

Hydrotropism and Its Interaction with Gravitropism in Maize Roots¹

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ABSTRACT

We have partially characterized root hydrotropism and its interaction with gravitropism in maize (*Zea mays* L.). Roots of Golden Cross Bantam 70, which require light for orthogravitropism, showed positive hydrotropism; bending upward when placed horizontally below a hydrostimulant (moist cheesecloth) in 85% relative humidity (RH) and in total darkness. However, the light-exposed roots of Golden Cross Bantam 70 or roots of a normal maize cultivar, Burpee Snow Cross, showed positive gravitropism under the same conditions; bending downward when placed horizontally below the hydrostimulant in 85% RH. Light-exposed roots of Golden Cross Bantam 70 placed at 70° below the horizontal plane responded positively hydrotropically, but gravitropism overcame the hydrotropism when the roots were placed at 45° below the horizontal. Roots placed vertically with the tip down in 85% RH bent to the side toward the hydrostimulant in both cultivars, and light conditions did not affect the response. Such vertical roots did not respond when the humidity was maintained near saturation. These results suggest that hydrotropic and gravitropic responses interact with one another depending on the intensity of one or both factors. Removal of the approximately 1.5 millimeter root tip blocked both hydrotropic and gravitropic responses in the two cultivars. However, removal of visible root tip mucilage did not affect hydrotropism or gravitropism in either cultivar.

Very early work showed that roots of many plant species bend tropistically toward more moistened sources (1, 5, 10, 13, 16). The hydrotropic response by which roots protect themselves from drying likely has important adaptative value especially in dry areas or in dry soil. However, little attention has been paid to root hydrotropism for many decades, probably because of the limited response in a limited moisture gradient, and because of the possible counteraction with the gravitropic response.

Recent studies with agravitropic roots of a pea mutant, *ageotropum*, showed that root hydrotropism occurs without the interference of gravitropism (7, 19). Furthermore, it has been reported that there exist common elements which function for both hydrotropism and gravitropism in pea roots (19). For example, the tip seems to be an essential sensory

site for both gravitropism and hydrotropism in roots (1, 5, 7, 8, 13, 19), though the signal perception mechanism for the two tropisms may well differ. Also, chemicals such as TIBA² and EGTA inhibit both gravitropism and hydrotropism in roots (11, 14, 19). In addition, roots respond tropistically not only to gravity or moisture gradients but also to other environmental stimuli such as thermogradients (3), magnetic fields (9), electric fields (6), and mechanical force (1). The root tip was again thought to be a sensory site for root thigmotropism (1). To understand the nature of root growth as well as the adaptative value of root tropisms, interactions among tropisms and their respective mechanisms need to be elucidated.

In the present study, we have partially characterized hydrotropism and its interaction with gravitropism in roots by using two different cultivars of maize. We have examined the interaction of gravitropism and hydrotropism by: applying hydrostimulation and gravistimulation to both dark-grown or light-exposed roots of normal and light-requiring orthogravitropic cultivars, and applying hydrostimulation to roots placed at various angles. Because the root tip is very likely essential for the sensing of both moisture and gravity, the roles of the root tip as well as of root tip mucilage in hydrotropism and gravitropism of maize roots were also examined.

MATERIALS AND METHODS

Plant Material

Seeds of maize, *Zea mays* L. cv Golden Cross Bantam 70, provided by Sakata Seed Co., Yokohama, Japan, and cv Burpee Snow Cross obtained from W. Atlee Burpee & Co., Warminster, PA, were germinated on wet filter paper in a covered glass container (19 cm i.d., 7 cm deep) at 24 ± 1°C in the dark. Three-day-old seedlings were selected for uniform root length between 2.0 and 3.0 cm. Shoots were removed from the endosperm with a razor blade before the roots were used.

Experimental Apparatus and Procedures

For each experiment, the chamber described by Takahashi and Suge (19) was used as modified and shown in Figure 1. A block of styrofoam (20 × 13.5 × 4 cm) with one end slanted at 55°, was wrapped with a layer of filter paper (Whatman 40; Whatman International Ltd., Maidstone, England) and 12

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² Abbreviation: TIBA, 2,3,5-triodobenzoic acid.

