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Hormones and *Cuscuta* Development: Interaction of Cytokinin and Indole-3-Acetic Acid in the Growth and Curvature of Subapical Stem Segments

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Abstract. *Cuscuta* stem (vines) exhibits two modes of growth—longitudinal elongation forming free-hanging vines, or coiling growth to twine around the host. The elongation zone of free-hanging vine extended up to 160 mm from the stem apex and in vivo growth rate (during 8 h of growth) was maximal in the 20-to-40-mm region. While gibberellic acid (GA_3) or fusicoccin (FC) could maintain (GA_3) or enhance (FC) the growth rate of apical (10 or 25 mm) segments, indole-3-acetic acid (IAA) (10 μM) induced growth only in subapical (5–160 mm) segments. In vitro growth rate induced by IAA (10 μM) was similar to the in vivo growth rate up to 40 mm. Thereafter, up to 100 mm, IAA induced growth rate exceeded in vivo growth.

Subapical segments (~13 mm) from 5- to 40-mm regions responded to a cytokinin (BA, Z, or iP) or to low IAA (0.1 μM) with curved growth, whereas the segments grew straight in the presence of high IAA (10 μM). Curvature (measured as the angle subtended at the center of the circle of which the segment formed an arc) induced by BA and low (0.1 μM) IAA was greater than either added separately. Besides, segments induced to curve in BA + low-IAA solution could be made to straighten out by transferring to a solution containing high IAA (10 μM) with or without BA. Thus in vivo patterns of straight and coiling growth could be mimicked

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reversibly in vitro by adjusting the relative concentrations of cytokinin and auxin; low auxin and cytokinin induced coiling growth, whereas high auxin and cytokinin induced straight growth.

Beyond 40 mm, BA had no growth-promoting or curvative-inducing effect. *Cuscuta* vine segments thus showed sequential sensitivity to applied hormones, the apical region (0–25 mm) to GA_3, the subapical (5–40 mm) region to BA and IAA and the region beyond (40–160 mm) to IAA alone.

An enormous body of experimental evidence indicates that exogenously supplied plant growth substances (hormones) elicit a variety of developmental responses in plants, from organogenesis, growth, and differentiation to the acquisition and directed transport of nutrients, depending on the plant, its part, and its stage of development. This has led to the general concept that endogenous hormones have a similar role to play—namely, to influence and integrate all aspects of plant development (Thimann 1977). Though much evidence exists in support of this concept, it is far too incomplete and the problem too complex to establish any general theory on it as yet.

The increasing awareness that both hormone concentration (Cleland 1983) and tissue sensitivity (Trewavas 1983) are important in the realization and regulation of a developmental process (Trewavas 1982) underscores the importance of both temporal (historical) and spatial (positional) factors in such a control, especially in a system with continued organogenesis such as a plant. Besides, almost invariably, hormones interplay in the control of any developmental event (Leopold and Nooden 1984), underscoring the need to know their sites and rates of production, translocation, and destruction to come to any overall conclusion.

The usefulness of the "simple" morphology of the rootless and leafless parasitic vines of *Cuscuta* to study its development has been highlighted (Mahadevan 1983). Successive stages of cellular growth and differentiation can be studied in successive segments of a linear, cylindrical vine in a basipetal sequence from the apex, as these comprise a series of cell populations that represent in space, a developmental sequence in time. Besides, the application of a single hormone (cytokinin) evoked all developmental events needed for its survival—namely, the induction of coiling growth (to twine around a host) and production of haustoria (for penetration and abstraction of nutrients from it) (Paliyath et al. 1978, Mahadevan 1983).

The involvement of a gibberellin (GA_3) and its interaction with auxin (IAA) for the continued growth of the apical segment of *Cuscuta* under aseptic culture conditions have been described (Maheshwari et al. 1980). In this paper we describe the action of auxin and cytokinin on the growth and curvature of the apical and subapical segments of the vine, and the conditions of their interaction to elicit the interconvertible straight and coiling modes of growth exhibited by the vine in nature. Part of this work has been reported elsewhere (Rajagopal et al. 1982).

