

# Gravitropism in Higher Plant Shoots

## I. A ROLE FOR ETHYLENE<sup>1</sup>

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### ABSTRACT

It has long been known that applied ethylene can redirect the gravitropic response, but only occasionally has it been suggested that ethylene normally plays a role in gravitropism. Two inhibitors of ethylene synthesis [ $\text{Co}^{2+}$  and aminoethoxyvinylglycine (AVG)] and two inhibitors of ethylene action ( $\text{Ag}^+$  and  $\text{CO}_2$ ) were shown to delay the gravitropic response of cocklebur (*Xanthium strumarium* L.), tomato (*Lycopersicon esculentum* Mill.), and castor bean (*Ricinus communis* L.) stems. Gentle shaking on a mechanical shaker does not inhibit the gravitropic response, but vigorous hand shaking for 120 seconds delays the response somewhat. AVG and  $\text{Ag}^+$  further delay the response of mechanically stimulated plants. AVG delays the response of defoliated and of decapitated plants. Plants laid on their side and restricted so that they cannot bend upward store both bending energy and gravitropic stimulus; they bend immediately when released from restriction (stored energy) and continue to bend for some hours after (stored stimulus). AVG retards the storage of bending energy but not of stimulus. In gravitropism, graviperception may first stimulate ethylene evolution, which may then influence bending directly, or responses involving ethylene could be more indirect.

The link between ethylene and gravitropism (geotropism) has been known since the work of Neljubov in 1901 (23) and Knight *et al.* in 1910 (17), who described the triple response of pea plants (reviewed in ref. 1). Treated stems were reduced in height, increased in diameter, and prostrate in their growth habit. The prostrate growth was called "ageotropic," but pea shoots actually grew in a horizontal or diagravitropic orientation, regardless of the original orientation of the shoot. Thus, ethylene redirected shoot gravitropic response rather than simply destroying or disorienting it.

Other indirect evidence also exists, suggesting a role of ethylene in gravitropism. Crocker *et al.* in 1932 (8) observed reduced epinastic response in ethylene-treated tomatoes when plants were placed in an inverted position. Abeles and Rubenstein (2) showed that asymmetrical distributions of auxin in photo- and gravitropically stimulated hypocotyls have corresponding asymmetrical ethylene evolution, although such gradients could be results rather than causes of gravitropism (10, 11). Chadwick and Burg (7) reported that ethylene, produced by low concentrations of IAA, was responsible for auxin inhibition of root growth and proposed that ethylene was essential for gravitropic curvature in roots. They supported this proposal by showing that  $\text{CO}_2$ , a widely used inhibitor of ethylene action in plants (1), retarded gravitropic

response in pea and lima bean roots (at 5 and 10% concentrations), but they were unable to observe effects of  $\text{CO}_2$  on the gravitropic response of pea-shoot sections. Zobel (35) observed that treatment of a mutant diagravitropic tomato with ethylene ( $5 \text{ nl l}^{-1}$ ) normalized shoot gravitropic response, that is, ethylene was required to induce normal, negative, gravitropic shoot growth in this mutant tomato. And Wright *et al.* (34) and Kaufman *et al.* (16) have measured increases of ethylene evolution in plants placed on their sides. Wright *et al.* (34), however, concluded that the ethylene production was symptomatic of the gravitropic response, rather than regulatory.

Further indirect evidence for a connection between ethylene and the gravity response is that leaf epinasty develops in horizontally placed plants (9, 26) and in plants on a horizontal clinostat (19, 24), and ethylene has long been known to cause leaf epinasty. In the companion paper (27), we suggest that ethylene is produced in clinostated plants in response to disturbance of the gravity-perception mechanism, rather than being caused by the mechanical stresses of leaf flopping. Inasmuch as gravitropic bending is also caused by the gravity-perception mechanism, ethylene could be involved in gravitropism.

Both AVG<sup>2</sup> and cobaltous ion ( $\text{Co}^{2+}$ ) are known inhibitors of ethylene synthesis in some plant tissues (3, 18; for review, see ref. 20). Silver ion is known to be a powerful inhibitor of ethylene action (5), and  $\text{CO}_2$  has been widely used as an inhibitor of ethylene action (1). We report effects of these four inhibitors on the gravitropic response, as well as results of related studies.