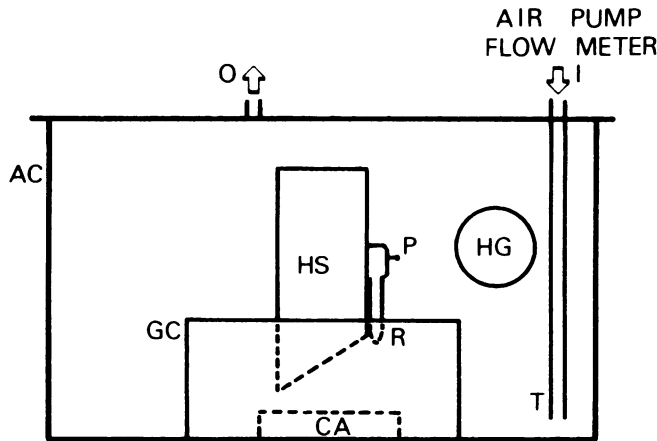


Figure 1. Apparatus used for experiments. AC, aquarium chamber; CA, CaCl₂-containing Petri dish; GC, glass container; HG, hygrometer; HS, hydrostimulant; I, inlet of air flow; O, outlet of air flow; P, insect pin; R, root; T, plastic tube for air flow. Dotted lines indicate those parts inside the glass container. See text for the details.

layers of cheesecloth. The filter paper and cheesecloth were moistened with distilled water and used as the hydrostimulant. Twelve to 14 roots were mounted on a single board by fixing the endosperms with insect pins (38 mm long). At the start, the tip-end of the root was placed approximately 1 mm away from the edge of the wrapped board (Fig. 1). In some experiments, the roots were placed apart from the hydrostimulant board at different distances so that the mechanical contact between root and hydrostimulant was avoided. The board with fixed roots was placed in a glass container (19 cm i.d., 7 cm deep) in a vertical or horizontal position. One or two whole root-holding assemblies were then placed in a glass aquarium chamber (41 × 24 × 23.5 cm) and covered by a sheet of Lucite L cast acrylic (6 mm thickness; E. I. Dupont De Nemours & Co., Wilmington, DE) with two holes (5 mm i.d.) for the inlet and outlet of air. Humidity inside the chamber was monitored by a hygrometer (model 605; Air-guide Instrument Company, Chicago, IL) placed 10 cm from the root tips.

Experiments were done at $24 \pm 1^\circ\text{C}$ room temperature under total darkness or continuous light. Roots of Burpee Snow Cross required no red light treatment for the induction of positive gravitropism. In experiments using dark-grown Golden Cross Bantam 70, seedlings were exposed to red light for 10 min prior to use in the dark. When the experiments were performed under light, these seedlings were also exposed to red light for 10 min prior to transfer to continuous white light. The red light was a 25 W red incandescent bulb (Westinghouse Electric Co., Bloomfield, NJ) at 12.5 W m^{-2} . Continuous white light was obtained from 34 W white fluorescent tubes (F40CW/RS/EW-II, Philips, Bloomfield, NJ) at 3.2 W m^{-2} . A dim green safelight was used for experiments in the dark during manipulations as necessary.

Hydrostimulation and Gravistimulation

In order to provide a moisture gradient, room air of approximately 50 to 60% RH was introduced into the chamber

by an aquarium pump (Whisper 800; Willinger Bros. Inc., Oakland, NJ). Air flowed through a plastic tube (4.8 mm i.d.) and a Visi-FLOAT flow meter (Dwyer Instruments, Inc., Michigan City, IN) at the rate of 0.15 to 0.2 L min^{-1} . In addition, one or two Petri dishes (9 cm i.d.) containing dihydrate calcium chloride (Fisher Scientific Co., Pittsburgh, PA) were placed 6 cm below the root tips. Accordingly, air humidity surrounding the roots resulted from the combination of the humidity of room air, the flow rate of this air, the amount of calcium chloride provided, and amount of water held by the hydrostimulant. After repeated trials, it was possible to control humidity inside the chamber at $85 \pm 3\%$ RH for the experimental period (3–14 h) by adjusting the amount of calcium chloride. In another chamber, the humidity was maintained near saturation by bubbling air through distilled water and by layering saturated filter papers inside the surface of the chamber. Therefore, the roots grew in nearly saturated conditions in this chamber.