Materials and Methods

Plant

The experimental material was from clonally propagating *Cuscuta reflexa* (Roxb)* free-hanging vines parasitizing *Tecoma stans* (Bignoniaceae) on the campus of Indian Institute of Science. Vines of uniform diameter were harvested and placed with cut ends in distilled water till use.

In Vivo Growth

Tagged, free-hanging vines of approximately equal length were marked at desired intervals with indelible ink using the shoot apex as reference point. Distances between markings were measured with a scale to the nearest millimeter at desired time intervals. Experiments were generally started between 9 and 10:30 a.m. to minimize variation due to diurnal fluctuation in growth rate.

In Vitro Growth

Stem segments were excised from required regions using a two-bladed cutter (12.7-mm blade distance) and floated in distilled water, and 15–20 segments were blotted and transferred to test solutions. Test solutions (2.5 ml in a 25-ml Erlenmeyer flask) contained 0.75 mM K_2HPO_4 citrate buffer, pH 5, 0.5 mM KCl and chloramphenicol, 50 μg/ml, (BKC solution) with or without the required hormone. The flasks were shaken at 27 ± 1°C in diffuse laboratory light on a reciprocal shaker (60 strokes/min) for the required time, normally 8 h. At the end of this time, the flasks were quickly chilled in crushed ice to minimize further growth until measurement.

Length and Curvature Measurements

The length of curved or straight segments was measured using a microcomparator (Gaertner Scientific Corp., Chicago, IL, USA). The length (A) of the × 15 magnified image of the segment was overlapped end to end along its curvature at midline with a flexible plastic tubing, and this length was measured to the nearest millimeter. Length A (in cm) times 1.5 gave the segment length in millimeters. Growth is expressed as a rate, micrometer growth (final-initial length)

* This species is the same as that used in earlier studies (Nagaiah et al. 1977, Paliyath et al. 1978, Maheshwari et al. 1980) but wrongly described as *Cuscuta chinensis* (Lamk). It has since been identified as *C. reflexa* by comparison of pollen exine pattern and floral characteristics with authentic *C. reflexa*.

per millimeter initial length of segment per hour (μm/mm/h) to accommodate variations in initial segment length and period of growth.

Two measurements of each segment—length (A) and the end-to-end linear distance (B)—were made. Assuming (A) as an arc of a circle and (B) as its chord, a simple FORTRAN program was written, and an HP 1000 Computer was used to compute θ, the angle (in degrees) subtended by A and B at the center of the circle, using an iterative procedure. θ, a measure of curvature, is 0° for a straight segment (where A = B and segment is an arc of a circle of infinite radius), 180° for a semicircle, and 360° for a circle (where B = 0).

Significance of difference (at 1% and 5% levels) between treatments was analyzed by the t-test, after correcting confidence interval by the F-test where variances were significantly different. All experiments have been repeated two or more times.

Chemical

Fusicoccin was a gift of Dr. Michieli, Montedison S.p.A., Milan. Hormones were purchased from Sigma Chemical Co., St. Louis, MO, USA. Other chemical were of analytical grade.

Results

Nature of Vegetative Vine Growth In Vivo

Cuscuta exhibited two interconvertible modes of growth—a normally rapid straight elongation, leading to the formation of free-hanging vines; and coiling growth, leading to its twining around the host. Two types of coiling growth occurred: a large pitched coiling with little or no haustoria formation, and a short pitched, tight coiling of stems bearing numerous haustoria. Coiling, genetically determined and related to its spiral phyllotaxus, was apparently always counterclockwise in the direction of growth. Circumnutation and a loosely curving growth of the shoot tip of the free-hanging vine led to efficient contact with new host regions, and the resultant thigmostimulus led to tight coiling and haustoria production. Once haustoria became functional, coiling growth ceased, and the shoot tip elongated linearly to form free-hanging vines once again.

