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Hormones and *Cuscuta* Development: In Vitro Induction of Haustoria by Cytokinin and Its Inhibition by Other Hormones

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Abstract. Cytokinins induced haustoria formation in excised 10-mm segments of *Cuscuta* vine, the subapical 25-to-50-mm region being most responsive, producing a mean of 4–6 haustoria per segment. The order of effectiveness of cytokinins continuously applied (72 h) was 6-benzylaminopurine (BA) ≥ isopentenyladenine (iP) ≫ zeatin (Z). Ribosides of BA and Z were as effective as the bases, whereas riboside of iP ([9R]iP) was half as effective as iP. Haustoria induction was influenced by weather and seasonal conditions at the time of vine collection; materials obtained on warm, sunny days responded better than those obtained on rainy, cloudy, or cool days. Haustoria were induced equally well all around the segment, and no thigmostimulus was needed for induction.

A 10-min pulse of 100 μM BA induced half as many haustoria as a 60-min pulse or continuous application of BA. White light inhibited haustoria induction elicited by a short (30-min) pulse of BA, whereas a longer (120-min) BA application overcame this light inhibition. Auxins (IAA or NAA, 1–10 μM), gibberellin (GA_3, 1–10 μM), ethylene (as ethrel, 10–100 μM), and abscisic acid (ABA, 100 μM) were individually inhibitory (60–80%) with respect to haustoria induction when given continuously with 50 μM BA. A 60-min pulse of auxins (10 μM), GA_3 (100 μM), or ethrel (10 μM), given at various time intervals during or after a 60-min pulse of 100 μM BA, showed that inhibition was maximal (70–95%) between 4 and 16 h of BA application and negligible (GA_3) or much reduced (auxin, ethrel) at 20 h, indicating a "commitment" to haustoria formation by this time.

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Application of benzyladenine (BA) to free-hanging vines or isolated stem segments of *Cuscuta reflexa* (erroneously reported as *C. chinensis*) induced *de novo* haustoria formation (Paliyath et al. 1978). Both prehaustorial and true haustorial tissues were formed, but the latter was not seen to penetrate the former. The cytokinin effect was unique and could not be replaced by auxin, gibberellin (GA_3), ethrel, or abscisic acid (ABA). In isolated segments, auxin and GA_3 reversed the cytokinin effect (Paliyath et al. 1979).

Jacob et al. (1975) reported the formation of smaller papillalike outgrowths on *Cuscuta reflexa* vines without differentiation of pre- or true haustorial cells when treated with 0.1% kinetin in lanolin. Tsivion (1978) was able to induce the emergence of true haustorium through its prehaustorial covering by the application of BA or kinetin to existing haustorial mounds of *Cuscuta campestris*. These structures formed naturally on the inner surface of a coiled region of the vine when induced to twine around a string support. Though cytokinin could not be replaced by any other hormone, continued haustorial development appeared to be aided by GA and indole-3-acetic acid (IAA). *De novo* haustoria induction by BA was also observed in *Cuscuta gronovii* (Mahadevan 1983) and *Cassytha filiformis* (Paliyath et al. 1978).

The interaction of cytokinin with low auxin in the induction of coiling growth in isolated segments of *Cuscuta* as a prelude to haustoria formation and its inhibition by high auxin has been described in the accompanying paper (Rajagopal et al. 1988). In this paper the conditions for in vitro haustoria induction, the effectiveness of various cytokinins, the inhibitions of the process by other hormones, and the timing of their response are described.

Materials and Methods

Clonally propagating *Cuscuta reflexa* vines on *Tecoma stans* were collected as described (Rajagopal et al. 1988).

