

# Gravitropism in Higher Plant Shoots<sup>1</sup>

## II. DIMENSIONAL AND PRESSURE CHANGES DURING STEM BENDING

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WESLEY J. MUELLER<sup>2</sup>, FRANK B. SALISBURY\*, AND P. THOMAS BLOTTER  
*Plant Science Department UMC 48 (W.J.M., F.B.S.) and Mechanical Engineering Department UMC 41 (P.T.B.), Utah State University, Logan, Utah 84322*

### ABSTRACT

Dimensional changes during gravitropic bending of cocklebur (*Xanthium strumarium* L.) dicot stems were measured using techniques of stereo photogrammetry. The differential growth is from an increased growth rate on the bottom of the stem and a stopping or contraction of the top.

Contraction of the top was especially evident upon release and immediate bending of horizontal stems that had been restrained between stiff wires for 36 hours. The energy for this could have been stored in both the top and bottom, since the bottom elongated, and the top contracted.

Forces developed during bending were measured by fastening a stem tip to the end of a bar with attached strain gauges and recording electrical output from the strain gauges. Restrained mature cocklebur stems continued to accumulate potential energy for bending for about 120 hours, after which the recorded force reached a maximum.

Pressures within castor bean (*Ricinus communis* L.) stems were also measured with 3.5-millimeter diameter pressure transducers. As expected, the pressure on the bottom of the restrained plants increased with time; pressures decreased in vertical controls, tops of restrained stems, and bottoms of free-bending stems. Pressures increased in tops of free-bending stems. When restrained plants were released, pressure on the bottom decreased and pressure on the top increased. Results suggest a possible role for cell contraction in the top of stems bending upward in response to gravity.

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Gravitropic responses can be thought of as involving a reaction chain beginning with perception of the gravitational stimulus, transduction of the stimulus to some form that can influence plant growth (e.g. one or more growth regulators), and finally the observed response (11). Mechanisms of perception and especially transduction are intriguing, but their elucidation depends upon a proper understanding of the actual plant response. When a stem is laid on its side, for example, does growth of the top remain fairly constant with bottom growth being accelerated, does the bottom continue at the same rate while the top stops or decreases, or do both growth rates change with the bottom rate always exceeding the top rate to account for bending? How do pressures (and tensions?) develop within the stem?

Historically, most measurements of the overall growth rates of

stems were obtained during the last century and the early part of this century. Some workers reported that overall growth rates remained fairly constant after stems were placed in the horizontal position (4, 8, 20, 26, 27). Others reported an overall decrease in growth rate when plants were displaced (2, 12, 18, 32).

De Vries (8) and Iwami and Masuda (14) emphasized the importance of the increased growth on the bottom of horizontal stems. Others reported that the top of horizontal stems grew less than the bottom (5, 10). Sachs (27) in 1872 stated that the top of an *Avena* coleoptile stopped growing, even contracted, while the bottom continued to elongate. In contrast, Navez and Robinson (20) in 1932 reported that the growth rate of the top of horizontal *Avena* coleoptiles is slowed but does not stop. In 1979, Digby and Firn (9) emphasized the rapidity with which the top growth of several stems and coleoptiles was halted when plants were turned to the horizontal. Because of these conflicting results, we report here our measurements of growth.

We serendipitously observed that, when mature plant stems are restrained in a horizontal position for some time (usually 36-48 h) and then suddenly released, they spring to a bent position (often a hook of approximately 130°) within 1 to 10 s (29, 33). We have used this phenomenon to study the development of pressure within the stem during gravitropic stem bending. Tensions develop during restraint. We have also examined the physical storage of energy during restraint, and this has provided insight into criteria that must be met by a proposed transduction mechanism. Our results have led to questions about what happens at the cellular level during gravitropic bending. Results of cellular studies on these questions are reported in the companion paper (30).

Although no one has used the technique of restraining plants during gravitropic bending in quite the same manner as we have, after our discovery we found many references to the use of restraint for various purposes in gravitropism research. Indeed, it seems as if almost as many reasons for restraint have been reported as researchers who have used them. Most reports are from the 1800s or the very early 1900s, however. For example, Johnson (15) in 1829 restrained roots to show that they do not bend passively in response to gravity as Knight (17) had suggested in 1806. With the *Phaseolus* root tip placed in a horizontal position and affixed to a balance, he added weight to counterbalance and thus showed that the force exerted was greater than the root's weight. Pfeffer (24) in 1906 repeated the experiments of Johnson, eliminating some flaws in the original experiments. Pfeffer's results showed that the root exerted a force that could be balanced with 13 g. We report forces developed by restrained stems measured with strain gauges attached to a recorder. We also report results obtained with pressure transducers inserted into stems.