Roots were gravistimulated by manipulation of the position of the root-holding hydrostimulant board vertically, horizontally, and at 30, 45, 60, and 70° below the horizontal. Except for the vertical placement, roots were always mounted on the lower side of the board. Accordingly, tropistic curvature would occur upward if positive hydrotropism overcame positive gravitropism but downward if positive gravitropism overcame positive hydrotropism. In vertical roots, sideward bending or straight growth would occur depending on the intensity of both hydrotropic and gravitropic stimulations.

Removal of Root Tips and Mucilage

Root tips, approximately 1.5 mm long, were cut off from dark-grown roots with a razor blade on a moistened filter paper in a Petri dish and discarded. To remove the root tip mucilage as completely as possible without damage to the root tip, the apical 10 mm of the intact roots were first immersed in distilled water for 5 min. Then, swollen mucilage at the tip was gently blotted and wiped off with a piece of filter paper. The root tip was washed with distilled water and wiped again with a filter paper. After repeating this washing twice, there was no swollen mucilage visible to eye. Both roots without tips or visible mucilage were stimulated hydrotropically or gravitropically as described above.

Curvature Measurement

Each treatment included 8 to 20 roots depending on whether one or two root-holding assemblies were used, and all experiments were repeated at least three times. Tropistic curvature of the roots at the desired time was measured by protractor. The data are presented as the mean \pm SE. Statistical differences were determined by the Student's *t* test.

RESULTS

It has previously shown that root hydrotropism occurs without interference of gravitropism in the agravitropic pea mutant, *ageotropum* (7, 19). However, little is known about an interaction between hydrotropism and gravitropism in roots. Resulting interactions may differ depending upon the

Table I. Hydrotropic Responses of the Roots of Maize, Golden Cross Bantam 70, Placed Vertically at Different Distances from the Hydrostimulant at Different Humidities

Roots were placed vertically touching the hydrostimulant, or 2 mm, 5 mm, or 10 mm from the hydrostimulant in 85% RH, 93% RH, or near saturation. Experiments were done under continuous light. Data represent the mean \pm SE ($n = 8$) of curvature 14 h after the start of the stimulation.

Distance between Root and Hydrostimulant	Humidity (RH)		
	85 \pm 3%	93 \pm 3%	>99%
<i>mm</i>			
0	54.9 \pm 1.7	22.0 \pm 4.1	No bending
2	61.0 \pm 3.4	7.8 \pm 5.3	No bending
5	9.5 \pm 4.2	1.6 \pm 1.8	No bending
10	Dehydrated	No bending	No bending

intensities of one or both of the stimuli, and the perception, transduction, and response to them.

The results of Table I show that vertically placed maize roots of Golden Cross Bantam 70 under the conditions of 85% RH and continuous light bent hydrotropically toward moist cheesecloth, although the intensity of the response changed as a result of differing chamber humidities and distances between the roots and the hydrostimulant. When the RH was controlled at approximately 85%, the roots touching or placed 2 mm from the hydrostimulant showed unequivocal hydrotropism. Increased distance between the roots and the hydrostimulant (5 and 10 mm) caused lesser hydrotropic response or dehydration of the roots. In 93% RH, the roots touching the hydrostimulant bent hydrotropically but only half of that compared to those in 85% RH. The roots did not respond when placed 5 or 10 mm from the hydrostimulant at 93% RH. Roots did not respond in humidity higher than 99% regardless of the distance from the hydrostimulant.

As shown in Table II, roots of Golden Cross Bantam 70 did not bend gravitropically when placed horizontally in moist air (>99% RH) under total darkness. However, roots previ-

Table III. Hydrotropic and Gravitropic Responses of Vertically or Horizontally Placed Roots of Maize, Burpee Snow Cross

Dark-grown roots were placed vertically by the side of the hydrostimulant or horizontally below the hydrostimulant under continuous light or total darkness. Data represent the mean \pm SE ($n = 8$) of curvature 14 h after the start of stimulation.