In Vitro Haustoria Induction by Cytokinins

Continuous Application of Hormones. About 20 segments (10 mm) were excised from the desired region of the vine, rinsed with distilled water, and placed in rows in a Petri dish (100 mm) lined with Whatman No. 1 filter paper over two adjoining microscope slides and moistened with 4–5 ml of test solution. The slides lifted the segments on the paper and prevented their becoming water-logged. In earlier experiments the test solution consisted of 1 mM KH_2PO_4-citrate buffer, pH 4, with 1 mM KCl, with or without the desired hormones. Later experiments used 0.75 mM K_2HPO_4-citrate buffer, pH 5, containing 0.5 mM KCl and 50 μg/ml chloramphenicol (BKC solution), with or without hormone (Rajagopal et al. 1988). Chloramphenicol was routinely added to minimize microbial contamination. It had no adverse effect on growth or haustoria formation by the segments. Following incubation in the dark for 72 h at 27 ± 1°C, the haustoria formed were scored.

Hormone Application as a Pulse. About twenty 10-mm-long segments were shaken in 2.5 ml of BKC solution with or without hormone in 25-ml Erlenmeyer flasks, as described (Rajagopal et al. 1988), for the desired time intervals (10–120 min) after which the segments were rinsed on a sintered glass funnel with plain BKC solution and transferred to Petri dishes as described above and incubated in the dark at 27 ± 1°C.

When a second hormone treatment had to be given, the segments were transferred to flasks as above and shaken in the second test solution (2.5 ml BKC solution plus second hormone) for 1 h, rinsed, and reincubated in Petri dishes. Haustoria were scored 60–72 h after the first treatment.

Hormone Application Through Cut Ends. Ten-millimeter-long segments were suspended horizontally like a bridge in a specially constructed holder, with their cut ends dipping in test solutions in tubes at both ends of the segments as shown in Fig. 1. Surface tension ensured constant contact of the solution in the tube with the cut ends of segments during 72 h of incubation in the dark (Fig. 1).

Scoring of Haustoria. Haustoria were scored visually with the aid of a hand lens (× 10) or under a dissecting microscope. A reasonably sized mound on the surface was counted as the haustorium; tiny papillae were ignored. Normally 30–40% of the haustoria scored were very well developed and had a saucer-shaped depression on the top of the mound, identifying the prehaustorial cell zone (Mahadevan 1983). Fifteen to 20 segments were used for each treatment. Values are given as mean number of haustoria per segment ± SE. All experiments were repeated at least twice, often several times.

Chemicals

Hormones and inhibitors were purchased from Sigma Chemical Co., St. Louis, MO, USA. Commercial ethrel (38% active ingredient) was obtained from Agromore Chemicals, Bangalore, India. Other chemicals were of analytical grade.

Results

Haustoria Formation in Segments from Various Regions of the Vine

Figure 2 depicts the average number of haustoria produced in 10-mm segments of the vine from the apex downward when treated continuously with optimal (50 μM) BA. Although the apical 10 mm never produced haustoria, the mean number of haustoria formed per segment increased to a maximum between 20 and 50 mm before declining to a negligible value around 100 mm. While in vivo

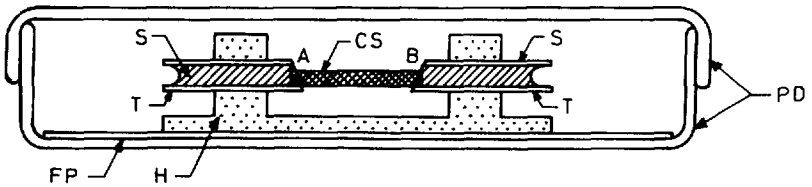

Fig. 1. Hormone application through cut ends. Diagrammatic representation of a U-shaped holder with stem segment. PD, Petri dish; H, holder; FP, filter paper; T, tube; CS, *Cuscuta* segment; A, apical end; B, basal end; S, solution.