On *Tecoma*, growth of free-hanging vines ranged from 50 to 150 mm per day, daylight growth (7 a.m. to 7 p.m.) being on an average 30% more than dark (7 p.m. to 7 a.m.) growth. Growth was greater on bright, sunny days than on cloudy or rainy days and was apparently related to host photosynthesis (Paliyath 1979).

At the start of a new flush of growth, a few thick vines (2–4 mm diameter) were produced, whose laterals secondarily infected and began covering the host. Numerous free-hanging vines of 1–2 mm diameter produced at this stage

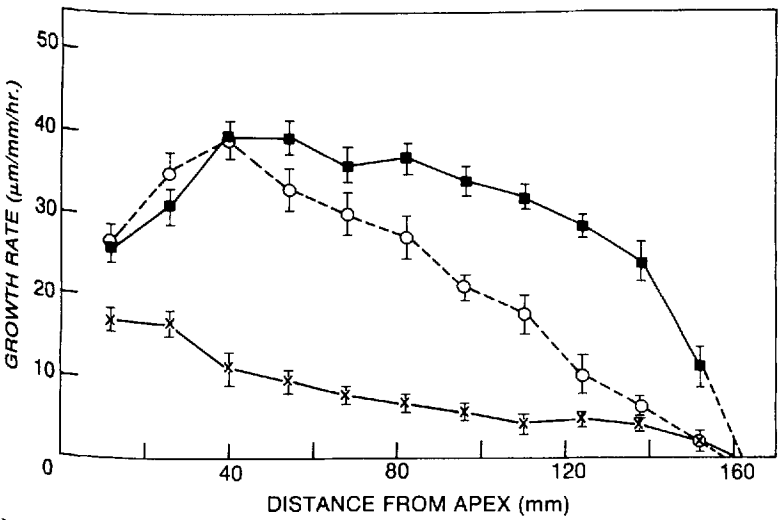

Fig. 1. In vivo and in vitro (±IAA) growth rates of various regions of the free-hanging vines in *Cuscuta*. For in vivo growth, vines marked at 14-mm intervals starting at 5 mm from apex and growth measured 8 h later. For in vitro growth, segments (12.7 mm) excised from the same 14-mm regions were incubated ±IAA (10 μM) and measured after 8 h as described in Methods and Materials. Growth expressed as μm/mm initial length/h. O——O, in vivo; X——X in vitro, controls; ■——■ in vitro, +IAA.

were normally collected for experimentation. Lateral branches became progressively numerous and thinner (<1 mm) as the host became completely covered and entangled with the vines. Eventually both host and the vines blackened and died as the flush ended.

Vine-marking experiments showed that the zone of elongation of the free-hanging vines extended up to 160 mm from the apex. In vivo growth rates, during 8 h, increased by 60% in the region 5 to 40 mm and thereafter declined to zero around 160 mm (Fig. 1).

Response of Excised Apical Segment to IAA, GA_3 and FC

IAA and GA_3 did not influence growth rate of the apical 0-to-10-mm segment during 10 h of incubation, but the fungal toxin fusicoccin (FC) enhanced the growth rate by 30% (Table 1, Column A). However, in longer segments (0–25 mm) incubated with their cut ends in solution for 72 h (Table 1, Column B), GA_3 maintained the initial growth rate, which fell off in controls. FC, promotive during the shorter period (10 h), became toxic during the longer, 72-h period. In subsequent experiments, the apical 5 mm of vines was discarded, and subapical segments alone were used. Besides providing a cut surface for basipetal entry of IAA and other materials, it removed the cluster of lateral buds located near the apex.

Table 1. Effect of IAA, GA_3, and FC on the growth rate of excised apical segments of *Cuscuta* incubated for short or long duration.