### MATERIALS AND METHODS

**Species and Growing Conditions.** All experiments reported here were performed with vegetative cocklebur plants, *Xanthium strumarium* L. (Chicago strain), and critical experiments were repeated at least three times with this species. Plants varied from 25 to 90 days old, although most experiments used younger plants (about 30 days old). Some experiments, especially those with AVG and  $\text{Ag}^+$ , were repeated with tomato (*Lycopersicon esculentum* Mill., var. Bonny Best) and with castor bean (*Ricinus communis* L.). Plants were grown in the greenhouse as described in the companion paper (27).

**Anti-Ethylene Treatments.** AVG, donated by Hoffmann-La Roche, Inc., Nutley, NJ, was applied as a simple solution (including 1 drop Tween 20/100 ml), but silver ion was complexed with thiosulfate (31) by pouring 2 mM  $\text{AgNO}_3$  into an equal quantity of 8 mM  $\text{Na}_2\text{S}_2\text{O}_3$  (or 1 mM  $\text{AgNO}_3$  into 4 mM  $\text{Na}_2\text{S}_2\text{O}_3$ ) and adding wetting agent. Other salts were simple solutions plus wetting agent. Plants were dipped in these solutions 30 min before being laid on their sides.  $\text{CO}_2$  was applied from a cylinder that contained 5%  $\text{CO}_2$ , 20%  $\text{O}_2$ , and 75%  $\text{N}_2$ . Plexiglas chambers were fitted tightly over clinostat turn-tables of a clinostat used in other

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<sup>2</sup> Abbreviation: AVG, aminoethoxyvinylglycine.

studies (27). The high CO<sub>2</sub> mixture was allowed to flow through three of the six chambers, while ambient air (from a tube outside the treatment room) was pumped at an approximately equivalent flow rate (about 100 ml min<sup>-1</sup>) through the other three chambers. In the gravitropic experiments reported here, the clinostat turntables remained stationary.

**Treatments and Measurements.** In most experiments, plants were placed in the dark room (usually held at 27 C). Plants were placed on specially built racks so that the normally horizontal tops of the plastic pots were within 2 or 3 degrees of the vertical. Most experiments were performed in the dark, measurements being made with the help of a green safelight (25-w incandescent bulb; light was filtered through a layer of green and a layer of blue Plexiglas). In spite of precautions to maintain dark or safelight conditions (to avoid complications of phototropism), gravitropic responses of plants in the light (typically in the greenhouse) were essentially the same as those in the dark. The angle formed by the nonelongating lower stem region and the growing terminal stem region was measured by shaping a pair of dividers to match the angle (without touching the plant), then measuring the angle of the dividers with a protractor. (Plants were sometimes photographed silhouetted against a dim, green background.) Measured angles could be expressed in two ways, as illustrated by the drawing on Figure 1.

In another set of experiments, plants were placed on a shaker that had a horizontal displacement of 3.7 cm, cycling 90 times min<sup>-1</sup>. In experiments on restricted gravitropism, plants were restricted by packing in buckets of vermiculite, by wrapping masking tape (sticky side out) around two wooden dowels 8 cm apart and parallel to a stem between, or by wrapping thread around two stiff wires 2.5 cm apart with a stem between.

## RESULTS AND DISCUSSION

**Results with Ethylene Inhibitors.** To begin with, we tested the effects of Na<sup>+</sup> and Mg<sup>2+</sup>, representative monovalent and divalent cations, and Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub>. There was no difference in the rate of gravitropic bending between plants so treated and untreated control plants. Figures 1 and 2 show results of treatments with two inhibitors of ethylene synthesis: Co<sup>2+</sup> and AVG. Cobaltous ion slowed gravitropic bending to 60° by about 3 h in the experiment of Figure 1 but, in some experiments, the delay was less than 1 h. The oscillating overshoot of controls in Figure 2 and in other figures represents a circumnutation and is real. Sustained average overshoot occurs because stems usually sagged below the horizontal, whereas the tips of the stems bent almost to the exact vertical, providing a stem-bending angle of over 90°. In Figure 2, AVG retarded gravitropic bending to 60° by 4 to 5 h. In general, results with AVG tend to be more striking than with the other three inhibitors.