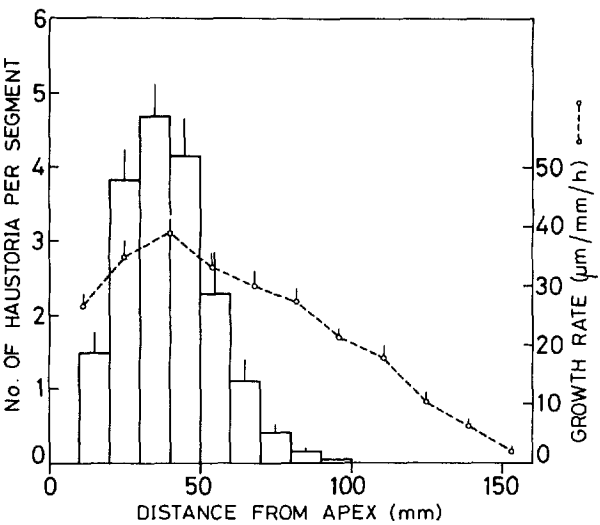

Fig. 2. BA-induced haustoria formation in excised 10-mm segments along the length of the *Cuscuta* vine. Haustoria induced by a 1-h pulse of 50 μM BA and scored after 72-h incubation at 27 ± 1°C in dark. Bars indicate number of haustoria/cm segments ± SE. Dashed line represents the in vivo growth rate of various regions of the vine. Values are given as μm/mm initial length/h ± SE.

growth rate also peaked between 20 and 50 mm (Fig. 2), elongation growth itself declined to zero value only around 160 mm (Rajagopal et al. 1988). In all further experiments, two 10-mm segments from the 25-to-45-mm region of a vine were used.

Effects of Various Cytokinins and Haustoria Formation

Representative results of the effects of varying concentrations of BA, benzyl adenosine ([9R]BA), trans-zeatin (Z), trans-zeatin riboside ([9R]Z), 2-isopentenyladenine (iP), and 2-isopentenyladenosine ([9R]iP), applied continuously, on haustorium formation are given in Table 1. Though variation in response between experiments was seen as with BA (see below), BA and iP were the most effective cytokinins, producing 4.5–5.5 mean number of haustoria per segment at the optimal concentration of 50–100 μM. However, they produced about 10% of this at 1 μM and about 50% at 5–10 μM concentrations. Surprisingly, zeatin was always a very poor inducer, eliciting no response at 10 μM

Table 1. Effect of various concentrations of cytokinins on haustoria formation during continuous application.

Cytokinin	Concentration (μM)				
	1	5	10	50	100
BA	0.6 ± 0.1	1.1 ± 0.3	2.8 ± 0.5	3.1 ± 0.7	4.3 ± 0.6
[9R]BA	0.5 ± 0.1	—	3.9 ± 0.6	—	4.2 ± 0.6
iP	0.4 ± 0.2	2.1 ± 0.5	3.5 ± 0.6	5.1 ± 0.4	3.7 ± 0.5
[9R]iP	0.1 ± 0.05	1.2 ± 0.3	2.4 ± 0.4	2.0 ± 0.5	2.3 ± 0.3
Z	0	0	0	0.4 ± 0.2	0.5 ± 0.2
[9R]Z	0	0	0	0.3 ± 0.1	0.3 ± 0.1

Replicates: 20; vine region, 30–50 mm; scoring after 72 h 10^{-3} M BA or Z toxic; results of experiments on various days. Values represent mean number of haustoria per 1-cm segment ± SE.

and 10% of the response of BA or iP at the optimal 50-to-100-μM range. All cytokinins tested were toxic at 1000 μM. Although the ribosides [9R]BA and [9R]Z were almost as effective as their respective bases, [9R]iP was only about half as effective as iP in haustoria induction. Rapid metabolism of [9R]iP to an inactive metabolite could partly explain its lowered activity (Ramasubramanian, unpublished results).

Factors Influencing Variation in BA-Induced Haustoria Formation

Using 50 μM BA, the mean number of haustoria produced per segment in 41 experiments conducted over a 9-month period (August to April), including a wet and cold season, ranged from 1.5 to 5.7 with an average response of 3.5. Separating them into above-average (19 experiments) and below-average response (22 experiments) sets, the mean number of haustoria in these two sets were 4.4 and 2.7, respectively.

The number of haustoria in individual segments ranged from 0 to 10. Scoring segments with no haustorium as nonresponders, 20% of the segments were nonresponders in the below-average compared to the 5% in the above-average set.