Other researchers who have restrained gravitroping plants for various reasons include Bateson and Darwin (3), Hofmeister

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<sup>2</sup> Present address: Crop Science Department, California, Polytechnic State University, San Luis Obispo, CA 93407.

(13), Pfeffer (24), and Sachs (28), all in the 1800s. Many researchers (5-7, 12, 19, 22), have restricted gravitropic bending of plant parts by placing them in glass tubes, two of these in the 1970s (16, 31). Several researchers used plaster of paris casts (e.g. 21) or grooves in plaster of paris (1).

## MATERIALS AND METHODS

**General.** Cocklebur (*Xanthium strumarium* L. Chicago strain) and castor bean (*Ricinus communis* L.) plants were grown in a greenhouse essentially as previously described (33). *Xanthium* fruits and *Ricinus* seeds were germinated in sand, then transplanted to individual 10-cm square pots when the cotyledons were fully expanded. Soil was a loam, mixed 3:1 with sand. Fertilizer was added to the pots at the time of transplanting (about 0.5 g Osmocote 14-14-14 and about 1.5 g super phosphate 0-20-0 per pot). Plants were subsequently fertilized every 10 to 14 d with 5 to 10 pellets of ammonium nitrate. The plants were watered daily, depending on need, and sprayed with Karathane when powdery mildew infected the leaves (*Xanthium*). The leaves were pruned to two or three fully expanded leaves during the growing period. The plants were kept under LD conditions (18-h days) with supplementary fluorescent lighting, which kept cocklebur plants vegetative but slightly promoted flowering of castor beans.

**Stereophotogrammetry.** Stereophotogrammetry was used to measure accurately the growth changes of plants over time. When the plants reached a height of 18 to 24 cm (about 30 d from planting), all but the uppermost mature leaf was removed. This exposed the stem to facilitate the photography and also reduced the weight at the tip of the plant.

The plants were then randomly assigned to one of three groups: vertical controls, horizontal unrestrained plants, and horizontal restrained plants. The stems of the plants in the last group were restrained by wrapping thread around two stiff support wires with the stem in between. A single wire was bent to a U-shape and its ends inserted into holes in wooden boxes built to hold the tapered square pots so stems would be horizontal when the box was placed on its side (Fig. 1). Opposite sides of each stem were marked with dots of india ink at approximately 2.5-mm intervals. Plants assigned to the vertical control treatment were photographed (beginning of the light controls), then placed back in the greenhouse for 36 h. At the end of that time, they were again photographed (end of light controls and beginning of dark controls). The plants of the other treatments were also photographed at that time, and all plants were placed in a dark room at 25°C for 36 h. All plants but vertical controls were turned 90° so stems were horizontal.

At the end of the experiment time, all plants were again photographed. The restraining threads were cut from the restrained plants, which were allowed to bend for 60 s and then photographed again.

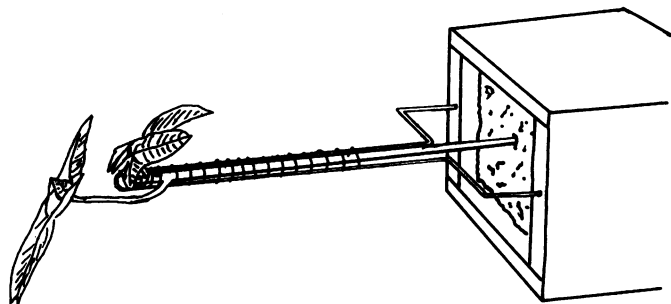


FIG. 1. Drawing of a plant restrained between wires and in the horizontal position.

The photographs were taken with two view cameras on 10.2 × 12.7-cm (4 × 5 inches) Kodak Tri-X pan professional film, ASA 320. Two plants were placed horizontally on a so-called stereograph table in such a way that none of the dots on one side of the stems were covered from the view of the camera by leaves, etc. After one side was photographed with both cameras, the plants were returned to the vertical position. The cameras were loaded and the plants were again positioned for photographs of the other side of the stem. The time that the plants were required to lay horizontally was about 25 s for each pair of pictures. The stereograph table had two bars for mounting the cameras. The bars were parallel to each other and above and parallel to the table surface. Distances between the bars and above the table could be adjusted, and camera positions were adjustable so the film plane could be exactly parallel to the table surface. The surface overlap of the two camera fields was 60%. Films were kept in the same environment and developed together. It was assumed that if all the films and prints were kept in the same environment, they would all expand or contract the same.

