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Vegetative/Parasitic Transition: Control and Plasticity in *Striga* Development[1]

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ABSTRACT

***Striga asiatica* (Scrophulariaceae), an obligate parasite of grasses including many of the world's major grain crops, switches from vegetative to parasitic development by the differentiation of the root meristem into the host attachment organ, the haustorium. This change was induced in culture by the exposure to a single, low molecular weight signal molecule, 2,6-dimethoxy-*p*-benzoquinone. A concentration of 10^{-6} molar quinone and an exposure time of ≥6 hours were required before the developmental process could be completed. With shorter exposure times, haustorial development was prematurely aborted and meristematic elongation was reestablished. The new meristem was capable of developing a second haustorium if reexposed to the signal molecule. These results are discussed in terms of the transition to the parasitic phase and the general control of plant cellular development.**

The initial gene expression events involved in the induction of both parasitic (7, 24) and symbiotic (14, 19, 20) relationships have been shown to be controlled in many cases by specific, structurally simple, signal molecules. These compounds must convey critical information required for host selection since, in most cases, the shift from a vegetative to a parasitic mode is both sudden and dramatic, requiring a significant recommitment of resources. The magnitude of this change is particularly striking in the parasitic angiosperms that are strictly dependent on the host for continued survival (15). In general, these plant holoparasites are dormant as seeds and apparently break dormancy only when exposed to a specific host-derived signal (10, 13). The change from the vegetative to a parasitic mode involved formation of a primary haustorium, an organ specialized for host plant attachment.

Several theories have been proposed for the mechanism of haustorial induction in parasitic plants, each generally involving haustorial inducing signals (2, 3, 8, 9, 12, 17, 26). In *Striga asiatica*, a simple quinone, 2,6-DMBQ,[2] is sufficient for quantitative induction of haustorial development in young seedlings (8, 9). Evidence has been presented consistent with the theory that a parasite-derived enzyme oxidatively releases 2,6-DMBQ from a host root surface (8, 9). Such a mechanism suggests an active screening process on the part of the parasite and ensures intimate host-parasite association before the induction of haustoria.

During primary haustorial induction, cellular expansion at the root meristem is redirected from longitudinal to radial dimensions followed closely by the formation of specialized haustorial hairs just distal to the swollen tip. The process is one of the most rapid differentiation processes known. *Agalinis purpurea* (Scrophulariaceae) has been shown to attach within 24 h following induction (22), and *Striga* attachment occurs at least as rapidly (8). Therefore, haustorial development is dependent to a large extent on cellular resources already present in the meristem. Nevertheless, the cost of this meristematic recommitment cannot be minimized. The redirection of meristematic growth results in a cessation of elongation. Therefore, host contact must be established for successful attachment (8, 9), and premature commitment to haustorial formation would certainly restrict the possibility of such contact. The importance of this differentiation event to *Striga* and its implications to plant cellular development in general have motivated our attempts to better define the control points involved in haustorial formation in *Striga*.

MATERIALS AND METHODS

Reagents

2,6-DMBQ was synthesized by the method of Bolker and Kung (6). Twice-distilled water and appropriate glassware were sterilized in a Market Forge Sterilmatic autoclave at 15 lb/in^2 and 121°C for 25 min. This water was used in all experiments with *Striga*.

Plant Material

Sorghum bicolor (L.) Moench seeds were grown aseptically on moist filter paper in the dark at 27°C for 7 d. The roots of intact plants were dipped in 100 mL of 0.5% CH_3COOH in CH_2Cl_2 for 2 s. The extract was evaporated *in vacuo* to give the biologically active germination stimulant (13).

Striga asiatica seeds were obtained from Dr. R. E. Eplee, USDA Witchweed Methods Development Laboratory, Whiteville, NC, and handled under quarantine. Pretreatment involved sandwiching two scoopulas of seeds between two 25-mm membrane filters, 10 μm pore size, in a Swin-Lock filter chamber and washing with 5 mL of 0.16% sodium hypochlorite containing 2% Tween 20 for 5 min followed by three washings with 5 mL of sterile water. The seeds were then transferred to a sterile Erlenmeyer flask, covered with steri-

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[2] Abbreviations: 2,6-DMBQ, 2,6-dimethoxy-*p*-benzoquinone.

lized water, the flasks capped with cotton gauze cap, and kept at ~27°C for 2 to 3 weeks.