Figures 3 and 4 show results of representative experiments with inhibitors of ethylene action, Ag<sup>+</sup> and CO<sub>2</sub>. Both inhibitors of ethylene action show clear retardation of the gravitropic response but in some of our experiments, CO<sub>2</sub> was only slightly effective (flow rates of CO<sub>2</sub> may have been too slow). Similar experiments with AVG and AG<sup>+</sup> have been performed over a dozen times, sometimes in slightly different contexts. Silver is always effective, and AVG is always highly effective.

Figure 5 shows results of AVG applied to tomato and castor bean. Delay of tomato stem bending is the more striking of the two.

Note that none of the inhibitors completely prevented gravitropic bending; they only delayed it. This is typical of inhibitor effects on ethylene production and action. AVG and Co<sup>2+</sup> never completely eliminate ethylene production, nor do Ag<sup>+</sup> or CO<sub>2</sub> ever completely eliminate ethylene effects. Ethylene responses are typically suppressed or delayed but not completely halted (e.g., refs 1, 5, and 20).

**Gravitropic Interactions with Mechanical Stress.** Figure 6 shows the results of treating cocklebur plants with AVG and then turning them on their side on a shaker. The gravitropic response of nontreated plants on the shaker is not retarded compared to control plants not on the shaker, but AVG inhibits the response of plants on the shaker as usual. In experiments not shown, Ag<sup>+</sup> was also effective.

Figure 7 shows gravitropic bending of plants treated with AVG compared to control plants when half the treated and control plants were subjected to vigorous hand shaking for 120 s just before plants were laid on their sides (but plants were dipped in the AVG solution 30 min before turning). There is initially a delay in gravitropic response caused by shaking, but both shaken and unshaken plants reach the vertical at about the same time. This roughly confirms the results of Jaffe and Biro (13), although they restored the normal bending rate with hypobaric conditions, implicating ethylene as an "inhibitor" of the gravitropic response. In our experiments, AVG again retarded the development of gravitropic bending, especially of the plants that had been shaken. Silver (not shown) was somewhat less effective in this and a similar experiment. Mechanical stresses are known to cause ethylene evolution (reviewed in refs. 13 and 27), and high ethylene might at first overload the system and, thus, inhibit the gravitropic response (35).

**Gravitropism of Defoliated and Decapitated Plants.** Brauner and Hager (6) have shown that sunflower hypocotyls respond gravitropically even after cotyledons and apical meristems have been removed (see also ref. 11). In several preliminary experiments, we have confirmed that stems of cocklebur, tomato, and castor bean will respond gravitropically when leaf blades are removed, when both petioles and blades are removed, and when apical meristems are removed. Figure 8 shows results of an experiment in which, first, plants were treated with AVG, then, after 1 h, entire leaves were removed (except the very youngest), and, 15 to 30 min later, plants were laid on their sides. Removing leaves delayed the response somewhat after 6 h, and AVG delayed it still more. When apical buds were also removed, the response was not only delayed but also reduced (i.e. stems stopped bending before reaching the vertical). Again, AVG reduced the response still more, but not much, in this experiment. Note that initial bending of defoliated and sometimes even decapitated plants is more rapid than in intact controls, as though weight of the leaves slowed bending at first. Do the leaves then supply something needed for bending (auxin?), which otherwise becomes depleted in defoliated and decapitated stems? Sometimes defoliated and decapitated plants bleed profusely at the cut surfaces and appear to lose turgor after several hours, but we have on occasion observed full (90°) and rapid bending of defoliated and decapitated plants that seemed unusually healthy.

**Restricted Gravitropism.** We noticed that restricting cocklebur plants laid on their sides so that they were unable to bend upward led to a storage of bending energy and of gravitropic stimulus. Although the phenomenon does not seem to be mentioned in the recent literature, Bateson and Darwin in 1888 (4) reported that restraining a *Plantago* inflorescence in a horizontal position and then releasing it resulted in a springing upward of the organ. They noted that the phenomenon was "well known."