Variation in response depended on the season, weather conditions, stage of flush, and flowering. Vines collected on sunny warm days were generally more responsive than those collected on rainy or cloudy days or on days with low minimum temperatures. Using local weather data and scoring days with precipitation, sunshine less than 1 h per day (average over the period 5 h), or a minimum temperature below 17°C (average 19°C) as unfavorable, twice (82%) as many unfavorable days were identified in the below-average set as in the above-average set.

In Vitro Haustorium Induction and Its Development

Following BA application, signs of haustorial induction could be detected in 48 h, and mounds were visible in 60 h. During this period, the segments thickened

at the region of the haustorium and usually near the cut ends. As with in vivo BA-induced haustoria formation (Paliyath et al. 1978, Mahadevan 1983), the top of the mound, initially smooth, became rough in appearance as the epidermal cells laterally separated and enlarged to form the prehaustorial cells (Fig. 3). A flattening at the top with a saucer-shaped depression occurred in 20–40% of the haustoria, often those in contact with filter paper (Fig. 3), when they were scored after 60–72 h. Still later (96 h), a true haustorium pushing through the center of the depression in mounds in contact with the filter paper was observed in a few instances, with the adherence of cellulose fibers to the prehaustorial cells following local degradation of the filter paper. Infection (and possibly depletion of reserves) prevented development beyond this stage in unsterilized segments.

Haustoria were induced on all sides of a segment, although those in contact with the filter paper developed better. To confirm that a touch stimulus was not needed for haustoria induction, BA was supplied through apical and/or basal cut ends of segments suspended like a bridge (see Materials and Methods and Fig. 1). The results are given in Table 2. Haustoria formed all over the segments (top, bottom, and sides) when BA was supplied through both ends. When BA was supplied through either apical or basal end, haustoria were induced only on the half of the segment that was in contact with BA, whereas the other half (in contact with buffer) was haustoria-free and remained unthickened like control vine segments. Only a few haustorial mounds developed prehaustorial cells, and even here, further development appeared restricted in comparison with those in contact with filter paper.

Duration of Cytokinin Application Needed for Haustoria Induction

Segments were shaken in 10-, 50-, or 100-μM BA solutions for various intervals of time (see Materials and Methods) before being rinsed and incubated in BKC solution. Table 3 shows that a 30- or 60-min exposure to 100 μM BA elicited a response comparable to the optimal continuous application of 50 μM BA, and a 10-min pulse gave a 40% response with 50 μM BA or a 65% response with 100 μM BA. Other experiments (Ramasubramanian, unpublished), using 8-[^{14}C]BA, showed that the amount of BA was taken up by the segments during a 60-min pulse computed to a tissue concentration of about 40 μM BA. In all later experiments a 60-min pulse of 100 μM BA was given for the induction of haustoria. Given as a pulse, iP, even at 100 μM, was only about 40% as effective as BA also given as a pulse (Table 4). The lesser effectiveness of iP compared to BA, when given as a pulse, appears to be due to its faster conversion to inactive metabolites (Ramasubramanian and Mahadevan 1985). Again, Z was the poorest inducer of haustoria formation. In all cases, the ribosides were poorer inducers than the corresponding free base.

Effect of Light on BA-Induced Haustoria Formation

Haustoria formed equally well under white light (cool white fluorescent lamps; about 150 lux at segment level) or darkness when BA was continuously present