The techniques of stereophotogrammetry were adapted from those used in other applications such as forest mensuration from aerial photographs (23). The  $x$  and  $y$  coordinates and the distance between dots on the stem were obtained from the image projected onto a series 7000 Houston-Instruments digitizer. The  $x$  and  $y$  axis of each picture had its origin at the nadir for its camera (the plumb point of the lens center). The  $y$  axis connected the nadirs of the two cameras, and the two  $x$  axes were parallel with each other (Fig. 2).

Several constants and measured parameters were needed to calculate the actual stem dimensions from each stereo pair of photographs. These include:

- $A$  = Distance between the nadirs (points directly below the center of the lenses) measured from a photograph.
- $F$  = Focal length of the lens.
- $H$  = The distance from the optical center of the camera (usually in the lens) to the base (surface of the table in this case).
- $I$  = The distance between two arbitrary points on the projected image or print.
- $L$  = The movement of the lens along its axis when focusing on an object closer than infinity.
- $M$  = The optical magnification (see below).
- $O$  = The distance on the negative between the same two arbitrary points used to measure  $I$ .
- $P$  = The absolute parallax at the base (see below).
- $P_1$  = The absolute parallax at a bench mark (any given point visible on both photographs of the stereo pair).

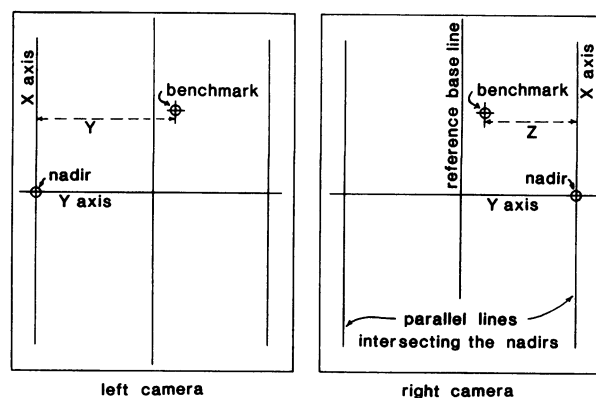


FIG. 2. An illustration of overlapping parts of a stereo pair of photographs showing the position of the nadirs (plumb points of the camera lenses), the parallel lines intersecting them ( $x$  axis), and the base reference line. The  $y$  axis connects the nadirs.

$R$  = Reduction of the image (see below).

$Y$  = The measured distance from a benchmark on one photograph to the  $x$  axis (see Fig. 2).

$Z$  = The measurement corresponding to  $Y$  from the second photograph of the stereo pair.

The height ( $H$ ) of the optical center of the lens above the base was determined empirically by measuring the distance from the film plane to the base and subtracting the focal length plus the movement of the lens ( $F + L$ ). As a check, equation 1 was used to determine  $H$  ( $H = 952.0$  mm):

$$H = \frac{(F + L)^2}{L} \quad (1)$$

The magnification,  $M$ , of the photograph was determined by measuring the distance between two points on the negative,  $O$ , and the corresponding points on the print or projected negative image,  $I$  ( $M = 4.7$ ):

$$M = \frac{I}{O} \quad (2)$$

The absolute parallax at the base ( $P$ ) was determined by finding a common point ( $X$ ) on the base in each stereo pair of photographs. The distance from  $X$  to the line intersecting the nadir of the first photograph (the  $x$  axis) was measured ( $Y$ ), and a similar measurement was taken from the same point ( $X$ ) on the second photograph to the line intersecting the nadir on that photograph ( $Z$ ). Measurements  $Y$  and  $Z$  were then added together and multiplied by the optical magnification ( $M$ ) to give  $P$ . A similar procedure was followed to give the absolute parallax ( $P_1$ ) at a bench mark (a point  $X_1$  on the plant).