Figure 9 shows results of an experiment in restricted gravitropism. Plants were packed in buckets of vermiculite. Upon release, they sprang within 1 to 10 s into a bent position. Beginning at 24 h, the angle formed began to exceed 90°. Bending continued for 2 h after release in response to stored stimulus, as illustrated for two of three plants measured after return to the greenhouse bench. In one case, maximum curvature exceeded 200°. After about 2 h, recovery began and was rapid. (Actually, bending after release should have been measured on a clinostat, which would probably have prevented recovery.)

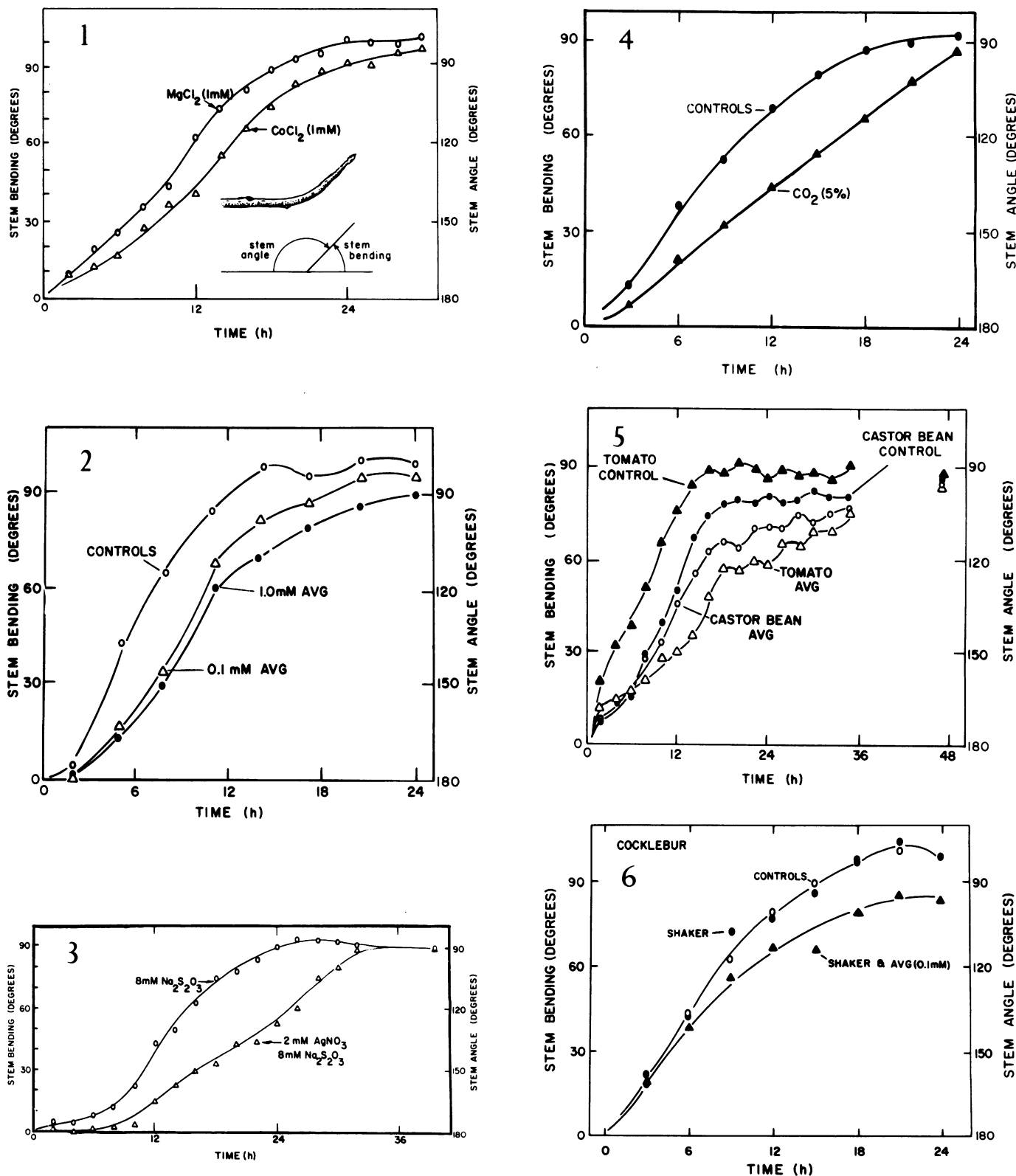


FIG. 1. Effects of cobaltous chloride on the gravitropic response of cocklebur plants (five plants per point). Although gravitropic bending to  $60^\circ$  is delayed 3 to 4 h, other  $\text{Co}^{2+}$  experiments showed less delay. The drawing illustrates the two ways bending can be expressed.