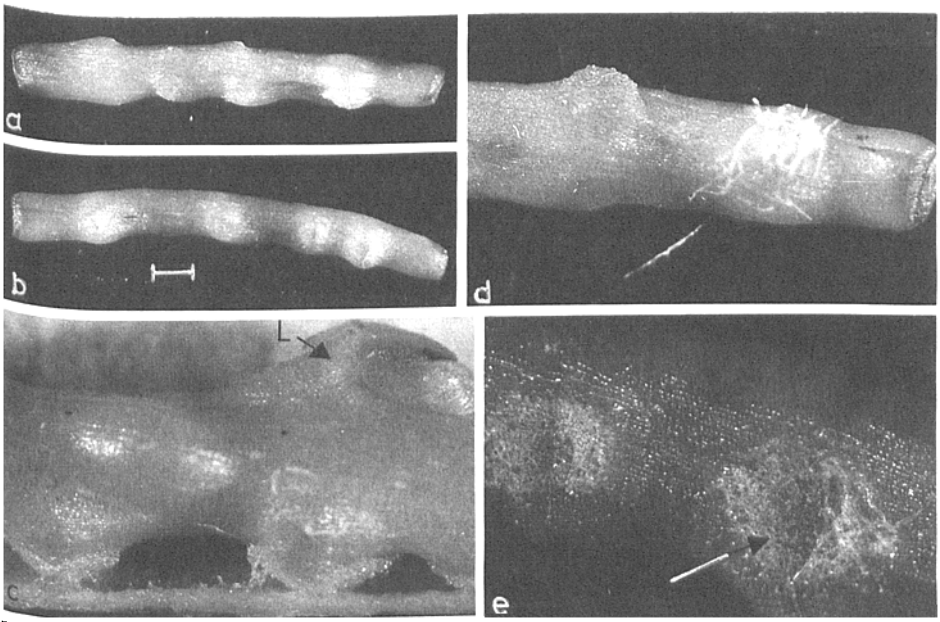

Fig. 3. Development of haustorium in excised 10-mm segment from the 25-to-45-mm subapical region of *Cuscuta*. Treatment: 50 μM BA for 1 h followed by incubation at 27 ± 1°C in dark for 60–72 h. (a, b) Formation of the haustoria mounds all over the segment. Bar indicates 1 mm. (c) Development of the prehaustorium and the establishment of contact with the filter paper. L, lateral bud. (d) View of the haustorial region when the filter paper contact (c) is disrupted. Fibers of the filter paper are sticking out from the prehaustorial tissue. (e) View of the haustorial region showing saucer-shaped depression (arrow) through which the true haustorium emerges.

during incubation. When BA was given as a pulse for 60 min or less, light inhibited haustoria formation significantly by about 40% (Table 5). However, with 120 min of BA application, the inhibition by light was overcome, as was seen with continuous BA application. In all other experiments, incubation was always performed in the dark to prevent any light effect.

Effect of Other Hormones on BA-Induced Haustoria Formation

IAA, NAA, GA_3, ethrel, and ABA were individually inhibitory to haustoria formation to varying degrees when supplied continuously with 50 μM BA (Table 6). The results of two or three experiments for auxins and GA_3 are included to show the type of variation observed. With IAA (or NAA), inhibition was 100% at 100 μM, nearly 80% with 10 μM, and up to 50% with 1 μM. They were either not inhibitory at 0.1 μM or, in a few instances, even slightly promotory, although variation between segments masked any significance. Significantly, at this concentration, IAA interacted with BA and promoted coiling growth, whereas at the higher concentration, growth promotion resulted in straight elongation of the segments (Rajagopal et al. 1988).

Inhibition by GA_3 was similar to that by auxin and was also variable. However, even at 100 μM, inhibition was not always complete. In contrast to auxin,

Table 2. Haustoria formation in suspended segments with BA application through cut ends.

Treatment	Mean number of haustoria ± SE
BA at both ends	5.6 ± 0.6
BA at apical end[a]	3.7 ± 0.3
BA at basal end[a]	2.8 ± 0.3

Replicates: 18; BA: 50 μM.
[a] BKC solution at other end.

Table 3. Duration of BA pulse on haustorial induction.

	Pulse (min)			
	10	30	60	120
Treatment	(Mean number of haustoria ± SE)			
BA 10 μM	0.1 ± 0.1	0.7 ± 0.2	0.6 ± 0.3	1.9 ± 0.3
BA 50 μM	2.1 ± 0.4	3.4 ± 0.7	4.0 ± 0.6	4.2 ± 0.5
BA 100 μM	3.5 ± 0.6	4.7 ± 0.6	4.8 ± 0.7	4.6 ± 0.8

Each datum is mean ± SE of three experiments each with 15–20 replicates.