$$P = M(Y + Z) \quad (3)$$

$$P_1 = M(Y_1 + Z_1) \quad (4)$$

The change in the absolute parallax ( $\Delta P$ ) at a bench mark was calculated by subtracting  $P$  from  $P_1$ :

$$\Delta P = P_1 - P \quad (5)$$

With the above information, the height of each bench mark above the base ( $h$ ) was calculated:

$$h = \frac{H \Delta P}{A + \Delta P} \quad (6)$$

The change in elevation of a bench mark from the base ( $\Delta h$ ) was determined:

$$\Delta h = \frac{(H - h) \Delta P}{A + \Delta P} \quad (7)$$

Since the reduction of the image,  $R$ , on the negative changes depending on the distance of the object to the camera,  $R$  must be determined for each bench mark:

$$R = \frac{F + L}{H - h} \quad (8)$$

The apparent length  $D_1$  between two points on the plant was obtained by averaging the digitizer measurements ( $D_2$  and  $D_3$ ) from the two photographs and multiplying that measurement by the magnification correction term,  $M$ . This apparent length ( $D_1$ ) and the change in elevation between the two marks ( $\Delta h$ ) was used in the Pythagorean theorem to determine the actual distance ( $D$ ).

$$D_1 = \frac{(D_2 + D_3)}{2} M \quad (9)$$

$$D = (D_1^2 + \Delta h^2)^{0.5} \quad (10)$$

A program was written in NorthStar GBASIC for carrying out the calculations described above. (This is printed in Mueller's dissertation and is available on request from the authors.) Two measurements were required at each dot on the stem—one from each photo of the stereo pair. To set up the stereograph table for taking these photographs, the nadirs were marked on the base, using a plumb line attached to the lens cap. Parallel lines were drawn, intersecting the nadirs and at right angles to a line connecting the nadirs (Fig. 2). The measurements were taken by projecting the negatives onto a digitizer interfaced with a micro-computer. A digitizer is a device that, among other things, gives  $x$ ,  $y$  coordinates for any point that is indicated with a cursor. The raw data were transferred to the computer and stored on disc files for analysis.

**Measurement of Developing Forces in Gravitropism.** Castor bean stems were restrained between wires in a horizontal position by wrapping with threads below the region of bending, then a thread was tied near the tip of the plant and secured to a metal bar below. Two strain gauges were affixed to each bar (one on top and one on the bottom of the bar in a half-bridge configuration) to measure the strain exerted by the plant as it responded (Fig. 3). The strain was recorded with a ten channel switching unit and a digital strain indicator (Vishay/Ellis 20). Each bar was calibrated by hanging a weight at the point where the string was later attached (this gives an equal but negative reading). The strain measurements (a dimensionless unit), multiplied by the calibration factor, gave the force exerted on the bar by the plant. In order to calculate a pressure in the stem, two assumptions were made. First, that the stems are a homogenous medium (the equations are based on engineering principles for a metal rod). Second, the diameter of the stem is equal and does not change. Even though the assumptions aren't valid, this method should give a good approximation. The pressure ( $P$ ) was calculated at the centroid of the pressure prism (*i.e.* the center point of the perpendicular cross sectional plane of half of the plant stem; see

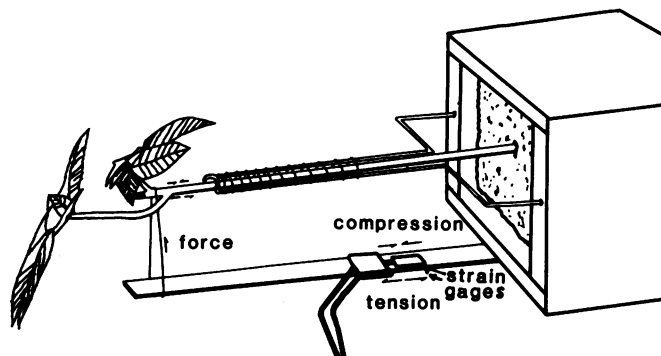


FIG. 3. A plant stem restrained between wires and tied to a metal bar with strain gauges attached (half bridge configuration) for measuring the forces of gravitropism.

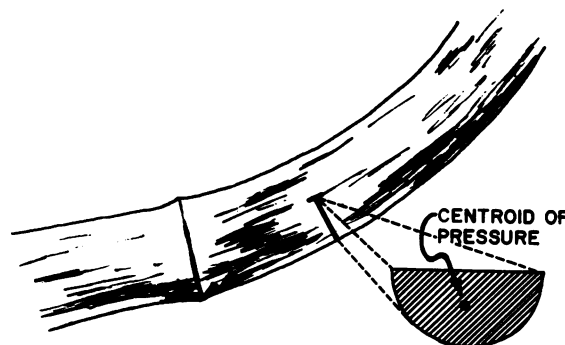


FIG. 4. Illustration of the centroid of pressure concept.

Fig. 4) according to equation 11.

