

# Rapid, bilateral changes in growth rate and curvature during gravitropism of cucumber hypocotyls: implications for mechanism of growth control

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**Abstract.** The growth response of etiolated cucumber (*Cucumis sativus* L.) hypocotyls to gravitropic stimulation was examined by means of time-lapse photography and high-resolution analysis of surface expansion and curvature. In comparison with video analysis, the technique described here has five- to 20-fold better resolution; moreover, the mathematical fitting method (cubic splines) allows direct estimation of local and integrated curvature. After switching seedlings from a vertical to horizontal position, both upper and lower surfaces of the stem reacted after a lag of about 11 min with a two- to three-fold increase in surface expansion rate on the lower side and a cessation of expansion, or slight compression, on the upper surface. This growth asymmetry was initiated simultaneously along the length of the hypocotyl, on both upper and lower surfaces, and did not migrate basipetally from the apex. Later stages in the gravitropic response involved a complex reversal of the growth asymmetry, with the net result being a basipetal migration of the curved region. This secondary growth reversal may reflect oscillatory and/or self-regulatory behaviour of growing cells. With some qualifications, the kinetics and pattern of growth response are consistent with a mechanism involving hormone redistribution, although they do not prove such a mechanism. The growth kinetics require a growth mechanism which can be stimulated by two- to three-fold or completely inhibited within a few minutes.

**Key-words:** *Cucumis sativus* L.; gravitropism; hypocotyl (cucumber); growth kinematics; cell expansion.

## Introduction

The growth asymmetry underlying plant tropisms has been studied in a number of systems on the principle that the pattern and kinetics of growth alteration can help to elucidate the mechanism of growth control in plants (Baskin *et al.*, 1985; Digby & Firn, 1979; Franssen *et al.*, 1981; Hart & MacDonald, 1981; Iino & Briggs, 1984). For example, during first positive

phototropism of maize coleoptiles, Iino and coworkers found that the growth rate was depressed on the irradiated side and stimulated on the shaded side, and this growth asymmetry migrated down the coleoptile at rates similar to those for basipetal auxin transport (Baskin *et al.*, 1985; Iino & Briggs, 1984). This pattern of growth asymmetry was viewed as compatible with the predictions of the Cholodny-Went hypothesis. Likewise, in maize roots, growth alterations have conformed to the hypothesis that endogenous growth regulators are laterally redistributed (Barlow & Rathfelder, 1985; Nelson & Evans, 1986).

On the other hand, Digby, Firn and coworkers (Digby & Firn, 1979; Firn & Digby, 1980; Franssen *et al.*, 1981) concluded that the growth asymmetry during phototropism and gravitropism (1) began simultaneously along the length of the organ and (2) resulted, in general, from an inhibition of one side of the organ, without a corresponding increase on the other side. These results were interpreted as being at odds with the Cholodny-Went hypothesis and stimulated renewed interest in the pattern and dynamics of growth changes during tropisms.

In phototropic bending, the growth pattern has been shown to be complicated by multiple light-growth responses. For example, Rich, Whitelam & Smith (1987) were able to modify the pattern of phototropic growth by use of various light treatments. In the absence of interfering light-growth responses, phototropism was caused by altered and opposing growth responses on both sides of the stem. Hence, the Cholodny-Went theory was indirectly supported by this and related work on phototropism (Baskin, Briggs & Iino, 1986).

In gravitropism, analogous complications are presumably missing, yet various studies are at odds with each other regarding the underlying growth patterns (Digby & Firn, 1979; Iwami & Masuda, 1974; MacDonald, Hart & Gordon, 1983; Mueller, Salisbury & Blotter, 1984). Even within a single species (cucumber), different groups have concluded that gravitropic curvature arises from a response of the upper (Digby & Firn, 1979), lower (Iwami &

Masuda, 1974) or both (MacDonald *et al.*, 1983) surfaces of the stem. However, because of differing methods, degrees of resolution, and time scales of measurements, it is difficult to resolve these differences.

This study was carried out to determine in detail the spatial and temporal patterns of growth alteration during gravitropism of cucumber hypocotyls. In particular, the work aimed to resolve (1) whether the growth response was localized to one side, (2) whether the growth asymmetry started at the tip and migrated basipetally, as reported for phototropism (Baskin *et al.*, 1985; Iino & Briggs, 1984), and (3) whether the growth pattern and kinetics were compatible with a mechanism involving hormone redistribution (Baskin *et al.*, 1985, 1986). The study also served as the foundation for a further investigation into the biophysical basis of the altered growth (Cosgrove, 1990). Cucumber was selected because it exhibits a fast and vigorous gravitropic response, which makes it particularly attractive for studying the underlying mechanisms of growth control. Using an improved method for high-resolution growth analysis, the growth pattern during the initial development of curvature was examined in detail.

## Material and methods

### Plant material

Seeds of cucumber (*Cucumis sativus* L. cv. Burpee Pickler, from W.A. Burpee, Warminster, PA, U.S.A.) were sown in 2 × 5 cm polyethylene vials filled with wet vermiculite and grown at 27–29°C for 3 d in the dark. Plants were handled under dim green overhead light (less than 0.01 µmol m<sup>-2</sup> s<sup>-1</sup> at plant level) obtained from a 40 W cool-white fluorescent lamp filtered through one amber and two green acetate filters (Roscolene No. 813 and 874; Roscoe, Port Chester, NY, U.S.A.).