Humidity	Orientation	Curvature	Bending Direction ^a
% RH		degrees	
Experiment I (continuous light)			
>99%	Vertical	0.7 \pm 0.5	No bending
>99%	Horizontal	78.0 \pm 2.7	Downward (PG)
85%	Vertical	53.0 \pm 3.5	Sideward (PH)
85%	Horizontal	83.3 \pm 1.7	Downward (PG)
Experiment II (total darkness)			
85%	Vertical	48.3 \pm 7.8	Sideward (PH)
85%	Horizontal	53.0 \pm 5.6	Downward (PG)

^a PH, positive hydrotropism; PG, positive gravitropism.

ously exposed to red light for 10 min showed positive gravitropism under the same conditions of nearly saturated air. When dark-grown roots were made hydrotropically sensitive by reduced humidity, horizontally placed roots below the hydrostimulant bent upward under total darkness. On the other hand, dark-grown roots with prior exposure to red light bent downward when placed horizontally below the hydrostimulant. Vertically placed roots showed no bending in either dark-grown or red light-exposed roots when humidity was maintained higher than 99% RH. However, vertical roots in 85% RH bent to the side toward the hydrostimulant in both dark-grown and red light-exposed roots.

In Burpee Snow Cross, roots placed horizontally below the hydrostimulant in 85% RH bent downward under both total darkness and continuous light (Table III). Vertical roots bent toward the hydrostimulant in 85% RH but did not in nearly saturated air (Table III).

Thus, red light-exposed roots of Golden Cross Bantam 70 or roots of Burpee Snow Cross maintained either in the dark

Table II. Hydrotropic Responses as Affected by Gravistimulation in the Roots of Maize, Golden Cross Bantam 70

Dark-grown roots were placed vertically by the side of hydrostimulant or horizontally below the hydrostimulant with or without preexposure to 10 min red light. Data represent the mean \pm SE ($n = 10$) of curvature 14 h after the start of the stimulation.

Humidity	Light	Orientation	Curvature	Bending Direction ^a
% RH			degrees	
>99%	Dark	Vertical	0.5 \pm 0.4	No bending
>99%	Dark	Horizontal	2.1 \pm 0.9	No bending
>99%	Light	Vertical	0.9 \pm 0.7	No bending
>99%	Light	Horizontal	54.0 \pm 5.3	Downward (PG)
85%	Dark	Vertical	40.5 \pm 4.1	Sideward (PH)
85%	Dark	Horizontal	36.4 \pm 8.0	Upward (PH)
85%	Light	Vertical	49.1 \pm 6.5	Sideward (PH)
85%	Light	Horizontal	41.4 \pm 6.0	Downward (PG)

^a PH, positive hydrotropism; PG, positive gravitropism.

Table IV. Gravitropic Responses as Affected by Pretreatment with Different Duration of Hydrostimulation in the Roots of Maize, Golden Cross Bantam 70

The roots were first placed vertically by the side of the hydrostimulant in 85% RH and continuous light conditions. After various durations of the hydrostimulation, the roots together with the hydrostimulant were reoriented in a horizontal position so that the horizontal roots with or without hydrotropic bending were positioned below the hydrostimulant. See also Figure 2. Data represent the mean \pm SE ($n = 9$) of curvature 3 h after the start of the gravistimulation.

Duration of Hydrostimulation <i>h</i>	Curvature	
	1st curvature ^a (hydrotropism)	2nd curvature ^b (gravitropism)
0	No bending	40.3 \pm 0.8
1	No bending	42.0 \pm 9.6
3	5.0 \pm 1.2	34.0 \pm 8.0
6	27.3 \pm 4.2	57.3 \pm 7.0
10	42.9 \pm 2.4	40.8 \pm 2.7

^a Sideward bending caused by hydrostimulation in a vertical position. ^b Downward bending caused by gravistimulation after horizontal reorientation.

or in the light bent gravitropically when placed in a horizontal position at 85% RH and bent hydrotropically when placed vertically at 85% RH. In subsequent experiments, therefore, the effects of pretreatment with hydrostimulation or root angle on the induction of both tropisms were examined using light-exposed roots of Golden Cross Bantam 70. Roots placed vertically, which were stimulated hydrotropically for various durations, were then stimulated gravitropically by reorienting the root-holding board to a horizontal position (Table IV; Fig. 2, A–D). All roots, with (Table IV; Fig. 2, B-2) or without (Table IV; Fig. 2, B-1) hydrotropic bending, were then positioned below the hydrostimulant (Fig. 2, C-1 and C-2). In such experiments, positive hydrotropism appeared 3 to 6 h after the start of hydrostimulation in the vertical roots, and

after 10 h the hydrotropic curvature reached greater than 40° (Table IV). However, the duration of hydrostimulation or hydrotropic curvature did not affect the subsequent gravitropic response of the roots when reoriented in a horizontal position in 85% RH; all roots bent downward gravitropically (Table IV; Fig. 2, D-1 and D-2).