Treatment	A	B
	Growth rate (μm/mm initial length/h ± SE)	
None	13 ± 1.0	5 ± 0.3
IAA 10 μM	13 ± 1.1	ND
GA_3 100 μM	13 ± 1.1	13 ± 0.7**
FC 0.1 μM	17 ± 1.1**	6 ± 0.3[a]

A—Short duration: 20 segments (0–10 mm) incubated in solutions with shaking for 10 h. B—Long duration: 20 segments (0–25 mm) placed with cut ends dipping in solution for 72 h.
**Significance: 1% of corresponding control.
[a]FC became toxic during 72 h.
ND: Not determined, since IAA is not taken up through the basal cut end.

Response of Subapical Segments to IAA

Figure 1 depicts the effect of 10 μM IAA, determined to be growth-optimal, on the growth rate of segments from a 5- to 160-mm region of the vine. The in vitro rate in the presence of IAA paralleled the in vivo rate in the region 5–40 mm from the apex, increasing from 25 to 40 μm/mm/h. The elevated rate was maintained in segments up to 80 mm before declining gradually until 140 mm and steeply thereafter to 160 mm. Growth rates in the region 40–140 mm was appreciably greater than in vivo rates, but response to IAA ceased where in vivo growth ceased. A similar pattern of response was seen with FC, which promoted growth of segments only in the growth zone (0–160 mm) and not thereafter (data not shown).

Growth response of segments from the subapical 5-to-40-mm zone was qualitatively different from low (0.1 μM) and high (10 μM) IAA concentrations when compared with that from later regions. Low IAA induced growth with curvature, whereas high, growth-optimal IAA produced straight segments, as seen in Fig. 2A. Segments from two regions, 5–19 mm (region I) and 25–39 mm (region II) within this zone, were therefore compared in further experiments, as these regions were also differentially sensitive to cytokinin (see below).

Tables 2 and 3 give the growth and curvature response of segments from these two regions to 0.1 and 10 μM IAA (in the absence and presence of 10 or 50 μM BA) in two experiments. Growth rate in 10 μM IAA was 50% greater in region II than in region I, though at the lower IAA concentration the response was variable. Curvature of segments from both regions were three- to fourfold greater in 0.1 μM IAA than in 10 μM IAA. Figure 3 compares curvatures (and growth rates) induced by 0.1 μM and 10 μM IAA concentration in segments from regions I and II with those from later, older (40–86 mm) regions. Curvature of control segments fell along the vine, reflecting their reducing growth rate (Fig. 1). The large curvatures induced by low IAA in segments from regions I and II declined in the later (40–86 mm) region, but they were always higher than either that of controls or those treated with high IAA.

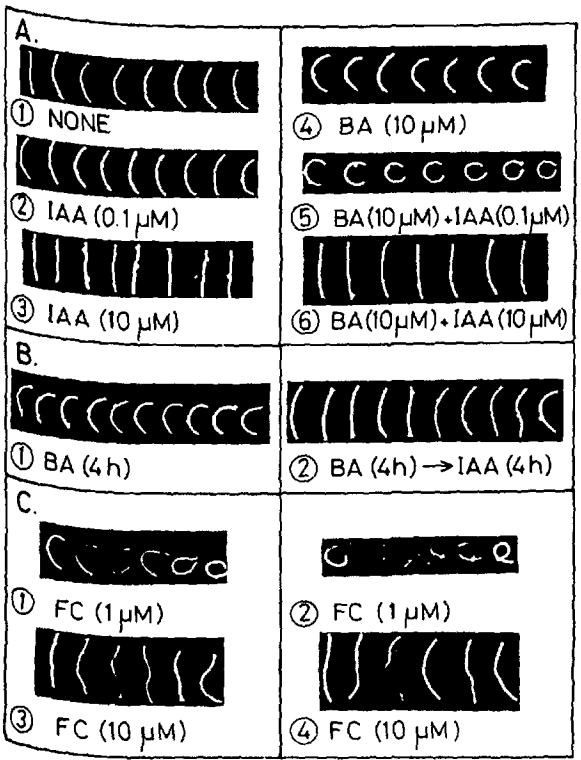

Fig. 2. Shadow graphs showing the effect of different hormones on the curvature of excised subapical segments of *Cuscuta*. (A) IAA (0.1 μM and 10 μM) and BA (10 μM) given separately and in combination. Segments (12.7 mm) from 5-to-40-mm subapical region of the vine. Treatment was for 8 h at 27 ± 1°C in diffuse laboratory light. (B) IAA (10 μM) on BA (10 μM) induced curvature on 5-to-19-mm subapical segments. BA given for 4 h followed by IAA for 4 h. All treatments at 27 ± 1°C in diffuse laboratory light. (C) FC (1 and 10 μM) on subapical segments from the regions 5–19 mm (1 and 2) and 25–39 mm (3 and 4).