**Growth measurements.** Hypocotyls of vigorous, symmetrical seedlings were marked by hand into 12 zones of approximately 2 mm each, using oil-based block-printing ink (Speedball, Hunt Manufacturing, Stateville, NC, U.S.A.) and a glass fibre (30 µm thickness) or an eyebrow hair as a brush. Seedlings were marked and positioned in front of the camera with the aid of a small, green light-emitting diode (emission maximum at 560 nm). The marked zones are designated as 1=most apical, through 12=most basal. Photographs were made at 15-min intervals with Kodak Tri-X film and a green-filtered horizontal flash for illumination. The intermittent green flashes did not significantly alter the growth rate of the seedlings during the 3-h time course of these experiments. This was demonstrated by comparing the growth of marked seedlings kept in the dark for 3 h with those exposed to 15-min flashes for 3 h. Growth rate of the most apical 1-cm region

was 9.9% h<sup>-1</sup> for the dark plants versus 9.7% h<sup>-1</sup> for the intermittently flashed plants ( $n=20$ ; SEM = 0.2% h<sup>-1</sup>).

Photographs of the marked seedlings were analysed by projecting the negatives onto a digitizing table (DigiPad 5, GTCO, Rockville, MD, U.S.A.) and recording the positions of the marks with the instrument's cursor and custom-made software (written in Pascal on an IBM AT microcomputer). The program fitted a cubic spline to the coordinates of each mark (Atkinson & Harley, 1983) and from the resulting polynomial equations the distances between marks were calculated along the curved surface by breaking each zone into 10 straight-lined segments and summing the length of the segments. Curvature in each marked zone was estimated by averaging the curvature at 10 equidistant points within each zone. Curvature (K, units: mm<sup>-1</sup>) was calculated using the standard formula:

$$K = \frac{|d^2y/dx^2|}{[1 + (dy/dx)^2]^{3/2}}$$

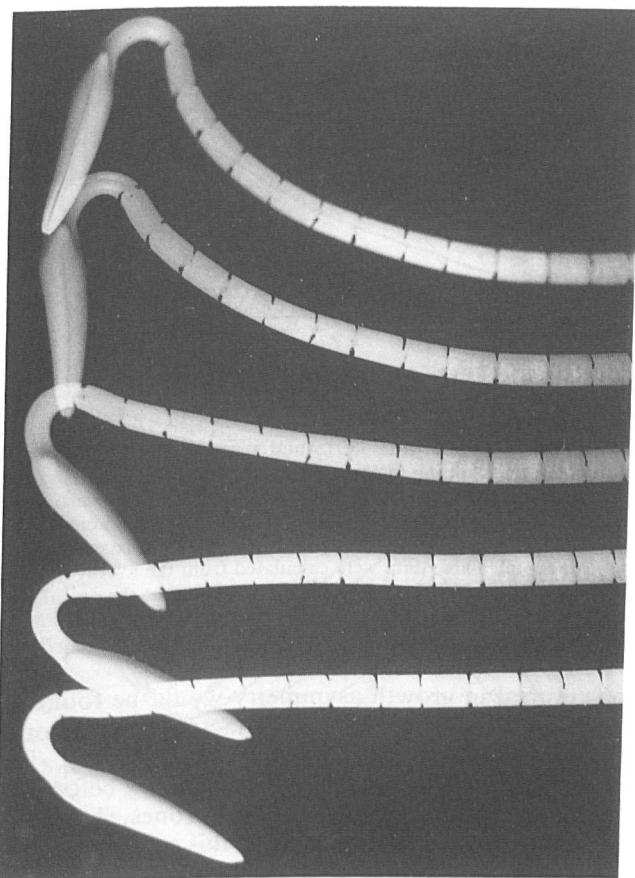
where dy/dx and d<sup>2</sup>y/dx<sup>2</sup> are the first and second derivatives of the cubic polynomial. Distances and curvatures were recorded in data files on disk, and subsequently were displayed or averaged by other custom software. As noted in some cases, growth data were smoothed in the space or time domains by a least-squares method using Chebyshev polynomials, implemented with a commercial library of numerical routines.

For some experiments, the start of gravitropism was detected by turning a seedling horizontally, bracing the basal part of the stem with a small amount of clay, and placing on the upper surface of the apical end of the seedling a counterbalanced lever-arm attached to a rotary variable differential transformer (RVDT model R30A, Schaevitz, Pennsauken, NJ, U.S.A.). The RVDT output was proportional to upward motion of the stem, which was recorded on a strip chart recorder.