The effect of root angle on the induction of hydrotropic or gravitropic response is shown in Figure 3. When the roots of Golden Cross Bantam 70 were placed at 30° and 45° below the horizontal plane in 85% RH, the roots bent downward as in horizontally placed roots (Fig. 3, A and B). In contrast, the roots placed 70° below the horizontal (Fig. 3D) bent to the side toward the hydrostimulant as in vertically placed roots. However, the roots placed at 60° below the horizontal (Fig. 3C) showed an irregular tropistic response; 25% of the roots did not bend, 42% bent about 20° toward the hydrostimulant, and 33% bent about 12° downward. The ratio of the irregularity was slightly variable in the repetitions of the experiment, but generally similar results were obtained. When the roots were placed vertically on a hydrostimulant board with an angle of 90° instead of 55° (Fig. 3E), 75% of the roots bent to the side toward the hydrostimulant and the hydrotropic curvature reached greater than 70°. However, 25% of the roots showed two types of bending; hydrotropic curvature (65.6 \pm 8.8°) followed by gravitropic curvature (28.6 \pm 6.8°).

Roots of Golden Cross Bantam 70 decapitated by removing approximately 1.5 mm of the tip did not respond to either hydrostimulus or gravistimulus under continuous light (Table V). The hydrotropic response of vertical roots under total darkness was also blocked by the decapitation. Decapitated roots tended to bend slightly away from the hydrostimulant. Horizontally placed intact roots bent downward in air of near saturation (>99% RH) but the decapitated roots did not. Likewise, hydrotropic bending toward the hydrostimulant was seen in the vertically placed intact roots in 85% RH air but not in the decapitated roots. In contrast, removing the root tip mucilage did not change the root sensitivity to hydrostimulus or gravistimulus (Table VI). Similar results by the decapitation and removal of the root tip mucilage were obtained also in the roots of Burpee Snow Cross (Table VII).

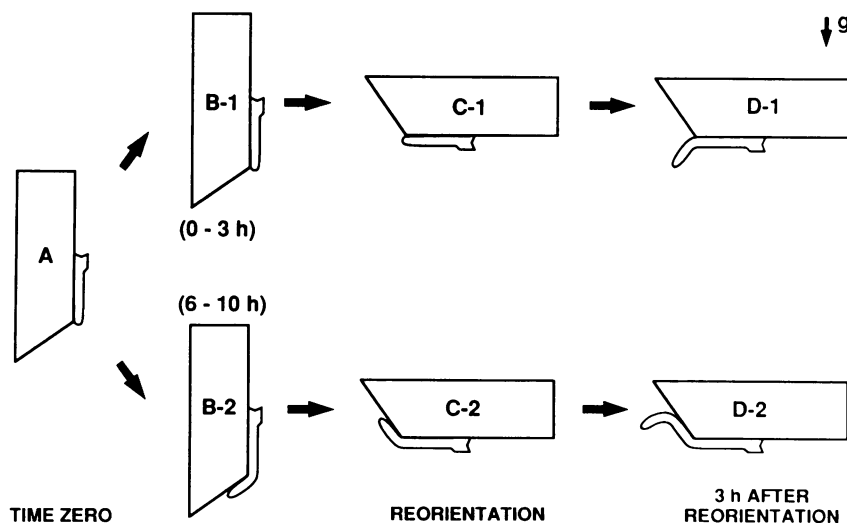


Figure 2. Effect of the time of pretreatment of hydrostimulation on subsequent gravitropic response of Golden Cross Bantam 70 maize roots. Light-exposed roots (A) were hydrotropically stimulated for various durations in a vertical position (B-1, B-2), then oriented horizontally (C-1, C-2). Vertically placed roots 0 to 3 h following hydrotropic stimulation do not have clear bending (B-1), but roots placed vertically for 6 to 10 h develop hydrotropic curvature (B-2) before reorientation. Roots 3 h after the reorientation (D-1, D-2) develop gravitropic curvature. B-1 and C-1 show a representative root with no hydrotropic bending at zero time. The direction of gravity is shown by an arrow and *g*. Humidity was maintained at approximately 85% RH throughout the experiment.