Table 2. Interaction of IAA and BA on growth rate (μm/mm/h ± SE) of segments from regions I (5–19 mm) and II (25–39 mm) of *Cuscuta*

	Exp 1		Exp 2	
	Region		Region	
Treatment	I (5–19 mm)	II (25–39 mm)	I (5–19 mm)	II (25–39 mm)
None	16 ± 1.3[a]	11 ± 0.5[f]	13 ± 0.7[a]	7 ± 0.6[f]
BA*	22 ± 1.7[b]	12 ± 1.5[f]	23 ± 1.0[b]	9 ± 0.9[f]
IAA 0.1 μM	21 ± 1.0[c]	30 ± 1.5[h]	23 ± 1.1[b]	23 ± 0.9[h]
IAA 0.1 μM + BA*	32 ± 0.9[d]	24 ± 1.1[g]	27 ± 1.5[d]	20 ± 1.0[g]
IAA 10 μM	23 ± 1.1[c]	30 ± 1.2[h]	23 ± 0.5[c]	32 ± 0.9[i]
IAA 10 μm + BA*	49 ± 1.6[e]	36 ± 2.2[i]	40 ± 1.8[e]	42 ± 1.0[j]

* BA concentrations: 10 μM in Exp 1 and 50 μM in Exp 2. Incubation: 8 h.
Significance: Exp 1—1% (a–c), (b–d), (c–d), (d–e), (f–g), (f–h), (g–h), (h–i); 5% (a–b). Exp 2—1% (a–b), (c–d), (d–e), (f–g), (g–h), (g–i), (h–i), (i–j); 5% (b–d).

Table 3. Interaction of IAA and BA on curvature θ° ± SE of segments from regions I (5–19 mm) and II (25–39 mm) of *Cuscuta*

Treatment	Exp 1		Exp 2	
	Region		Region	
	I (5–19 mm)	II (25–39 mm)	I (5–19 mm)	II (25–39 mm)
None	76 ± 7[a]	55 ± 5[g]	69 ± 5[a]	52 ± 5[g]
BA*	137 ± 12[b]	82 ± 13[h]	161 ± 8[b]	81 ± 9[h]
IAA 0.1 μM	112 ± 9[c]	126 ± 12[i]	101 ± 9[c]	158 ± 8[i]
IAA 0.1 μM + BA*	245 ± 17[d]	159 ± 17[j]	210 ± 11[d]	129 ± 12[j]
IAA 10 μM	34 ± 6[e]	43 ± 4[k]	24 ± 5[e]	35 ± 7[k]
IAA 10 μm + BA*	54 ± 10[f]	38 ± 7[l]	37 ± 4[f]	48 ± 6[l]

* BA concentrations: 10 μM in Exp 1 and 50 μM in Exp 2. Incubation: 8 h.
Significance: Exp 1—1% (a–b), (a–c), (a–e), (b–d), (c–d), (b–e), (b–f), (g–i), (g–j), (h–i), (h–j), (h–k), (h–l); Exp 2—1% (a–b), (a–c), (a–d), (a–e), (a–f), (h–c), (h–d), (c–d), (b–e), (b–f), (g–h), (g–i), (g–j), (h–i), (h–j), (h–k), (h–l).