Table 4. Comparative effect of a pulse (60 min) of cytokinin on haustoria formation.

Cytokinin	% Response
BA	100
[9R]BA	85
iP	43
[9R]iP	2
Z	12
[9R]Z	4

Cytokinin concentration 100 μM.
Average of two experiments, each with 15–20 replicates.
Mean number of haustoria per segment in BA was 4.8.

GA_3 inhibition of haustoria induction was not accompanied by any effect on elongation growth (Rajagopal et al. 1988).

Ethrel was about 50% inhibitory at 10 μM and around 90% at 100 μM. ABA even at 100 μM was only 60% inhibitory and was toxic at higher concentrations. ABA was also ineffective on auxin-induced elongation growth.

Timing the Inhibition of BA-Induced Haustoria Formation by Other Hormones

Since haustoria induction was fully realized by a 60-min pulse of 100 μM BA, the second hormone was given as a 60-min pulse at various time intervals up to 24 h after the BA pulse in order to establish the period during which they were inhibitory to haustoria formation scored 72 h after BA treatment (Fig. 4).

Though varying in degree, a common period of maximal sensitivity to inhibition by the second hormone was observed between 4 and 16 h following the

Table 5. Effect of light (cool white) on BA-induced haustoria formation.

Treatment	Duration of BA (100 μM) pulse (min)			
	30	60	90	120
	(Mean number of haustoria ± SE)			
Dark	4.7 ± 0.4	4.1 ± 0.5	4.4 ± 0.4	4.4 ± 0.4
Light[a]	2.7 ± 0.3*	2.7 ± 0.4*	4.1 ± 0.5	4.5 ± 0.5

Replicates: 18–20.
* Significance: 1%—respective controls.
[a] Cool white fluorescent: about 150 lux.

Table 6. Effect of continuous application of other hormones on BA[a]-induced haustoria formation.

Exp No.	Treatment	Concentration of second hormone (μM)				
		0	0.1	1	10	100
		(Mean number of haustoria ± SE)				
1	IAA	3.8 ± 0.4	3.7 ± 0.2	1.7 ± 0.3	1.3 ± 0.3	0
2	IAA	4.6 ± 0.5	3.5 ± 0.4	2.0 ± 0.5	0.6 ± 0.2	0
1	NAA	2.5 ± 0.5	3.5 ± 0.5	0.8 ± 0.2	0.5 ± 0.2	0
2	NAA	4.9 ± 0.4	5.1 ± 0.6	4.9 ± 0.7	0.9 ± 0.4	0
1	GA_3	2.3 ± 0.4	2.4 ± 0.4	1.7 ± 0.4	0.9 ± 0.4	0.9 ± 0.3
2	GA_3	3.8 ± 0.5	3.9 ± 0.5	2.8 ± 0.5	1.3 ± 0.4	1.0 ± 0.3
3	GA_3	4.9 ± 0.4	4.8 ± 0.6	1.3 ± 0.5	0.5 ± 0.2	0
	Ethrel[b]	3.2 ± 0.5	3.7 ± 0.5	3.3 ± 0.5	1.9 ± 0.3	0.4 ± 0.2
	ABA	4.0 ± 0.5	3.0 ± 0.4	3.2 ± 0.6	2.0 ± 0.3	1.6 ± 0.4

Replicates: 20.
[a] BA (50 μM) ± second hormone applied continuously for 72 h.
[b] Computed from rated concentration (38% w/w) in commercial sample.

BA pulse for the auxins, GA_3, and ethrel. Inhibition by 10 μM IAA, negligible when given along with BA (0–1 h), was about 70% during the sensitive period and was reduced to less than 40% by 24 h. NAA (10 μM) was about 40% inhibitory at 0–1 h, 95% between 4 and 16 h, and 30% at 24 h. The somewhat greater inhibition by NAA possibly reflects slower metabolism, particularly oxidative breakdown.