FIG. 2. Delay of the gravitropic response by two concentrations of AVG. Each point represents five plants. Delays up to 12 h have been observed with 1.0 mM AVG (see Fig. 8).

FIG. 3. Effects of silver nitrate complexed with thiosulfate on the gravitropic response of older cocklebur plants (five plants per point). Older plants (about 8 to 10 weeks) were used in this experiment because younger plants are often burned by the silver solutions, but the control response time is slower for the older, slower-growing plants.

FIG. 4. Delay of the gravitropic response of cocklebur plants (three per point) by 5%  $\text{CO}_2$ . High  $\text{CO}_2$  was introduced into the chambers for 30 min with plants in the vertical position before plants were turned to the horizontal. Most tests with  $\text{CO}_2$  showed less delay than in this experiment.

FIG. 5. Delay of the gravitropic response by AVG applied to tomato and castor bean plants (five per point). AVG solutions were applied 30 min prior to turning plants on their sides. The waves in the curves after plants reach maximum bending are nutational movements. Note that plants treated with AVG began this movement even before they reached the vertical, beginning at about the same time as control plants.

FIG. 6. Gravitropic response of plants (four per point) placed on their sides on a shaker. The gentle shaking does not delay the response compared to unshaken controls, but AVG delays the response. Plants were dipped in AVG just prior to being placed on their sides, perhaps accounting for the small effect of AVG for the first few h.