Striga seeds were germinated by placing 100 pretreated seeds in each of 24 wells of a microtitre plate. Ten μg of the germination stimulant was dissolved in 1 mL of twice-distilled water overnight at 5°C. This solution was then placed over the seeds. After 24 h, the seeds were divided into wells of approximately 30 seeds each. The germination solution was replaced with 1 mL of sterile, twice-distilled water.

Photography

Seedlings were pipetted from culture wells and put on glass slides. Photographs were taken with a 35 mm Nikon FE through a Bauch and Lomb Photozoom inverted microscope with green filtered light.

Serial Exposures

Germinated *Striga* seedlings (20–30) were placed in each of 24 culture wells with 900 μL of sterile twice-distilled water. At time zero, 100 μL of 10^{-5} M 2,6-DMBQ was added to each of the wells. After 2 h, the seedlings in three wells were washed with water three times and covered with 1 mL of water. This procedure was repeated every 2 h for the duration of the experiment. Haustoria were counted under a dissecting microscope 24 h after the experiment began. All assays were performed in triplicate and values are expressed as ±SD.

Concentration Dependence

A 10^{-3} M solution of 2,6-DMBQ with 1% DMSO was serially diluted in culture wells containing 20 to 30 germinated *Striga* seedlings. The final volume in each well was 0.9 mL. The number of developed haustoria were counted after 24 h.

Data Analysis

The time exposure data were fit to the logistics function (Eq. 1) where the percent haustoria formed ($\%H$) ranged form zero to a maximal value of B (≤ 1).

$$\%H = \frac{B}{1 - Ae^{-kt}} \quad (1)$$

The constant A reflects the offset along the time axis and k is a rate term that is solely associated with the change in the population as a function of time (4, 5, 21, 29). The fit of the data was estimated from the linear form of the equation (Eq.