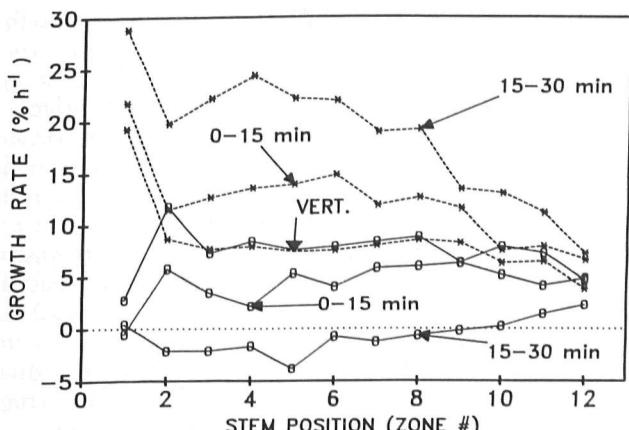
## Results

Figure 1 shows a sequence of time-lapse photographs of a cucumber hypocotyl during gravitropic bending. The ink marks were used to monitor growth and curvature on the two sides of the stem. Figure 2 shows the growth rate as a function of stem position for seedlings in the vertical position and during the initial period of gravitropic bending. For vertical seedlings, growth rates were symmetrical on the two sides of the hypocotyl, except in the most apical zone where unbending of the hook imparted a growth asymmetry. The gradient in growth rate in the marked region (ca. 2.3 cm) was rather small compared to other seedling stems (Cosgrove, 1985).

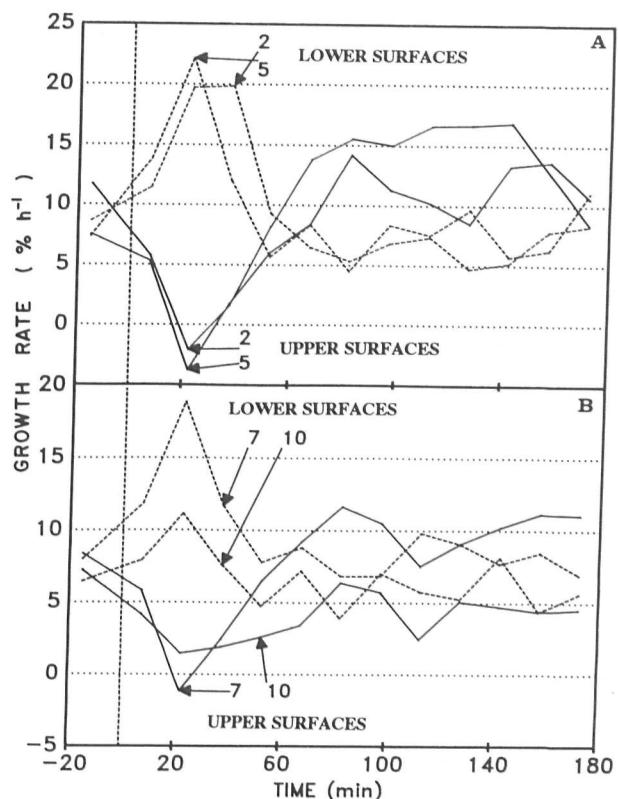
Figure 2 illustrates several points about the start of cucumber gravitropism. First, both upper and lower



**Figure 1.** Multiple-exposure, time-lapse sequence of photographs of a gravitroping cucumber stem. Photographs were taken at 15-min intervals starting at time zero and the seedling was displaced vertically between photographs. The marks were typical of those used to measure surface expansion along the length of the hypocotyl.



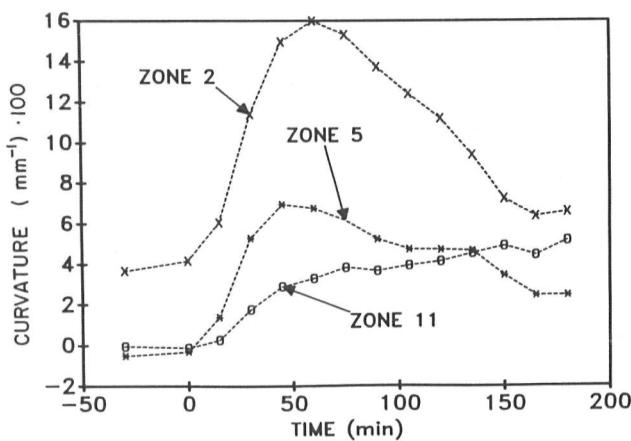
**Figure 2.** Profile of growth rate of upper and lower surfaces along the length of the hypocotyl in cucumber seedlings in the time period 30–0 min before, 0–15 min after, and 15–30 min after horizontal placement. These graphs are the composite responses of 18 seedlings, averaged by computer (no smoothing). The zone designated '1' is the apical zone. Solid line, upper surface; broken line, lower surface. Standard errors are typically 2–3%  $\text{h}^{-1}$ .



**Figure 3.** Time course for growth rate changes on upper and lower hypocotyl surfaces following horizontal placement at time=0. Apical (zone 2), intermediate (zones 5 and 7) and basal regions (zone 10) exhibit similar responses. These graphs are the composite of 18 seedlings, averaged by computer (no smoothing). Each point is plotted in the middle of the time interval. Standard errors were typically 2–3%  $\text{h}^{-1}$ .

stem surfaces responded to the gravitropic stimulus by reducing or increasing growth rate, respectively. The reduction in growth rate on the upper surface was nearly symmetrical with the increase on the lower surface. Secondly, the growth response did not originate in the apex and migrate slowly downward as in the case of maize phototropism (Baskin *et al.*, 1985; Iino & Briggs, 1984). Rather, growth changed simultaneously along the length of the plant (see also Fig. 3). A very fast migration, within 5 min, however, might not be detected with these methods. Thirdly, at the peak of the response (15–30 min), the lower surface increased its growth rate by two- or three-fold, whereas the upper surface ceased growth entirely, and in places contracted. Finally, although all the marked zones began to react at the same time, the magnitude of the response varied with stem position, with the basal region responding less vigorously.