- $A$  = the area of half of the stem cross section ( $\text{mm}^2$ ).  
 $F$  = the force calculated from the strain readings ( $\text{g cm s}^{-2}$ ).  
 $L$  = the length of the stem from the last restraining threads to the point of thread attachment from the bar (mm).  
 $M$  = the moment of force or torque ( $\text{mm s}^2$ ).  
 $P$  = pressure at  $r_{cm}$  (Pa).  
 $r$  = the average radius of the stem (mm).  
 $r_{cm}$  = the centroid of the pressure prism (mm; see Fig. 4).

$$\begin{aligned}
 M &= LF = r_{cm}PA \\
 r_{cm} &= \frac{4r}{3\pi} \\
 LF &= \left(\frac{4r}{3\pi}\right) (P) \left(\frac{\pi r^2}{2}\right) \\
 P &= \frac{3LF}{2r^3}
 \end{aligned}
 \tag{11}$$

These measurements were compared with bending of plants treated in three ways: (a) twelve sets of plants (five plants per set) with stem restrained between wires, each set being released at a different time interval, measured, and then discarded; (b) a single set of five plants restrained in a similar way, released, and allowed to bend for 10 s, measured, then straightened (forceably, using fingers) and restrained again to be released along with the next set of restrained plants later, this being repeated until the end of the experiment; and (c) a single set of five horizontal free-bending plants. Measurements were taken every 6 h for the first 36 h and then every 12 h to the end of the experiment (120 h). Stem bending (in degrees) was the measure of the response to gravity in the treatments, excepting the strain-gauge treatment.

**Pressure Transducers.** A small pressure transducer (3.5-mm diameter), marketed by Precision Measurement Co.<sup>3</sup>, offered another means of measuring the pressure changes in larger stems, such as castor beans. The pressure was measured and recorded periodically with a digital strain indicator combined with a 10-channel switching unit (the same unit used to measure strain with the strain gauges).

These are miniature pressure transducers, but they are still very large when compared to the diameter of the stem (about 8-

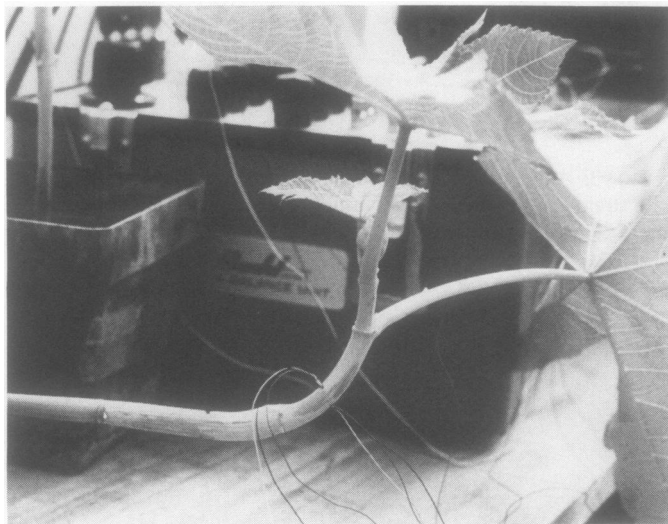


FIG. 5. Photograph of pressure transducers in a bending castor bean stem.

mm diameter). In spite of this, the plants still respond readily to gravity. Two transducers were inserted into the stem, one on each side, with the sensitive surface perpendicular to the axis of the stem and in the region of bending (Fig. 5). Plants were assigned to one of three treatments: vertical controls, horizontal unrestrained, and horizontal restrained plants. Horizontal stems had pressure transducers inserted in tops and bottoms of the bending region. Each of the three experiment replications was carried out in a dark growth chamber at 27°C.

## RESULTS

**Growth Changes of *Xanthium* Measured with Stereophotogrammetry.** Figure 6 shows the growth patterns of the vertical controls in the stereophotogrammetry experiments. The average initial length of all of the stems is represented by the axis of each graph, and the per cent growth is shown for each internode along the stem. The overall growth was slightly reduced when the plants were in the dark. Variabilities on opposite sides of vertical stems (third to sixth internode from the tip) account for nutational movements and crooked stems in *Xanthium*. The horizontal unrestrained plants (Fig. 7) bent as a result of increased growth on the bottom and a corresponding cessation of growth on the top, when compared to the controls. In the zone of bending, the upper surface of the stem actually shrank. The measurements of the tips of the plants were variable. This was because of the difficulty of taking measurements when the stem was bent upward so the apparent distances between dots was