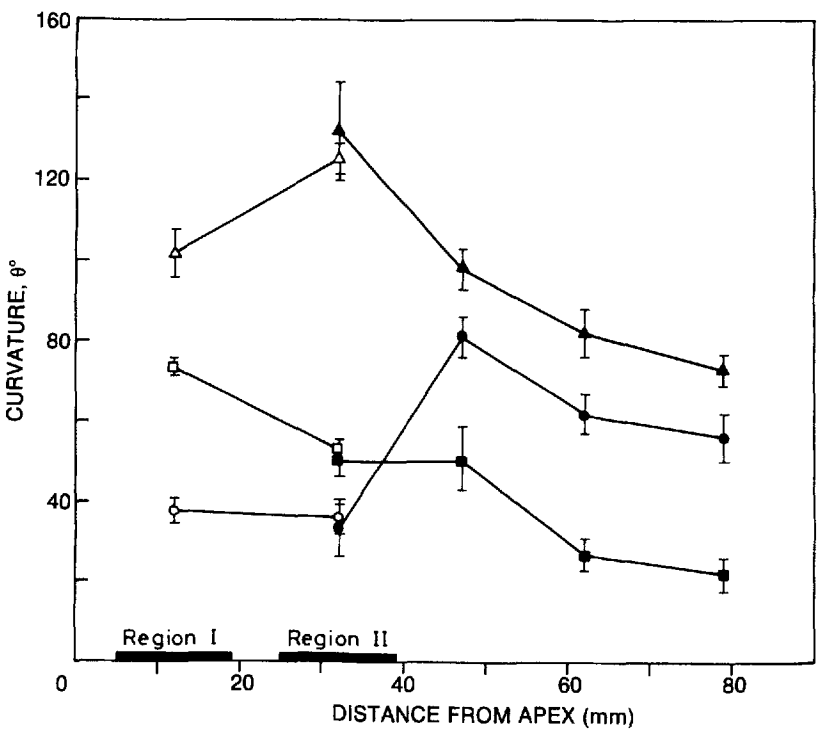

Fig. 3. Effect of low (0.1 μM) and high (10 μM) IAA concentration on curvature in segments from 5 to 86 mm region of *Cuscuta* vine. □, ■—not treated (controls); △, ▲—IAA (0.1 μM); ○, ●—IAA (10 μM). Open symbols (regions I and II) represent average values (±SE) of four separate experiments. Representative growth rates (μm/mm/h) of these regions appear in Table 2. Growth rates (μm/mm/h) of segments from regions 40–50 mm, 56–70 mm, and 72–86 mm were: controls—9, 4, 5; IAA (0.1 μM)—20, 22, 14; IAA (10 μM)—33, 30, 25.

Table 4. Effect of zeatin and isopentenyl adenine on growth and curvature of segments from region I (5–19 mm) of *Cuscuta*

Treatment	Growth (μm/mm/h ± SE)	Curvature (θ ± SE)
None	20 ± 1.7 (100)	57 ± 11 (100)
Z 1 μM	26 ± 1.7* (130)	155 ± 19** (272)
Z 10 μM	26 ± 2.5* (130)	166 ± 23** (291)
iP 1 μM	25 ± 1.8* (125)	153 ± 25** (268)
iP 10 μM	31 ± 3.0** (155)	184 ± 33** (323)

Incubation 8 h. Percent of respective control values in parentheses.
Significance: **1% and *5% of respective controls.