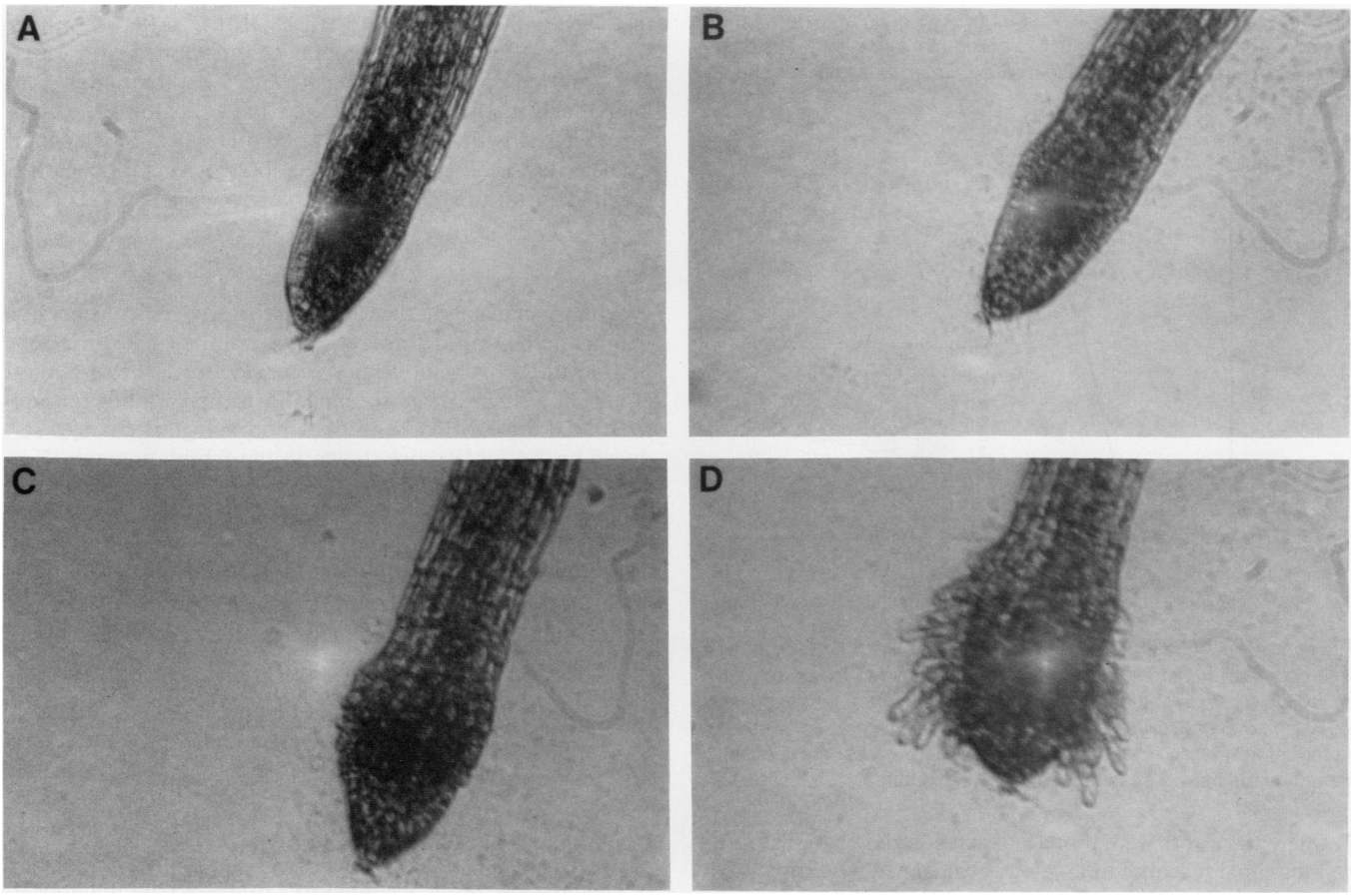

Figure 1. Time course of haustoria induction. *St. asiatica* seeds were germinated as described in "Materials and Methods," and at time zero, seedlings were transferred to a Petri dish containing 10^{-5} M 2,6-DMBQ. The photographs are of a single representative seedling at times: A, 0 h; B, 8 h; C, 12 h; D, 20 h.

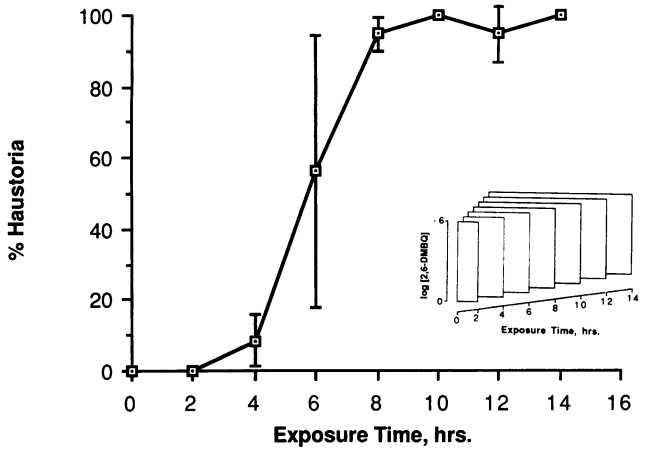

Figure 2. Course of haustoria induction with various exposure times to 2,6-DMBQ. *S. asiatica* seeds were germinated as described in "Materials and Methods", and 20 to 30 seedlings were placed in each of 24 culture wells. Sterile, twice-distilled water (900 μL) was then added along with 100 μL of 10^{-5} M 2,6-DMBQ. Every 2 h this solution was removed from three of the wells, the seedlings were rinsed three times with sterile twice-distilled water, and then the seedlings were covered with another portion of water. These various time exposures are represented by the inserted bar graph. The number of seedlings that made haustoria 24 to 48 h after initial exposure were counted using a dissecting microscope. A seedling was counted as having a haustorium if it possessed both a swollen meristem and haustorial hairs. Exposure to sterile, twice-distilled water was the zero-hour exposure control.