Growth rates are displayed as a function of time for selected marked zones in Fig. 3A & B. Note that the data show that growth is altered within the first 15-min interval after horizontal placement, but the temporal resolution is not adequate to determine the exact start of the response (but see below). The



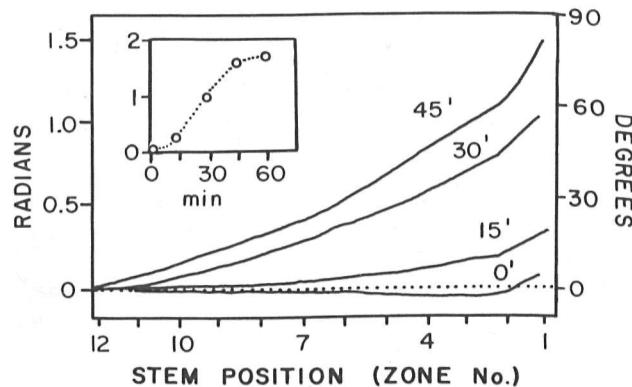
**Figure 4.** Curvature of different marked zones as a function of time after horizontal placement at time = 0. These are the composite responses of 18 seedlings, averaged by computer (no smoothing). Standard errors are typically  $0.01 \text{ mm}^{-1}$ .

growth alteration was very transient and the asymmetry quickly reversed itself in the apical zones. This reversal began during the 30–45 min interval, but did not actually reverse the growth asymmetry until the 60–75 min interval, i.e. after the stems had curved more than  $90^\circ$  and overshot the vertical. Thus, the reversal would appear to be part of the straightening reaction of the hypocotyl.

Changes in the local curvature of various marked zones (Fig. 4) were consistent with these growth patterns. All regions began to curve at the same point in time, but the apical zones curved more strongly because of the stronger asymmetry in growth rate. The curvature of apical zones reached a maximum, then declined in a manner consistent with the reversal in the growth asymmetry and the straightening of the apical hypocotyl region. In contrast, the more basal zones showed little or no decline in curvature.

As an aside, it is possible to convert these data on local curvature to the more common form of stem angle. This is done by integrating the values for curvature over the length of the stem, as shown in Fig. 5.

Two aspects of these growth kinetics seemed remarkable and worth further examination. First, the growth asymmetry of the basal zones was quickly diminished or even reversed (e.g. Fig. 3B), even though these zones were displaced only slightly from the horizontal in this time (see Fig. 1). Such ‘premature’ growth reversal is inconsistent with a simple growth response directed by a local gravity sensing system, and suggested that the growth of the basal regions might depend on gravity sensing by the apical zones, which attain a vertical posture at about the time of the growth reversal. To test this possibility, the two most apical zones (1 and 2) of marked plants were maintained in a horizontal position by rotating the seedling as it began to bend gravitropically. If the gravity sensor were localized to the apical zones, then

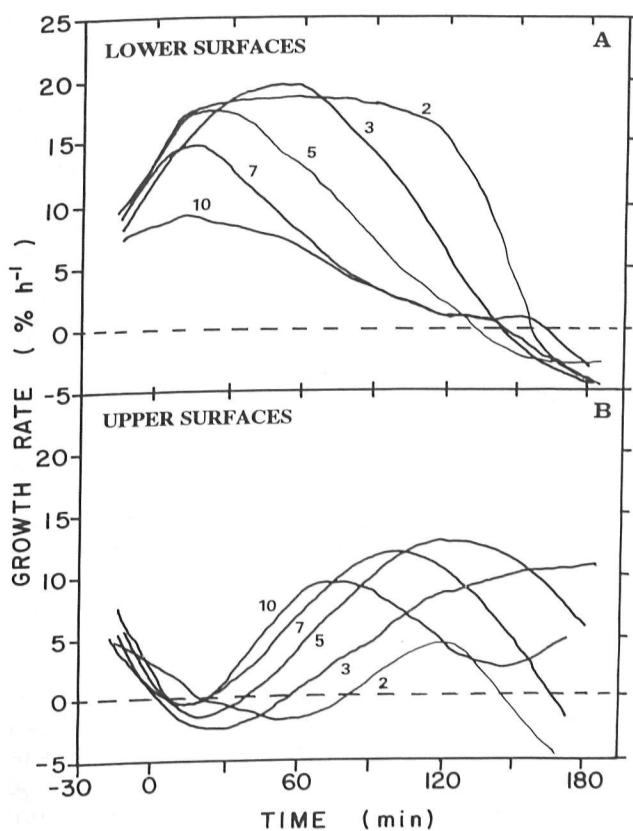


**Figure 5.** Curvature integrated over the length of the stem, at different time points after horizontal placement. Curvature was integrated by summing the product of the curvature and length of each zone. The result has units of radians, which is convertible to degrees. Inset shows a time course for total integrated curvature, i.e. the angle (in radians) formed by the apical and basal parts of the hypocotyl. These data were calculated from the average curvatures and lengths of 18 marked seedlings. Note that the apical part of the seedling is on the right part of the graph.