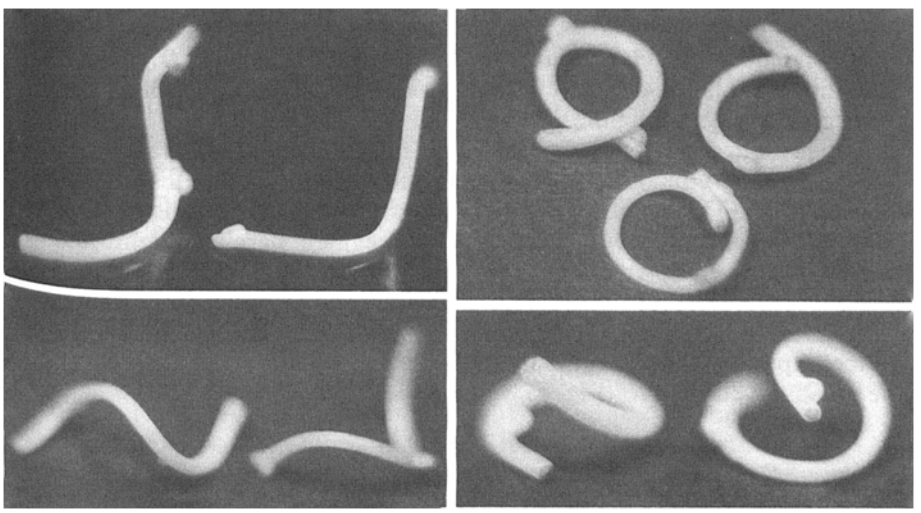

Fig. 4. Photographs of BA (50 μM) and IAA (0.1 μM) induced spirally coiled segments from the 5-to-19-mm region of *Cuscuta* vine. Segments of 12.7 mm were treated for 2 h with hormones and set out on a filter-paper-lined Petri dish containing buffer for 24 h.

On the other hand, the curvature induced by high IAA was below that of the control segments in the initial (I and II) regions but increased to values near them in later (40–86 mm) region. Growth-optimal (10 μM) IAA concentration induced symmetric growth, resulting in linear extension, whereas low IAA induced unequal growth, leading to curvature of segments in this subapical 5–40 mm zone.

Response of Subapical Segments to Cytokinins in the Absence and Presence of IAA

Like low (0.1 μM) IAA, BA (10 or 50 μM) enhanced growth rate and induced curvature in segments from regions I (5–19 mm) and II (25–39 mm) (Fig. 2A; Tables 2, 3). But unlike IAA, the responses of the two regions were reversed; region I responded more than region II. The pattern was qualitatively similar at

Table 5. Reversal of BA-induced curvature by IAA in segments from region I (5–19 mm) of *Cuscuta*

Treatment A	Incubation (h)	Treatment (h) B	Curvature ($\theta \pm$ SE) (% control)
None	8	—	92 ± 8 (100)[a]
IAA$^+$	8	—	48 ± 8 (52)[b]
BA$^+$	8	—	178 ± 14 (193)[c]
None	4	IAA (4)	70 ± 7 (76)[d]
BA	4	None (4)	152 ± 26 (165)[e]
BA	4	IAA (4)	67 ± 12 (73)[f]

IAA$^+$—10 μM; BA$^+$—10 μM.
Significance: 1% (a–b), (a–c), (a–e), (e–f).

all BA concentrations (1–100 μM) and with 1–10 μM zeatin (Z) or isopentenyladenine (iP) (Table 4). The effect of BA on elongation growth of segments beyond 50 mm was negligible.

In the presence of low (0.1 μM) IAA, BA-induced growth and curvature were significantly enhanced in segments from region I but to a lesser extent for those from region II. On the other hand, in the presence of high (10 μM) IAA, though BA enhanced growth maximally, the segments grew straight, just as in high IAA alone (Fig. 2A; Tables 2, 3).

Segments from region I treated for 2 h with a combination of 50 μM BA and 0.1 μM IAA and set out on filter-paper-lined Petri dishes containing buffer produced spirally coiled segments in 24 h, the sense of the spiral being the same as observed in vivo (Fig. 4).

Reversal of BA-Induced Curvature by High Concentrations of (10 μM) IAA

Segments from region I were incubated with 10 μM BA for 4 h, when curvatures were induced. One-half of the segments were shadow-graphed, and the others were rinsed and transferred to a solution containing 10 μM IAA and incubated for a further 4 h. Shadow graphs of segments in Fig. 2B show that BA-induced curvature was reversed by IAA. The results of a separate experiment expressing curvature in θ is given in Table 5. Symmetric growth in high IAA thus overrides asymmetric growth in BA, to produce linear segments.