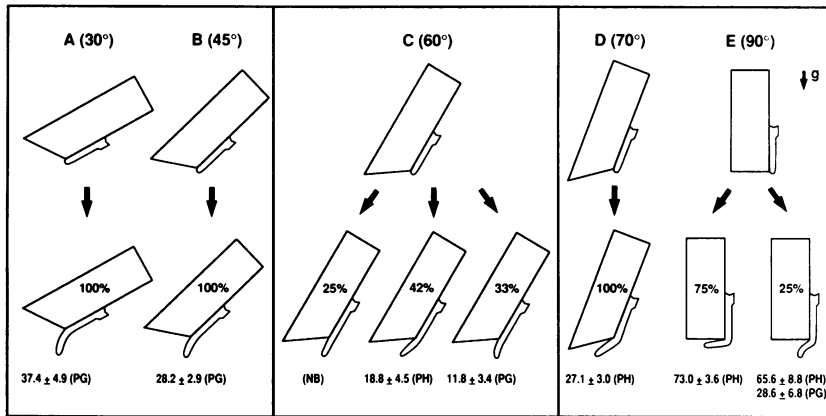


Figure 3. Effect of root angle on the induction of hydrotropism in Golden Cross Bantam 70 maize roots. Light-exposed roots were hydrotropically stimulated at various angles at 85% RH. The upper row shows the roots at zero time, and the lower row 8 h after the start of stimulation. A to E, roots placed at 30°, 45°, 60°, 70°, and 90° (vertical) below the horizontal, respectively. The gravitational direction is shown by an arrow and g. The percentages shown in the hydrostimulant "board" indicate the number of roots which showed the representative responses. Curvature is represented as the mean \pm SE ($n = 10$ in A–D and $n = 20$ in E) 8 h after the stimulation. PH, positive hydrotropism; PG positive gravitropism; NB, no bending.

The hydrotropic response of the roots with no swollen mucilage was significantly greater than that of intact roots in Burpee Snow Cross.

DISCUSSION

Although an existence of root hydrotropism has long been recognized, little is known about the mechanism of hydrotropism and its interaction with gravitropism. Regarding the interaction with gravitropism, Hooker (5) observed positive hydrotropism but not gravitropism when he placed *Lupinus* roots on a horizontal clinostat. Because the roots on the clinostat ultimately bent equally to those of the stable control, he concluded that gravitropic response did not interfere with hydrotropism in roots. However, the results of the present study show that hydrotropism is strongly affected by the gravitropic response and vice versa. The clearest evidence is that roots of Golden Cross Bantam 70 bend upward when placed horizontally below the hydrostimulant under the conditions of 85% RH in the chamber and in total darkness (Table II). On the other hand, the light-exposed roots under the same conditions bend downward. Roots placed in a horizontal position or vertical position with the tip downward in nearly saturated air, however, did not bend in the dark (Table II). In addition, horizontally placed roots of Burpee Snow Cross bent downward under both total darkness and continuous light conditions at 85% RH as well as under saturated conditions (Table III). Because the roots of Golden Cross Bantam 70 require red light for orthogravitropism (18) as in many other maize cultivars (2, 12, 17), positive hydrotropism might take place without gravitropic interference in the dark. On the other hand, the red light-exposed roots placed in a horizontal position might bend gravitropically but only by overcoming hydrotropism.

In vertically placed roots with the tips down, however, light stimulation did not affect the appearance of the hydrotropic response in Golden Cross Bantam 70 (Tables I, II). The roots bent sideward to the hydrostimulant under both total darkness and lighting conditions. The roots of Burpee Snow Cross also bent hydrotropically when started from a vertical position (Table III). These results suggest that there is a difference in the intensity of gravistimulation between vertical roots and horizontal roots. The reaction time for hydrotropism appears

to be somewhat longer than 3 h (Table IV), similar to that of pea roots (19), while gravitropic curvature of maize roots is reported to commence approximately 30 min after horizontal orientation (15). If so, the gravitropic response would begin well before the commencement of the hydrotropic response, which would result in gravitropic bending in the horizontal roots in 85% RH. However, this possibility seems unlikely since the pretreatment with hydrostimulation for various durations with roots in a vertical position did not change the extent of the gravitropic response in the subsequent horizontal exposures (Table IV; Fig. 2). Further, roots that had already bent hydrotropically also responded positively to subsequent gravistimulation. Because the intensity of hydrostimulation cannot be altered by angle, the intensity of the gravity-generated signal is that which differs between vertical and horizontal roots. Even though roots always undergo a 1g gravitational force regardless of their positioned angle, the intensity of the stimulus produced by gravity will differ depending on the