no reversal in growth asymmetry would be found in either apical or basal zones. In fact, the basal zones did reverse their growth asymmetry (Fig. 6). The most basal zones reversed their asymmetry before the middle zones, whereas the apical zones showed a prolonged growth asymmetry. In this experiment, the basal zones were the first to be displaced into a vertical (but upsidedown) position. With further bending they tilted beyond the vertical and thus the gravitropic stimulus became reversed for them. The same happened to the middle zones of the hypocotyl, but at a later time. This pattern of growth reversal indicates that gravity is sensed locally in the cucumber hypocotyl.

This conclusion contradicts the hypothesis (above) that gravity is sensed primarily in the apical zones of the stem. The reason for the ‘premature’ growth reversal in the basal zones during normal gravitropism (Fig. 3B) remains uncertain. A possible clue is that even though the apical zones were kept horizontal, they were not able to sustain their large growth symmetry indefinitely (Fig. 6), despite continued gravitropic stimulation. Apparently, other growth regulatory responses are involved (see ‘Discussion’).

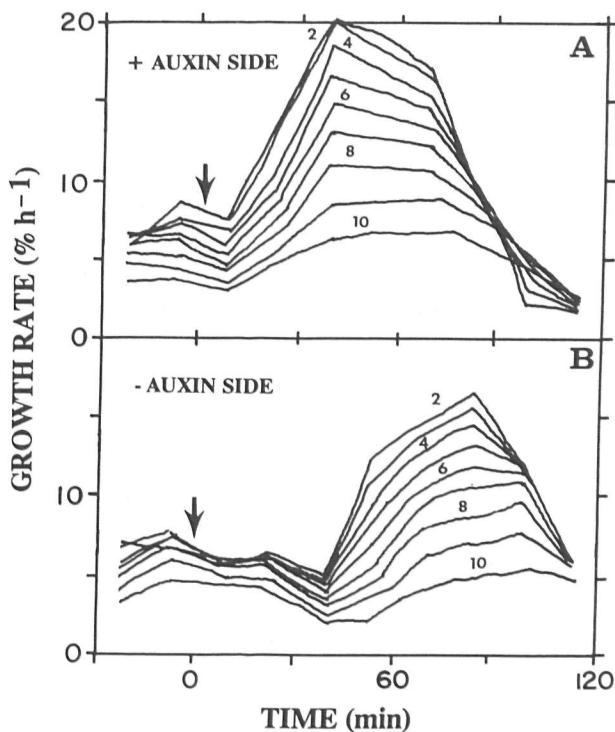
A second curious aspect of cucumber gravitropism is that the upper stem surface not only ceased growth, but actually contracted transiently (Figs 2 & 6). This contraction might result from turgor loss in the upper cells or from mechanical compression (due to bending moments) of an otherwise nongrowing surface. To test this latter idea, auxin solution was applied as a droplet to one side (zone 3) of the hypocotyl of a set of vertical seedlings, and the growth rates on the two sides were measured as before. Assuming the untreated side was not directly affected by the auxin, any reductions in growth rate could be interpreted as due to passive compression



**Figure 6.** Growth responses of different stem regions when zones 1 and 2 were maintained in a horizontal position, starting at time = 0. The small numbers indicate the zone. Photographs were taken 15-min intervals. These are composites of three seedlings, averaged by computer, with seventh-degree polynomial smoothing in the temporal and spatial domains. The temporal smoothing leads to a slight spread of the response; for example, in comparison with Fig. 3. A: lower surface; B: upper surface.

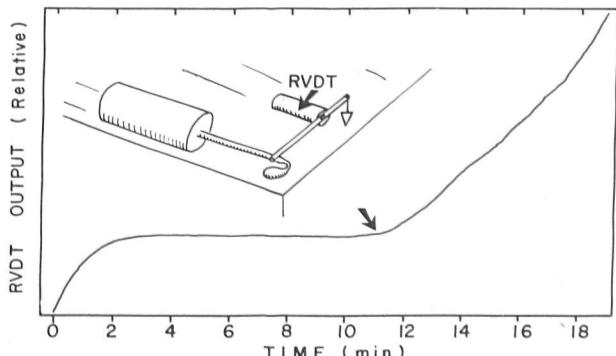
from bending of the stem. Figure 7 shows that, as expected, the side with applied auxin increased in growth rate, by two- to three-fold at 30–45 min after application. Interestingly, zones apical and basal to the site of auxin application were stimulated to grow faster at the same time as the treated region. The maximum rate of curvature was about one half of the rate of gravitropic bending in the plants used in Fig. 2. The untreated side reduced its expansion rate by  $2.9\% \text{ h}^{-1}$  (average of zones 1–10, significant at the 0.002 level by ANOVA). This (presumably passive) growth reduction is similar to the rate of contraction of the gravitroping stems. These results are consistent with the view that the transient contraction in Fig. 2 is a passive mechanical effect, arising from bending moments generated in the curving stem and superimposed upon a nongrowing surface. The curvature caused by the unilateral auxin application subsequently induced a secondary gravitropic response, leading to stimulation of the untreated side and inhibition of the treated side (Fig. 7).