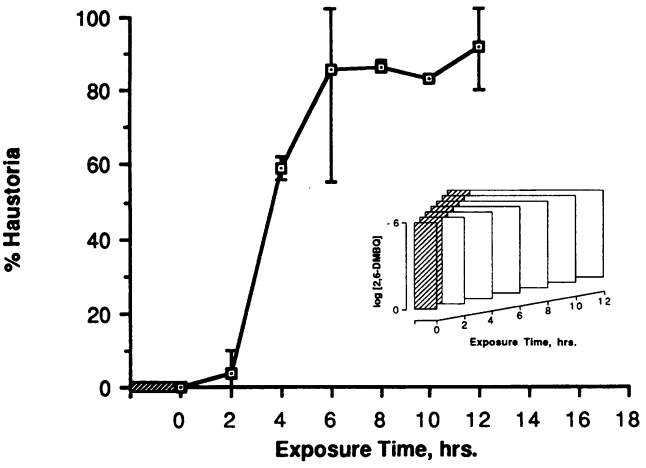

Figure 3. Effect of a 2-h pretreatment with 10^{-6} M 2,6-DMBQ on the time course of haustoria induction. This experiment was performed as in Figure 1 except that the germinated seeds were first exposed to 10^{-6} M 2,6-DMBQ for 2 h and rinsed three times with distilled water before the incremental exposures. This pretreatment is represented by the heavily shaded area in the bar graph.

2) where the errors were propagated standard deviations. The half maximal response time, $t_{1/2}$, was calculated by setting $\%H = 0.5B$

$$\ln\left(\frac{B}{\%H} - 1\right) = \ln A - kt \qquad (2)$$

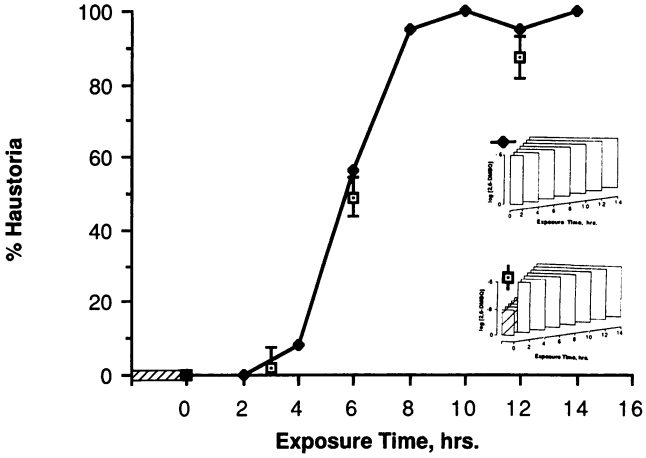

Figure 4. Effect of a 2-h pretreatment of 10^{-8} M 2,6-DMBQ on the time course of haustoria induction. This experiment was performed as in Figure 2, except that 10^{-8} M 2,6-DMBQ was used as the pretreatment. This is represented in the bar graph by the lightly shaded area. The normal time course for haustoria induction is shown (●) with the pretreatment (□).

Double Haustoria

One-day germinated *Striga* seedlings (20–30) were placed in a well with 1 mL of 10^{-6} M 2,6-DMBQ. After 12 h, the solution was removed, the seedlings were washed with water (3×), and covered with 1 mL of water. Approximately 2 d later, a new meristem had appeared and the bathing medium was replaced with 1 mL of 10^{-6} M 2,6-DMBQ. Twenty-four h later, the seedlings were scored for the formation of the second haustorium.

RESULTS

Primary haustorial development in *Striga* fits generally within the described framework for terminal haustoria formation in the parasitic angiosperms. Figure 1 shows photographs of a single *Striga* seedling during its 24 h of exposure to 10^{-6} M 2,6-DMBQ. The first morphological changes induced by 2,6-DMBQ are shown in the 8-h photograph (Fig. 1B). Radicle elongation has been terminated and the radial expansion of the root meristem initiated. Cells located concentrically around the distal end of the swollen tip develop into the characteristic haustorial hairs. The hairs appear after about 12 h of incubation (Fig. 1C) and reach their maximum length and density approximately 12 h later (Fig. 1D). Development has been shown to be arrested at this point in the absence of a host (18). Even though the entire host-parasite interface is generally defined as the haustorium (27), we have, for simplicity, referred to the haustorium as this prematurely arrested stage that is still competent for host attachment.