GA_3 (100 μM) was 50% inhibitory when given with BA, about 80% during the sensitive period (5–16 h), and negligible at 24 h. Ethrel (100 μM) was inhibitory at all times, about 70% when given along with BA or at 24 h, and over 90% during the middle phase. ABA (100 μM) was hardly inhibitory except at 16–20 h (about 30%) and was not inhibitory at 25 h.

Discussion

The subapical region (5–19 mm) of a *Cuscuta* vine was maximally responsive to BA in exhibiting coiling growth (Rajagopal et al. 1988), and it preceded the 20-to-50-mm region most responsive to BA-induced haustoria formation. This sequence of differential response of the vine segments to exogenous cytokinin

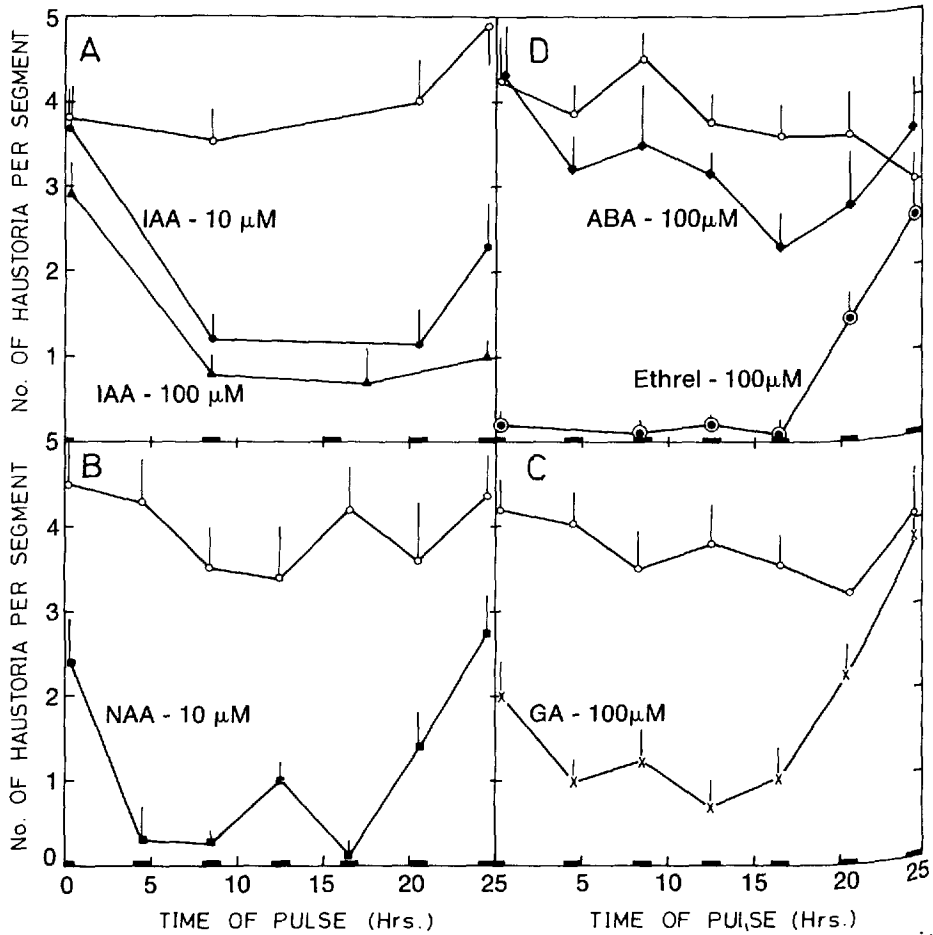

Fig. 4. Effect of various hormones given as a pulse, on BA-induced haustoria formation in *Cuscuta*. Segments were treated with BA (100 μM) between 0 and 1 h. Lots of 20 segments were treated either with the second hormone in BKC or in BKC solution alone (control) for 1 h at indicated time points (■), before being washed and transferred to BKC for further incubation up to 72 h before scoring for haustoria. Respective controls indicated as (—○—○—). Bars indicate SE of mean.

in a way parallels the temporal sequence of events, when *Cuscuta* parasitizes a host, and where coiling growth precedes haustoria formation.