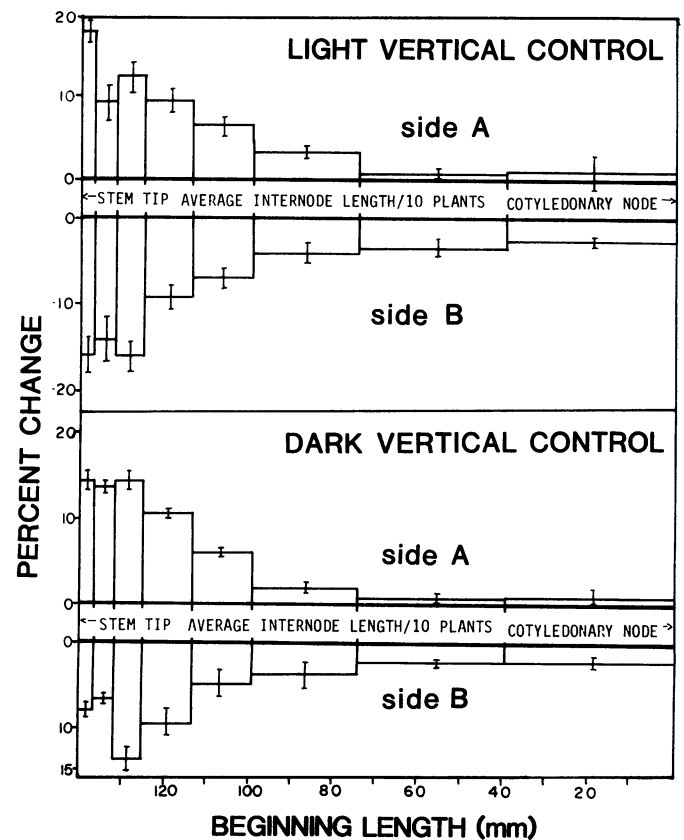


FIG. 6. Graph showing the growth of the control plants in stereophotogrammetry experiments. Distances of nodes along the stem (measuring from the tip) at the beginning are indicated on the abscissa of each graph, and the per cent change (after 36 h) is represented by the bars and the figures on the ordinate. Each bar shows the growth change of that particular internode. The measurements were taken using techniques of stereophotogrammetry.

<sup>3</sup> Precision Measurement Co., 885 Oakdale, Ann Arbor, MI 48107.

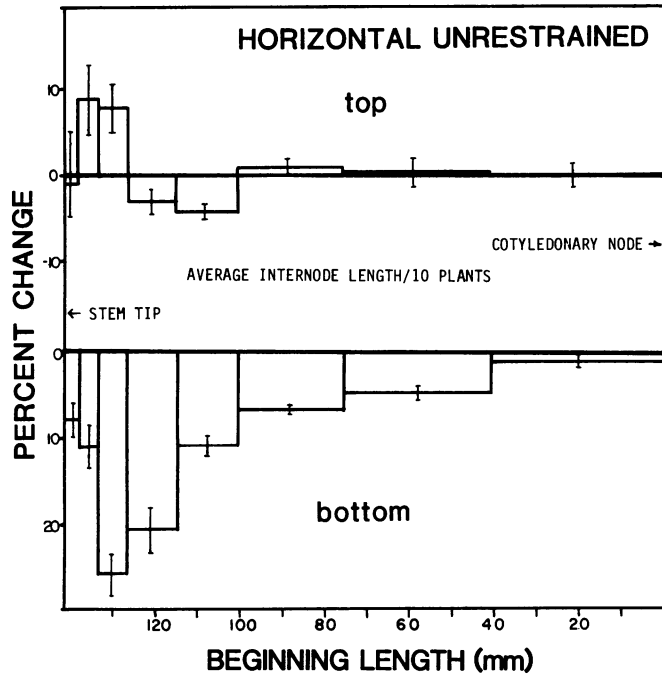


FIG. 7. Graph showing the growth of horizontal unrestrained plants in stereophotogrammetry experiments. See caption of Figure 6 for explanation.