Dependence on Signal Exposure Time

The response of the seedlings to 2,6-DMBQ did not appear to be instantaneous. The initial swelling of the meristems appeared only after about 8 h, but from that point development continued quite rapidly. To investigate the role of the

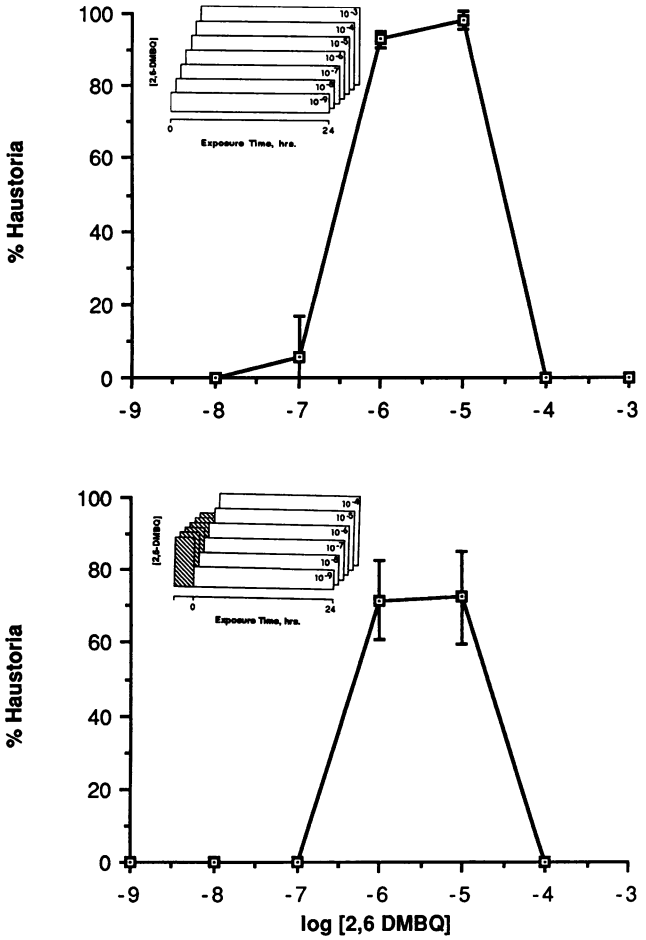

Figure 5. Effect of a 2-h pretreatment of 10^{-6} M 2,6-DMBQ on the dose response curve for 2,6-DMBQ. The upper plot shows the dose response curve obtained by exposing 2-d-old *Striga* seedlings to serially diluted 2,6-DMBQ for 24 to 48 h (8). The lower plot shows a similar experiment in which the seedlings have been exposed to 10^{-6} M 2,6-DMBQ for 2 h and then rinsed three times with sterile twice-distilled water before the dose response experiment was performed. This pretreatment is denoted by the heavily shaded area in the bar graph.

signal molecule throughout this time period, serial exposure experiments were conducted. A plot of exposure time as a function of the percentage of the seedlings forming haustoria is shown in Figure 2. In every case, the percentage was measured 24 h after the start of the experiment.

In the seedlings exposed for 2 h, the root meristems had begun radial expansion, and the seedlings resembled those shown in Figure 1B. After 4 to 6 h, the majority of the root tips were swollen, but the ones that made haustoria produced hairs which were small and few in number similar to the one shown in Figure 1C. However, with longer exposure times, these hairs reached normal lengths and densities. The half-maximal exposure time was 6 h. Only with exposures to 2,6-DMBQ for 8 h or more did high percentages of the seedlings develop complete haustoria.

Dependence on Signal Molecule Concentration

It had been previously shown (8, 9) that the concentration dependence of the response to 2,6-DMBQ was biphasic; concentrations below 10^{-8} M were ineffective, while 10^{-4} M and above were inhibitory. The half-maximal stimulation occurred at 3×10^{-7} M. Greater than 95% of the seedlings respond to these concentrations within 24 h. These dose-response experiments established that long exposures to low concentrations of 2,6-DMBQ were not capable of inducing haustoria. Within the active range, both 10^{-5} M and 10^{-6} M 2,6-DMBQ required ≥6 h exposure time. These experiments argued against simple metabolic conversion of 2,6-DMBQ into an active metabolite, analogous to the mechanism proposed for the release of the quinone (8, 9). Removal of the signal within the 6-h time period could further exclude such a mechanism. Washing the seedlings after 2 h of 2,6-DMBQ treatment followed by immediate replacement with fresh 2,6-DMBQ resulted in the same 6-h time requirement for haustorial development (Fig. 3).