Table V. Hydrotropic and Gravitropic Responses as Affected by the Removal of Root Tips in the Roots of Maize, Golden Cross Bantam 70

Root tips approximately 1.5 mm long were removed from dark-grown or light-exposed roots. The roots were then stimulated gravitropically in a horizontal position in nearly saturated air or stimulated hydrotropically in a vertical position in 85% RH. Data represent the mean \pm SE ($n = 10$) of curvature 8 h after the start of the stimulation.

Humidity and Orientation	Light Conditions	Removal of Tip	Curvature ^a
% RH			degrees
Experiment I			
>99%; Horizontal	Light	Intact	55.7 \pm 2.0 (PG)
>99%; Horizontal	Light	No tip	No bending
Experiment II			
85%; Vertical	Light	Intact	36.0 \pm 1.4 (PH)
85%; Vertical	Light	No tip	-3.4 \pm 1.7 (NH)
Experiment III			
85%; Vertical	Dark	Intact	42.5 \pm 6.6 (PH)
85%; Vertical	Dark	No tip	-10.2 \pm 3.3 (NH)

^a PH, positive hydrotropism; NH, bending away from the hydrostimulant; PG, positive gravitropism.

positioned angle, because the quantity of the gravistimulation is a function of time and mass acceleration, with mass acceleration determined by its absolute value and stimulus angle (20). According to the sine rule, the optimum angle of stimulation is about 90° from vertical orientation (20). Therefore, if the roots are oriented in a vertical position (least stimulus), hydrotropism may easily overcome gravitropism. If they are oriented in a horizontal position (greatest stimulus), gravitropism may overcome hydrotropism.

If the above hypothesis is true, there should be a critical angle where the hydrotropic response and gravitropic response become equal and competitive. The present results support this hypothesis. When the light-exposed roots were placed at various angles in 85% RH, the roots placed at 70° below the horizontal still showed positive hydrotropism as in the vertical roots (Fig. 3D), while roots at 30° and 45° below the horizontal showed positive gravitropism (Fig. 3, A and B). Furthermore, the roots placed at 60° below the horizontal showed a mixed response; roots with no bending, hydrotropic bending, and gravitropic bending (Fig. 3C). In these hydrotropic or gravitropic responses of some roots at a 60° angle, the curvature was smaller than that of the roots placed at 30, 45, or 70° below the horizontal. The results indicate that these two tropisms are truly competitive when the intensity of the gravistimulus is reduced. Nevertheless, the hydrotropic curvature reached far more than 45°, namely 73°, in vertically placed roots when the edge of the hydrostimulant had an angle 90° perpendicular to the root axis (Fig. 3E). Although one-quarter of the roots bent gravitropically after the roots had bent hydrotropically 65°, 75% of roots showed only a hydrotropic response and did not bend downward even when they reached angles greater than 45° from the vertical (Fig. 3E). This would seem to contradict the hypothesis put forward above. However, a consistent explanation may be that when roots are reoriented to a horizontal position, it takes only seconds for their statoliths to sediment to their new "basal" positions. When roots reach a horizontal position from a vertical orientation by bending hydrotropically, statoliths

Table VII. Hydrotropic and Gravitropic Responses as Affected by the Removal of Root Tip or Root Tip Mucilage in the Roots of Maize, Burpee Snow Cross

Root tip or mucilage was removed from dark-grown roots. The roots were then stimulated gravitropically or hydrotropically under continuous light.

Humidity and Orientation	Removal of Root Tip or Mucilage	Curvature†
% RH		degrees
Experiment I		
>99%; Horizontal	Intact	82.7 ± 6.6 ^a (PG)
>99%; Horizontal	No tip	2.3 ± 1.5 ^a (NB)
85%; Vertical	Intact	44.6 ± 2.2 ^a (PH)
85%; Vertical	No tip	4.0 ± 2.1 ^a (NB)
Experiment II		
>99%; Horizontal	Intact	76.7 ± 4.0 ^b (PG)
>99%; Horizontal	No mucilage	76.9 ± 3.3 ^b (PG)
85%; Vertical	Intact	31.9 ± 3.0 ^{c*} (PH)
85%; Vertical	No mucilage	43.2 ± 3.0 ^{c**} (PH)