Absence of Influence of GA_3 on the Growth and Curvature of Subapical Segment

GA_3 in the concentration range 1–100 μM had no significant influence on the growth and curvature of segments from regions I and II, either by itself or in the presence of low (0.1 μM) or high (10 μM) IAA, or BA at 50 μM (data not shown).

Discussion

In vivo growth rate *Cuscuta reflexa* on *Tecoma* was determined to be highest around 40 mm from the apex during an 8-h growth period, coinciding with the

region most responsive to growth-optimal IAA in vitro. However, greater growth rates were obtained in segments from region I (5–19 mm) in the presence of both BA and IAA. The region of maximal growth rate in vivo would therefore be variable depending on both auxin and cytokinin status in this subapical zone.

Factors limiting growth apparently exist in vivo beyond 40 mm from the apex, as excised segments from this region responded to IAA with enhanced growth rate. Besides, the different regions of the growth zone of *Cuscuta* were sensitive to different hormones or their combinations in eliciting elongation growth. Thus, the apical region responded to GA_3 (and IAA) (Maheshwari et al. 1980), subapical (I and II) region to BA and IAA, and the later 40-to-160-mm region to IAA alone. Sequential sensitivity of the apical portion of the shoot to gibberellin, cytokinin, and auxin, first shown in wheat coleoptiles by Wright (1966), appears to be involved in *Cuscuta* also.

The differential response of subapical segments to low and high IAA is novel. Low IAA induced curvature in segments from all regions up to 90 mm, but maximally in those from region II. In contrast, high IAA concentration induced "straight" growth in segments from regions I and II. Low-IAA-induced curvatures are not sufficient to allow coiling around a host stem, but they are sufficient to form a sweeping arc to intercept it. Free-hanging vines in the morning after a nocturnal period of reduced growth were usually found with a loosely curving shoot apical portion, whereas the same vines extended out in a linear fashion, often perpendicular to gravity, during peak growth later in the day (Mahadevan 1983). These patterns of in vivo growth may be reflections of low and high internal auxin status, respectively.

Though symmetrically applied, *Cuscuta* subapical segments responded to low IAA and/or BA with asymmetric growth leading to curvature and coiling—a nastic response. Differential sensitivity of tissues to ethylene, IAA, or GA is now widely accepted as the basis for the curvature that characterizes epinastic and hyponastic responses such as tendril coiling or apical hook maintenance in seedlings (Palmer 1985). Whatever the basis for the differential sensitivity is, it proves to be of a temporal nature. The apical hook of seedlings is believed to be the result of cells on one side being temporarily retarded in their elongation growth (possibly by ethylene), but they catch up later, leading to the straightening of the stem at the base of the hook. The hook, a half coil, thus "moves up" as growth proceeds until this differential sensitivity is abolished by yet another factor such as light when the hook opens. In *Cuscuta,* with a longer zone of differential sensitivity extending up to 40 mm from the shoot apex and an inherent (genetic) spiral "sense," a differential growth response leads to spiral coiling that is counterclockwise and acropetal in direction. The condition that induces growth-retaining differential sensitivity is low auxin along with cytokinin, whereas the condition that obliterates this differential sensitivity is high IAA, irrespective of the level of cytokinin. It is significant that high IAA, besides preventing coiling growth, also inhibits cytokinin-induced haustoria formation in segments from this region, as described in Ramasubramanian et al. (1988).

That differential sensitivity, and thus differential growth rate, rather than growth rate *per se* controls coiling was seen in the response of the segments

from regions I and II to FC (Fig. 2C). FC at 1 μM caused pronounced coiling growth, whereas with 10 μM FC, the segments grew longer but straight, paralleling the response to low and high IAA in the presence of BA. However, the growth rate (80–90 μm/mm/h) in 1 μM FC was almost twice that in high (10 μM) IAA and BA. Since FC is not reported to be transported like IAA, its entry into the segment would be expected to be more uniform. Differential growth leading to curvature should all the more be due to differential sensitivity. As with IAA and BA, the older growing regions of the *Cuscuta* vine did not exhibit this differential growth response to high and low FC.

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