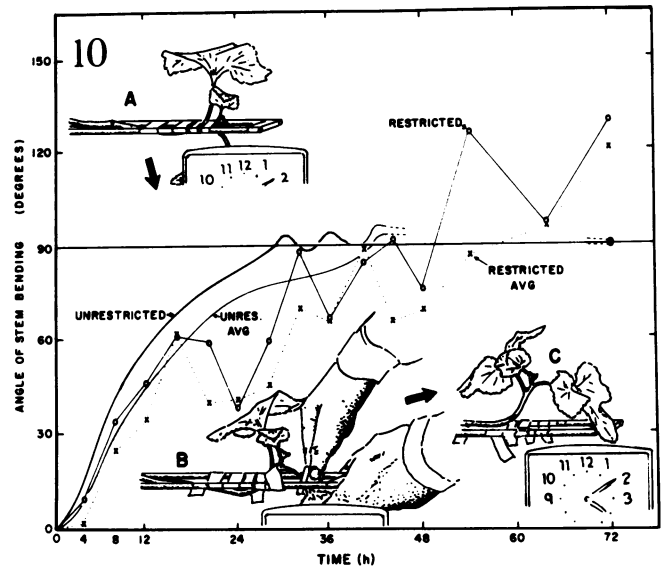
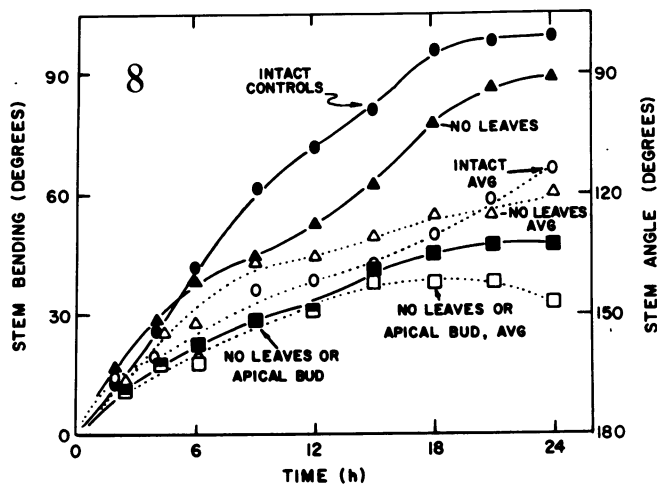
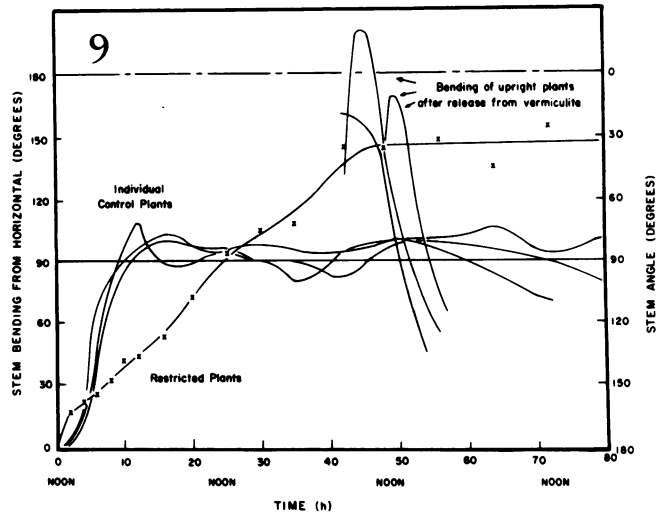
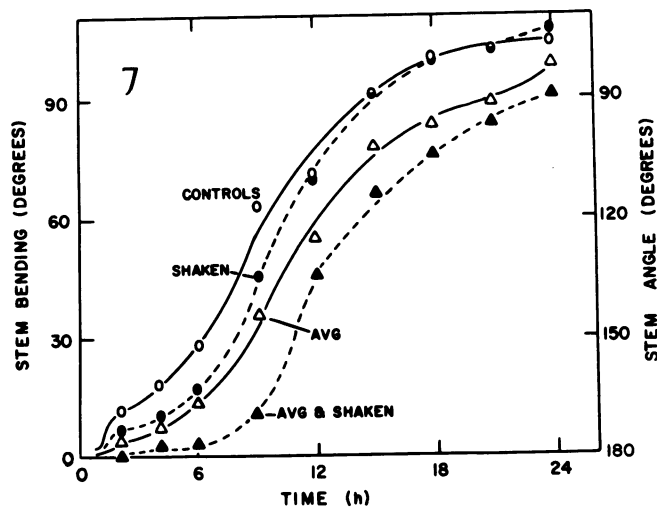


FIG. 7. Effects of vigorous hand shaking for 120 s on the gravitropic response of cocklebur plants (four per point). The severe mechanical stress initially delayed the gravitropic response, but shaken and control plants reached the vertical at about the same time. AVG delayed the response, especially of shaken plants.

FIG. 8. Gravitropic response of defoliated (all leaves removed except those less than about 0.5 cm long) and defoliated-decapitated (all leaves plus apical bud removed) plants, compared to control plants (pruned to three fully expanded leaves). Each point represents three plants. Note that defoliated and decapitated plants initially bent as fast or faster than controls, indicating that the weight of leaves may slow bending at first, but controls usually surpass the two pruning treatments after 4 to 6 h; defoliated and especially decapitated plants also often stop bending well before reaching the vertical. AVG delays bending of all treatments, but perhaps somewhat less for the defoliated and/or decapitated ones. Plants were dipped in AVG 1 h before pruning and laid on their sides 30 min after pruning.  $AgNO_3$  (1.0 mM) or lower concentrations of AVG were less effective in delaying bending of defoliated and/or decapitated plants (not shown).

FIG. 9. Gravitropic response of cocklebur plants packed in buckets of vermiculite to restrict their gravitropic bending, compared with three unrestricted control plants (control points not shown; all fall almost exactly on the lines as drawn). Points (x) are averages of three plants unpacked at the indicated times, measured within 5 min of unpacking. Bending occurred within seconds (less than 10 s) after release from the vermiculite. (Slight bending occurred in the vermiculite.) Note that immediate bending after release is delayed compared to the three unrestricted control plants up to about 25 h, after which the stored bending energy produces curvatures that are well beyond  $90^\circ$  (to about  $150^\circ$ ). The three curves labeled "Bending of upright plants after release from vermiculite" (points not shown) show the expression of stored gravitational stimulus after plants were returned to an upright position in the greenhouse. One plant bent to an angle of over  $200^\circ$ . After about 2 h, plants begin to respond to their new position, reversing the direction of bending so that stems are nearly straight after about 24 h.