^{a-c} Represented as the mean ± SE ($n = 8$ in Experiment I and $n = 10$ in Experiment II) of curvature 12, 5, and 8 h after the stimulation, respectively. Statistically significant between * and ** at a 1% level. † NB, no bending; PH, positive hydrotropism; PG, positive gravitropism.

must move so slowly (it takes at least 6–8 h to get the position of the 45° angle) that stimulation by the replacement of the statoliths may not generate a biological signal of the same magnitude as that of quick-sedimenting statoliths. In terms of the gravistimulation, the intensity of the stimulus generated by the moving statoliths might be greater when the roots were reoriented in just a short moment to a horizontal position as compared to the roots which achieve a horizontal position by hydrotropic bending very slowly. We conclude that the hydrotropic response strongly interacts with the intensity of the gravistimulation.

Table VI. Hydrotropic and Gravitropic Responses as Affected by the Removal of Visible Root Tip Mucilage in the Roots of Maize, Golden Cross Bantam 70

Visible root tip mucilage was removed from dark-grown or light-exposed roots. The roots were then stimulated gravitropically in a horizontal position in nearly saturated air or stimulated hydrotropically in a vertical position in 85% RH.

Humidity and Orientation	Light Conditions	Removal of Mucilage	Curvature†
% RH			degrees
Experiment I			
>99%; Horizontal	Light	Intact	58.3 ± 7.6 ^a (PG)
>99%; Horizontal	Light	No mucilage	63.5 ± 1.5 ^a (PG)
Experiment II			
85%; Vertical	Light	Intact	43.1 ± 6.4 ^b (PH)
85%; Vertical	Light	No mucilage	45.0 ± 5.5 ^b (PH)
Experiment III			
85%; Vertical	Dark	Intact	30.5 ± 5.7 ^c (PH)
85%; Vertical	Dark	No mucilage	32.3 ± 5.2 ^c (PH)

^{a-c} Represented as the mean ± SE ($n = 10$) of curvature 3, 11, and 6 h after the start of the stimulation, respectively. † PH, positive hydrotropism; PG, positive gravitropism.

In this study, it was also shown that the degree of hydrotropism could be varied depending upon the intensity of hydrostimulation because the response decreased as the distance between the hydrostimulant and the roots became greater (Table I). A maximum hydrotropic response was obtained when the roots were placed at the hydrostimulant or 2 mm from it. Thigmotropism is not involved in the bending because the curvature occurs without direct touch to the hydrostimulant. Further, the roots which did touch the hydrostimulant did not bend in air of nearly saturated humidity. We were also concerned about thermotropism since a recent study has shown that maize roots bend toward the warmer side in response to temperature gradients of 0.5 to 4.2°C cm⁻¹ (3). We found a very slight temperature gradient no greater than 0.12 ± 0.01°C cm⁻¹, from the hydrostimulant board to a distance 7 cm from it in the chamber. However, the observed curvature in the present study was toward the hydrostimulant and away from the slightly warmer end of the temperature gradient. Thus, neither thermotropism nor thigmotropism interfere with the hydrotropic response.

At this time, the mechanism of root hydrotropism is not known, though there is an indication that the sensory site resides in the root tip (1, 5, 7, 13, 19). The root tip is likely involved in hydrosensing also in maize roots because the roots did not respond to either hydrostimulation or gravistimulation when tips approximately 1.5 mm long were removed (Tables V, VII). This is interesting because of its analogy to gravity sensing by roots (2, 8), though there is no evidence that statocytes in the root cap play a role in hydrosensing.

The root tips, especially of maize, produce an abundance of mucilage which has been reported to shrink or swell in response to a change of moisture (4). Accordingly, we were concerned whether an asymmetrical shrinkage or swelling of the mucilage is involved in the hydrotropic sensing or response. However, removal of the swollen mucilage did not affect either hydrotropism or gravitropism in either cultivar (Tables VI, VII). Since there was no swelling of any possible remaining mucilage (asymmetrical or otherwise) visible to the eye during the course of the experiments after its removal, swollen mucilage does not seem to be required for the hydrotropic or gravitropic response in maize roots. It is unknown whether any of the remaining small amount of the mucilage or its regeneration could still be responsible for the induction of the hydrotropic response.

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