The sites of action of cytokinin are apparently different in these responses. Coiling growth, involving differential cell expansion, was promoted equally well by Z or iP (Rajagopal et al. 1988), but iP was 5–10 times more effective than Z in haustoria formation.

That iP was a better inducer of haustoria than Z is interesting. In most systems, such as various bioassays for cytokinins (Letham 1978, Letham et al. 1983), or during phloem regeneration in decapitated *Coleus* stems (Houck and La Motte 1977) or the release of axillary bud inhibition in pea (Pillay and Railton 1983), Z was more effective than iP. However, iP was more effective

than Z in inducing "bud" formation in the moss *Funaria* (Spiess 1975) and in the inhibition of root elongation in *Linum* (Goran 1982). Significantly, the endogenous content of iP in the 50-mm shoot tips of *Cuscuta* was often five times higher than that of Z, suggesting an in vivo role for this cytokinin in haustoria induction (Ramasubramanian and Mahadevan 1985). However, Ihl et al. (1984), using a method not suitable for recovery of iP or [9R]iP, have reported the presence of Z and [9R]Z in *Cuscuta* shoot tips.

In contrast to the "sidedness" in the siting of the haustoria along the face in contact with the host in vivo, neither was sidedness observed nor a continuous thigmostimulus needed for their in vitro induction by BA. However, contact could have been stimulatory for their further development. Potential for haustoria formation was, therefore, present all around the cylindrical vine in the 10-to-100-mm sensitive zone, with the actual in vivo siting possibly dependent on local factors.

That a 10-min pulse of BA could induce haustoria formation indicated uptake of sufficient amount of BA within this period. The need for a cytokinin only during the early stages of adventitious bud differentiation in *Torenia* stem segments (Tanimoto and Harada 1982) or during sprouting of potato tubers (Turnbull and Hanke 1985) reflects the rapid uptake of cytokinin by tissues.

Although low auxin concentration promoted BA-induced coiling growth, in the subapical segments of *Cuscuta* (Rajagopal et al. 1988), high auxin inhibited both cytokinin-induced coiling growth and haustoria formation and induced longitudinal elongation in isolated segments. This ability of high auxin to overcome cytokinin action and promote the elongation growth is in contrast to the suppression of auxin-induced elongation growth by cytokinin in etiolated soybean hypocotyl segments (Vanderhoef and Stahl 1975).

In *Cuscuta,* the absence of haustoria formation on the outer face of a coiled vine in vivo is apparently a reflection of greater elongation growth on that side compared to the inner face. Using a *Xanthium* cotyledon expansion bioassay of partially purified extracts, Gupta and Singh (1985) have reported greater cytokinin activity in the inner face of *Cuscuta* vine coiling around the host *Lantana* than on the outer face. However, such high cytokinin activity in the haustorial region has not been detected in *Cuscuta* growing on *Vinca* (Ihl et al. 1984). Furthermore, inhibition of BA-induced haustoria induction without causing elongation growth as obtained with GA, ethrel, or ABA underscores the involvement of processes other than just a suppression of elongation growth as a prerequisite for haustoria formation.

Auxins, GA, and ethrel inhibited BA-induced haustoria formation. The inhibition by these hormones, though varying in degree, followed a similar temporal pattern, being effective only if applied within 16–20 h of BA treatment. Externally applied ABA was not very inhibitory to haustoria formation, probably because the tissue is already rich in endogenous ABA (Ihl et al. 1984). Apparently, a committed step in BA-induced haustorium differentiation occurred within this period, after which the process was no longer subject to inhibition by the other hormones. The interplay of the five hormonal classes during in vitro haustoria induction suggests that endogenous levels of all these hormones may similarly influence in vivo haustoria induction. The marked variability seen in BA-induced in vitro haustoria formation (depending on sea-

sonal and daily weather conditions when the vines were collected and in the absence of a controlled environment for the growth of the host plants) may be a reflection of the differences in the endogenous levels of these hormones.

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