FIG. 10. Gravitropic response of cocklebur plants restricted between strips of masking tape (drawing A, which was traced from a projected photograph). At the indicated times, tapes were rapidly cut with a razor blade (B), and the angle that developed (C) was measured within 5 min. (Bending actually occurred within 10 s.) Each point represents three plants, as do the unrestricted control curve and the unrestricted-AVG curve (points not shown). AVG (1.0 mM) delayed the unrestricted controls as usual and also delayed the extent of stored bending energy (although there is an unusual scatter in the data). The overshoot is less striking than when plants were restricted in vermiculite (Fig. 9), perhaps because virtually no stem bending was allowed by the masking tape. Note in drawing A that leaves, which were not restricted, have responded gravitropically by becoming horizontal.

Figure 10 illustrates results of another experiment in which plants were restrained by masking tape (note drawings) rather than by vermiculite. Little stem bending could occur against this restriction, but leaves responded gravitropically until they were virtually horizontal. Plants treated with AVG showed somewhat less stored bending energy at each time of release (average AVG points are lower than controls), but stored stimulus was virtually identical for controls and for plants treated with AVG. Controls bent an average of 12.4° by 2 h after release; AVG plants averaged 12.5°. The overshoot was less spectacular for plants restricted with tape than with vermiculite.

We have initiated an intensive study of the restricted gravitropic response (22, 28). Preliminary results show that tension builds on the upper side of the stem as pressure builds on the lower, so the upper side shrinks (cells decrease in length and increase in thickness) by as much as 40° when the restriction is removed and bending occurs. Cells on the bottom lengthen. These observations must be examined in the light of current theories of auxin-induced stem growth.

### CONCLUSIONS

The time-honored Cholodny-Went theory of gravitropism (reviewed in refs. 10, 14, 32, and 33) suggests that graviperception leads to more auxin and, thus, more growth on the lower side, resulting in upward bending of the stem. There is considerable evidence for auxin and/or gibberellin gradients as predicted by the model (reviewed in ref. 33). (Roots appear to have gradients in inhibitors rather than promoters.) Leaf epinasties that develop on clinostated plants also seem to develop in response to upsetting of graviperception (27) and, again, there is evidence for auxin gradients (15, 21).

Digby and Firn (10, 11) have questioned the Cholodny-Went theory, mostly on grounds that bending can be observed before auxin (or especially gibberellin) gradients can be measured, and that the hormone concentrations and gradients are not high enough to cause bending when they do occur.

Our results and those of others (see the introduction to the text) suggest that ethylene plays an essential role in the gravitropic response of shoots, although this never seems to be mentioned in reviews of gravitropism (10, 11, 14, 32, 33) or of ethylene action (1). Ethylene has also been clearly implicated in leaf epinasty of clinostated plants (19, 21, 27, 30). Ethylene may modify auxin transport in horizontal stems or in petioles and blades of leaves (12; reviewed in ref. 15) or, as others have suggested, it might act directly in growth response mechanisms (25, 39). Our preliminary results suggest a possible inhibition of cell elongation on the upper sides of horizontal stems by the ethylene. We have observed stem deflections up to 60° in tomatoes treated (swabbed) with a 1% ethephon solution on one side and then placed on a horizontal clinostat. The bending is directed toward the side of ethephon application. So a direct inhibition is a possible mode of action.

Our results clearly suggest that ethylene should be considered as a prime candidate for a role in stem gravitropism. For one thing, attempts should be made to measure ethylene evolution from different parts of plant stems as a function of time after changing the plant's orientation with respect to gravity. Such measurements might not be easy, but they could open important new avenues to an understanding of stem gravitropism and perhaps stem growth. A possible role for ethylene in phototropism should also be considered.

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