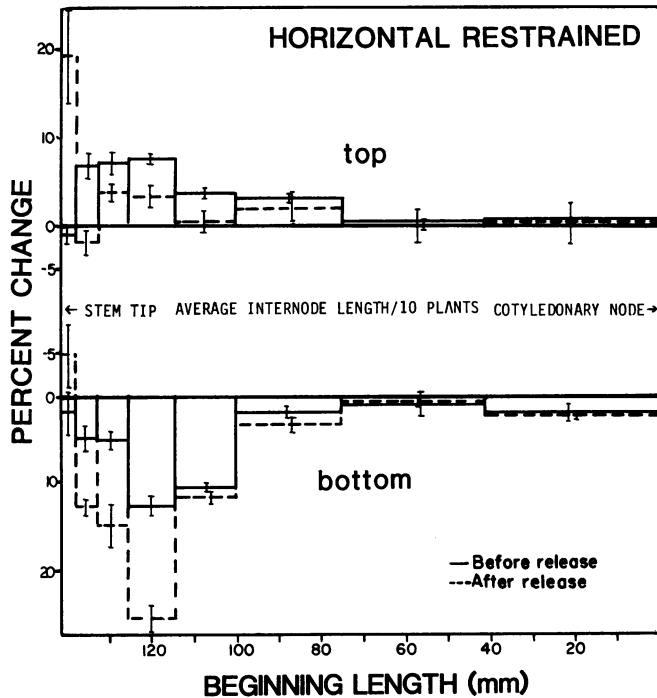


FIG. 8. Graph showing growth of horizontal restrained plants in the stereophotogrammetry experiments. See Figure 6 for explanation. (—), Growth changes after 36 h but before the plants were released; (---), the change in length (compared with the beginning) that occurred when the restraints were cut, and the stem was allowed to bend freely.

very small on the photographs. These results with cocklebur were confirmed with castor beans as well.

Upon release, bottoms of restrained stems rapidly elongated, and tops shrank (Fig. 8). The second and fifth internodes in this figure shrank to their approximate dimensions before bending, although this is somewhat variable in different experiments.

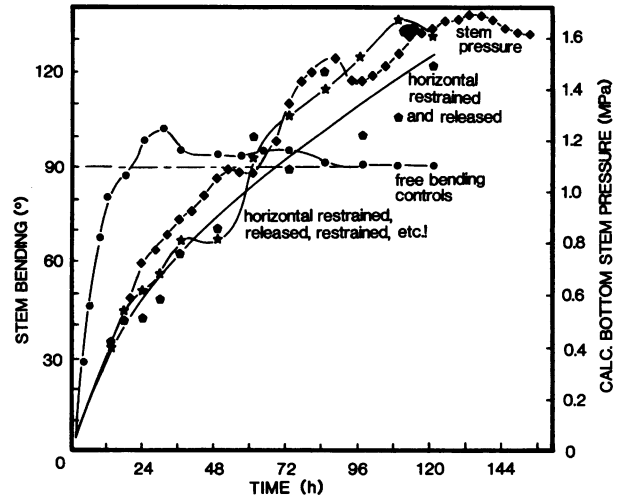


FIG. 9. Graph showing the gravity responses of horizontal plants to various treatments. The circles represent degrees of bending for five horizontal free-bending plants. The stars represent bending of a single set of five plants that were restrained, later released, then restrained again, to be released at the next measurement. The pentagons represent bending of different sets of restrained plants that were released at different time intervals. The squares represent calculated pressures at the bottom centroids of plants attached to the strain gauges. This pressure is calculated from the forces measured by the strain gauges.

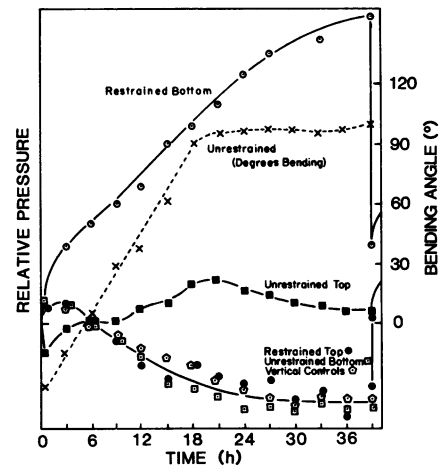


FIG. 10. Graph showing the results of the pressure transducer experiments. (●, ■), the top; (○, □), the bottom; (⊙), the vertical controls. (×), stem bending (in degrees) of the free-bending plants. The restrained plants were released at 40 h.

The gravity response of the plants occurred in the region of growth, primarily in the third to fifth internodes from the tip (the growing region of the stem). (Compare the growth patterns of the controls with those of the unrestrained and the restrained plants, Figs. 6–8.) There was also an increased growth of the sixth internode from the tip when compared to the controls. This is normally an area of slow growth.

**Measurements of Developing Forces in Gravitropism.** The force exerted on the metal bars by bending stems did not reach a maximum until about 120 h (Fig. 9). The plants that were restrained and released at different times followed the same pattern, bending to the maximum at about 120 h. Surprisingly, the plants that were restrained, released, then restrained again, again reaching a maximum bending at about 120 h.