From Figs 2 and 3 we know that stem growth was altered within 15 min of gravitropic stimulation, but



**Figure 7.** Response of different stem regions to local unilateral application of auxin ( $2 \text{ mm}^3$  of  $10 \text{ mmol m}^{-3}$  IAA) to zone 3. Numbers indicate the zone. These are the composite responses of 13 seedlings, averaged by computer, with fifth-degree polynomial smoothing in the spatial domain.

exact determination of the start of the response is not possible from these data. More precise timing of the lag period prior to the start of gravitropic bending was obtained by placing the end of the lever arm of an RVDT on the upper surface of the apical end of a horizontal seedling. As shown in Fig. 8, the start of the upper movement was clearly discerned and usually was quite abrupt. In 10 experiments, the lag period ranged from 9 to 15 min, with an average value of 11.3 min.



**Figure 8.** Measurement of lag time preceding initiation of curvature. Inset shows the connection of the RVDT to the upper, apical part of the hypocotyl. Lag times were estimated by eye for each curve, as shown by the arrow in this example.

## Discussion

These results show that gravitropic stimulation elicited a simultaneous, bilateral growth response along the length of the cucumber hypocotyl. The deviation from normal (vertical) growth rates was nearly symmetrical, but of opposite sign, on the upper and lower stem surfaces. Thus, unlike Iwami & Masuda (1974), who concluded that the lower cucumber epidermis was the gravitropically-responsive site, and Digby & Firn (1979), who concluded that the upper surface of the cucumber hypocotyl was the responsive region, this study found that both sides of the organ were involved in the gravitropic response: specifically, a transient, total cessation of expansion on the upper surface and a doubling or more of the expansion rate on the lower stem surface.

What accounts for these differing conclusions? One factor might be the magnitude of the gravitropic response, which was greater in the current study than in the previous ones (Digby & Firn, 1979; Iwami & Masuda, 1974; MacDonald *et al.*, 1983). Iwami & Masuda (1974) did not measure growth on the two sides of the stem, but based their conclusion that the lower epidermis was the gravitropically responsive one on results from stress-relaxation measurements of isolated, methanol-boiled epidermal strips. From recent work on light-growth responses in cucumber (Cosgrove, 1988), it appears that such mechanical assays of wall characteristics do not always reflect the relevant wall properties that control growth. In the study by Digby & Firn (1979), it may be that temporal variations in growth, as noted in other studies (Gaba & Black, 1979; Kristie & Jolliffe, 1987; MacDonald *et al.*, 1983), hid the predominant gravitropic pattern, since Digby & Firn showed only responses of single seedlings. Likewise, MacDonald *et al.* (1983) examined the gravitropic responses of single cucumber hypocotyls and, although their data are also troubled by large variations, they concluded that cucumber stems responded bilaterally. In the current study, the finer resolution and the ability to average multiple data sets leaves little room for doubt about the bilateral response during cucumber gravitropism. Thus, cucumber behaves like most other bending shoots, including maize, cress, sunflower and cocklebur (Baskin *et al.*, 1985; Digby & Firn, 1979; Gordon *et al.*, 1984; MacDonald *et al.*, 1983; Mueller *et al.*, 1984).

For the initiation of bending, there was no indication of a downward migration of the growth asymmetry, as in phototroping maize coleoptiles (Baskin *et al.*, 1985; Iino & Briggs, 1984); rather, the growth asymmetry developed simultaneously in apical and basal regions. This confirms in greater detail previous observations of dicot stem gravitropism (Digby & Firn, 1979; MacDonald *et al.*, 1983). Also of interest is the abruptness of the start of bending (e.g. Fig. 8), which suggests that the transition to altered growth rates was very quick, 1–2 min.

After the cucumber hypocotyl righted itself (45–60 min after horizontal placement), there ensued a complicated reversal in the growth pattern, which in part may be due to a straightening response to overshooting the vertical position and in part may result from a growth reaction to the initial (15–45 min) growth perturbation. This behaviour, sometimes termed autotropism (Firn & Digby, 1979; MacDonald *et al.*, 1983), appeared to be superimposed on local gravitropic responses along the length of the stem. Possibly related to this, straight growth of cucumber and other stems frequently exhibits oscillatory patterns and signs of 'stored growth' (Cosgrove, 1988; Kristie & Jolliffe, 1987), which have sometimes been interpreted as evidence for feedback regulation of cell expansion. These complicated behaviours may be responsible for the unexpected reversal in the basal growth regions during gravitropism and may be independent of hypothetical hormone asymmetries.

Although gravitropic bending is initiated simultaneously along the length of the stem, the reversal in the growth pattern is stronger in the apical regions than in the basal regions, with the result that the curved region of the stem migrates downward; this late stage in gravitropism is similar to the one documented by MacDonald *et al.* (1983) in cress and cucumber hypocotyls, wherein a basipetal migration in the growth asymmetry was noted.