The results of the experiment shown in Figure 3 suggested that it was possible to manipulate the signal exposure by placing the seedlings in new medium within the 6-h time frame without altering the developmental process. In the experiments shown in Figures 4 and 5, this observation was exploited in order to provide a better understanding of the concentration requirements of the 6-h time period. Pretreatment of the seedlings for 2 h with 10^{-8} M 2,6-DMBQ, followed by an increase to 10^{-6} M, found the timing dependent only upon the length of the exposure to the micromolar concentrations (Fig. 4). There was also no change in the concentration dependence for the completion of the 6-h time (Fig. 5). Addition of the quinone at 10^{-6} M for 2 h, followed by washing the seedlings and the addition of a range of concentrations of the quinone, gave a dose-response identical to that previously reported (8, 9).

Plasticity in Haustorial Commitment

Seedlings which had developed a complete haustorium were found to form a new meristem when cultured in the absence of the quinone for 1 to 2 d (Fig. 6B). Generally, the new meristem originated at the terminus of the haustorium and developed colinearly with the initial radicle. However, cells of the root axis immediately behind the haustorium also appeared to organize into the new meristem. This regenerated meristem was capable of developing a new haustorium when reexposed to 10^{-6} M 2,6-DMBQ. By controlling the exposure times within the first 5 d following germination, it was possible to induce at least two distinct haustoria on a single seedling (Fig. 6D).

When haustorial development was prematurely arrested by signal removal, these seedlings also reverted to meristematic growth. Again, the new meristem usually formed at the terminus of the swollen area and grew colinearly with the initial radicle (Fig. 6A) but was also found to develop laterally (Fig. 6C). In either case, this new meristem was capable of differentiating into a new haustorium.

In an attempt to quantify the transition between haustorial commitment and meristematic redifferentiation, the initial