**Pressure Transducers.** One of the most striking results of this experiment was that the plants were able to respond at all. Even

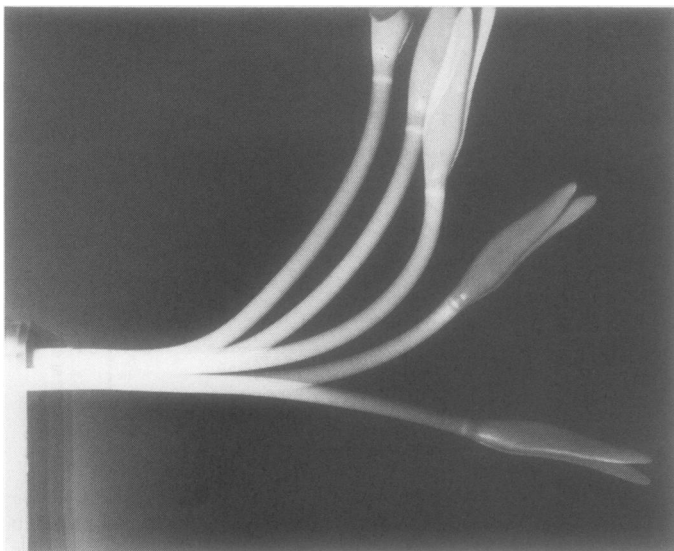


FIG. 11. A multiple exposure of a bending stem (cocklebur seedling) showing the pattern of localization of bending. Exposures were 0, 1, 2, 4, and 6 h after the stem was turned to the horizontal position.

though the transducers are small (3.5 mm), they are quite large when compared to the stem diameter of *Ricinus* (about 8 mm). The first time an experiment was conducted, the transducers were inserted 48 h before the experiment to allow healing, but callus tissue formed, pushing the transducer from the wound.

The pressure in the vertical control plants changed over the duration of the experiment. There was first an increase in pressure, followed by a steady decline that leveled off after about 24 h (Fig. 10), at which time bending was complete in free-bending plants. This is consistent throughout the experiments.

The bottom of the free-bending plant stems showed the same pressure changes as in the controls, while the top pressure increased. The maximum pressure was recorded at the time when the plant stem bend reached 90°. Initially, when the plants were placed horizontally, the weight of the stem and leaves caused pressure at the bottom to be higher than when vertical, and that of the top to be lower. After bending reached about 25°, the top then had a higher pressure than the bottom.

## DISCUSSION

The use of photogrammetry in measuring plant growth makes it possible to measure more concisely where the growth changes occur than by conventional methods. When a plant is allowed to bend freely, the bend is first noticeable as a smooth curve all along the growing region of the stem. Then the bend begins to localize and move basipetally (Fig. 11).

The horizontal restrained plants demonstrate the elastic properties of the stems. The stored energy for the rapid bending when the threads are cut is apparently in the stretched top cells and the compressed bottom cells.

It should be pointed out that elongation would be equal in the top and bottom of restrained plants before release if the restraints were perfect. There is some bending that occurs during restraint, however, and this appears in Figure 8 as slightly different elongations on top and bottom during restraint. (We have restrained stems in grooves between blocks of wood, observing bending upon release when restraint was nearly perfect.)

Even with the imperfect restraint, the results (shrinkage on top, stretching on bottom, upon release) show that during restraint the top is being stretched by the growing bottom of the stem while the bottom is being compressed by the tension (resistance) of the top. As expected, the plant stem isn't com-

pletely elastic; the top does not contract to the same dimensions as free-bending unrestrained plants.

The plants that were restrained, released, and restrained again clearly show the elastic nature of the stem. Some plant movements are caused by rapid movement of water into or out of cells (as is the case with *Mimosa* leaf movements). Because of the demonstrated reversibility of bending in this particular experiment, however, water movement has been discounted in favor of a change in cellular dimensions (relative length to width) during restraint, which predisposes the stem to bending when released (30).

With the unrestrained horizontal plants, there was a region where the top of the stem shortened during bending (Fig. 7). Since the pressure on top apparently exceeded that on the bottom (Fig. 8), the top pressure and shrinkage could not be caused by growth on the bottom exerting a force on the top. These results suggest that the tissues on top of a bending stem are actively contracting—although the pressure measurements must surely be repeated when smaller pressure transducers become available. (Cellular shortening was also observed in the companion study [30].) We are also following other approaches to investigate the possible role of active contraction on top of a free-bending stem.

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