With regard to the Chodlony-Went theory, the timing of the growth response is just barely sufficient to allow the cells to respond to changes in auxin, if it were redistributed quickly (within a few minutes). It is not clear, however, that endogenous auxin is so quickly redistributed, or that its redistribution could account for the cessation of growth on the upper side and doubling of the growth on the lower side. For example, Mertens & Weiler (1983) reported that endogenous auxin is not detectably redistributed between the upper and lower halves of gravitroping cucumber hypocotyls. On the other hand, auxin applied exogenously does appear to become asymmetrically distributed, at least in some systems (for review, see Pickard, 1985). If one accepts the typical curves relating applied auxin concentrations to the growth rate of excised segments (Baskin *et al.*, 1986; Cosgrove, 1981), a rather large auxin differential might be predicted to account for the striking growth differences on the upper and lower surfaces during cucumber gravitropism. These apparent discrepancies have been rationalized by proposals invoking intracellular redistribution of auxin (Mertens & Weiler, 1983) or subtle shifts in auxin between the cortex and the epidermis (MacDonald & Hart, 1987; Mertens & Weiler, 1983). These hypotheses remain largely conjectural and without direct support. In favour of these ideas, new studies have supported the old notion (Masuda & Yamamoto, 1972) that the epidermis may regulate organ expansion and be the site of initial auxin action (Kutschera, Bergfeld &

Schopfer, 1987; Kutschera & Briggs, 1987). Also, McClure & Guilfoyle (1989) have reported that auxin-induced mRNA transcripts are increased on the lower side and decreased on the upper side of gravitroping soybean hypocotyls, particularly in the outer cell layers. Thus, while some aspects of the Chodlony-Went theory vis-a-vis hormone redistribution in dicot stems remain in doubt, the gravitropic growth pattern in cucumber cannot rule out the theory, and other new results contribute circumstantial support for the theory (McClure & Guilfoyle, 1989).

The upper surface of the bending cucumber hypocotyl undergoes a transient contraction, as reported previously (MacDonald *et al.*, 1983; Mueller *et al.*, 1984). While it is possible that the contraction is associated with a transient turgor loss on the upper stem surface, direct measurements with the pressure probe have shown that turgor remains high in these cells (Cosgrove, 1990). Instead, if we assume that the upper surface stops all active growth during this period of gravitropism, then the experiments with local auxin application (Fig. 7) indicate that the small contractions can arise passively by compressive bending moments generated by the asymmetry in expansion rates on the two sides of the stem. Analogous contractions may also be observed in circumnutations (Millet, Melim & Badot, 1988).

Finally, it is worth comparing the methods of growth analysis used here with some of those used in previous studies. One obvious comparison is between the photograph/digitizing-tablet approach versus video analysis (Gordon *et al.*, 1984; Jaffe *et al.*, 1985; Nelson & Evans, 1986). The primary advantage of the digitizing tablet is its higher resolution—conceptually 11 000 lines in each dimension versus about 500 for most video systems. The practical resolution of the digitizing tablet is limited by the positioning of the cursor, which in our hands yields an effective resolution of about 2500 lines. This figure can be improved somewhat by averaging multiple measurements of the same photograph. The better resolution of the digitizing tablet means that growth rates can be measured more accurately on more zones and over shorter time intervals than is feasible with video methods. This advantage is partly offset by the greater effort needed to make the tedious measurements.

The mathematical analysis by cubic spline, used here, has the distinct advantage that the local curvature can be readily calculated, and curvature along the stem can be integrated to give an accurate measure of total angle formed by the stem and to identify the region of maximum curvature. Thus, the method yields more information than the common method of recording total angle of the stem (Jaffe *et al.*, 1985) and does not have the analytical defects of the 'curvature index' method of Woitzik & Mohr (1988); for example, the curvature index may yield faulty and misleading values when straight regions of

the organ are included in the measured region and also is not fundamentally related to the growth differential on the two sides of the stem, as is local curvature (Silk & Erickson, 1978).

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### References

- Atkinson, L.V. & Harley, P.J. (1983) *An Introduction to Numerical Methods with Pascal*. Addison-Wesley, London.
- Barlow, P.W. & Rathfelder, E.L. (1985) Distribution and redistribution of extension growth along vertical and horizontal gravireacting maize roots. *Planta*, **165**, 134–141.
- Baskin, T.I., Briggs, W.R. & Iino, M. (1986) Can lateral redistribution of auxin account for phototropism of maize coleoptiles? *Plant Physiology*, **81**, 306–309.
- Baskin, T.I., Iino, M., Green, P.B. & Briggs, W.R. (1985) High-resolution measurement of growth during first positive phototropism in maize. *Plant, Cell and Environment*, **8**, 595–603.
- Cosgrove, D.J. (1981) Rapid suppression of growth by blue light: occurrence, time course, and general characteristics. *Plant Physiology*, **67**, 584–590.
- Cosgrove, D.J. (1985) Cell wall yield properties of growing tissues. Evaluation by in vivo stress relaxation. *Plant Physiology*, **78**, 347–356.
- Cosgrove, D.J. (1988) Mechanism of rapid suppression of cell expansion in cucumber hypocotyls after blue-light irradiation. *Planta*, **176**, 109–116.
- Cosgrove, D.J. (1990) Biophysical mechanism of altered growth during gravitropism of cucumber hypocotyls. *Plant, Cell and Environment*, **13**, 235–241.
- Digby, J. & Firn, R.D. (1979) An analysis of the changes in growth rate occurring during the initial stages of geocurvature in shoots. *Plant, Cell and Environment*, **2**, 145–148.
- Firn, R.D. & Digby, J. (1979) A study of the autotropic straightening reaction of a shoot previously curved during geotropism. *Plant, Cell and Environment*, **2**, 149–154.
- Firn, R.D. & Digby, J. (1980) The establishment of tropic curvatures in plants. *Annual Review of Plant Physiology*, **31**, 131–148.
- Franssen, J.M., Cooke, S.A., Digby, J. & Firn, R.D. (1981) Measurements of differential growth causing phototropic curvature of coleoptiles and hypocotyls. *Zeitschrift für Pflanzenphysiologie*, **103**, 207–216.
- Gaba, V. & Black, M. (1979) Two separate photoreceptors control hypocotyl growth in green seedlings. *Nature*, **278**, 51–54.
- Gordon, D.C., Macdonald, I.R., Hart, J.W. & Berg, A. (1984) Image analysis of geo-induced inhibition, compression, and promotion of growth in an inverted *Helianthus annuus* L. seedling. *Plant Physiology*, **76**, 589–594.
- Hart, J.W. & Macdonald, I.R. (1981) Phototropism and gravitropism in hypocotyls of cress (*Lepidium sativum* L.). *Plant, Cell and Environment*, **4**, 197–210.
- Iino, M. & Briggs, W.R. (1984) Growth distribution during first positive phototropic curvature of maize coleoptiles. *Plant, Cell and Environment*, **7**, 97–104.
- Iwami, S. & Masuda, Y. (1974) Geotropic response of cucumber hypocotyls. *Plant Cell Physiology*, **15**, 121–129.
- Jaffe, M.J., Wakefield, A.H., Telewski, F., Gulley, E. & Biro, R. (1985) Computer-assisted image analysis of plant growth, thigmomorphogenesis, and gravitropism. *Plant Physiology*, **77**, 722–730.
- Kristic, D.N. & Jolliffe, P.A. (1987) A rapid phytochrome-mediated growth response in etiolated *Sinapis alba* hypocotyls. *Canadian Journal of Botany*, **65**, 2017–2023.

- Kutschera, U., Bergfeld, R. & Schopfer, P. (1987) Cooperation of epidermis and inner tissues in auxin-mediated growth of maize coleoptiles. *Planta*, **170**, 168–180.
- Kutschera, U. & Briggs, W.R. (1987) Differential effect of auxin on *in vivo* extensibility of cortical cylinder and epidermis in pea internodes. *Plant Physiology*, **84**, 1361–1366.
- MacDonald, I.R. & Hart, J.W. (1987) New light on the Chododny-Went theory. *Plant Physiology*, **84**, 568–570.
- MacDonald, I.R., Hart, J.W. & Gordon, D.C. (1983) Analysis of growth during geotropic curvature in seedling hypocotyls. *Plant, Cell and Environment*, **6**, 401–406.
- Masuda, Y. & Yamamoto, Y. (1972) The control of auxin-induced stem elongation by the epidermis. *Physiologia Plantarum*, **27**, 109–115.
- McClure, B.A. & Guilfoyle, T. (1989) Rapid redistribution of auxin-regulated RNAs during gravitropism. *Science*, **243**, 91–93.
- Mertens, R. & Weiler, E.W. (1983) Kinetic studies on the redistribution of endogenous growth regulators in gravireacting plant organs. *Planta*, **158**, 339–348.
- Millet, B., Melin, D. & Badot, P.-M. (1988) Circumnutation in *Phaseolus vulgaris*. I. Growth, osmotic potential and cell ultrastructure in the free moving part of the shoot. *Physiologia Plantarum*, **72**, 133–138.
- Mueller, W.J., Salisbury, F.B. & Blotter, P.T. (1984) Gravitropism in higher plant shoots. II. Dimensional and pressure changes during stem bending. *Plant Physiology*, **76**, 993–999.
- Nelson, A.J. & Evans, M.L. (1986) Analysis of growth patterns during gravitropic curvature of roots of *Zea mays* using a computer-based video digitizer. *Journal of Plant Growth Regulation*, **5**, 73–83.
- Pickard, B.G. (1985) Roles of hormones, protons and calcium in geotropism. In *Encyclopedia of Plant Physiology, New Series, Hormonal Regulation of Development III. Role of Environmental Factors* (eds R.P. Pharis & D.M. Reid), pp. 193–281. Springer-Verlag, Berlin.
- Rich, T.C.G., Whitelam, G.C. & Smith, H. (1987) Analysis of growth rates during phototropism: modifications by separate light-growth responses. *Plant, Cell and Environment*, **10**, 303–311.
- Silk, W.K. & Erickson, R.O. (1978) Kinematics of lettuce hypocotyl curvature. *American Journal of Botany*, **65**, 310–319.
- Woitzik, F. & Mohr, H. (1988) Control of hypocotyl phototropism by phytochrome in a dicotyledonous seedling (*Sesamum indicum* L.). *Plant, Cell and Environment*, **11**, 653–661.

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