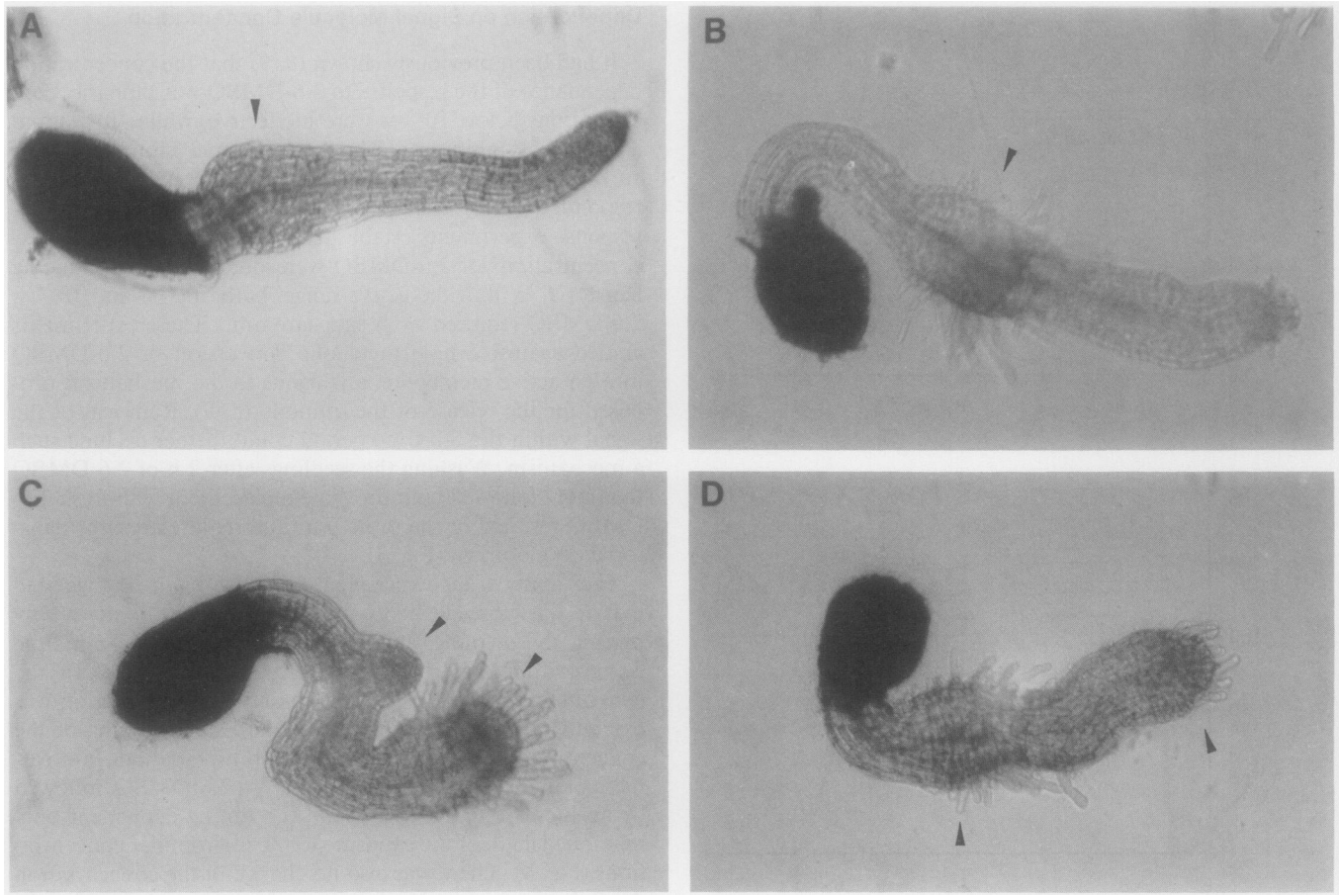

Figure 6. Ability of *Striga* seedlings to make more than one haustorium. A and C show *Striga* seedlings which had an initial 2,6-DMBQ exposure of 10^{-5} M for 2 h. A remained in sterile, twice-distilled water for the remainder of the assay. 10^{-5} M 2,6-DMBQ was reapplied to C after 10.5 h in water. The photographs were taken 36 h after the beginning of the assay. B and D are seedlings which had a 12-h initial exposure to 10^{-5} M 2,6-DMBQ. B remained in distilled water for the remainder of the assay while D was reexposed to 2,6-DMBQ for 36 h after washing with water (3×). The photographs were taken 72 h after the beginning of the assay. Each seed is approximately 100 μm in diameter. Arrows indicate both the areas of initial swelling and the haustoria.

exposure to 10^{-6} M 2,6-DMBQ was followed by a variable delay time, τ, which was then followed by the same serial exposure experiment as in Figure 2. If the quinone was reapplied immediately after the initial 2 h exposure, *i.e.* $\tau = 0$, completely normal haustorial differentiation was observed. The same normal development occurred with $\tau = 2$ h (Fig. 7A). As the delay time was increased, however, the distance between the initial swelling and the developing haustoria increased (Fig. 7, B, C, and D). After 8.5 h, haustorial hairs no longer formed on the initially swollen area. After a 10.5-h interruption, a length of radicle was visible between the two distinct swollen regions.

The time dependence for haustorial formation was also varied with τ. With $\tau = 0$, the expected 4 additional hours of exposure to the quinone was required, whereas with $\tau \geq 4$ h, 6 additional hours was required. In this case, the response data were fit to a logistics function in order to calculate a more accurate $t_{1/2}$. It was found that the overall shape of these curves, indicated primarily by the variance of the value of k ($3.44 \pm 0.41 \times 10^{-4}$ s^{-1}), changed very little even though the delay times changed significantly. A plot of $t_{1/2}$ *versus* the delay between the exposures, τ, is shown in Figure 8.

DISCUSSION

In recent years, there has been a dramatic increase in the efforts directed at understanding recognition events both in plant/bacteria interactions (7, 14, 19, 20, 24) and in plant cell-cell recognition (1). Advances in molecular genetics have revealed new strategies for the study of these processes and have motivated much of this increased interest. The parasitic plants share many of the essential elements of the host-pathogen interaction and, at the same time, encompass some of the fundamental processes of plant cellular development. Within this context, we have attempted to define the sequence of events regulating the developmental transition from vegetative to parasitic growth in *Striga asiatica.*

S. asiatica shows two early developmental commitments that are induced by chemical signals from its host, germination and haustorial formation. In each case, further development is arrested at a stable stage and continues only in the presence of an independent host-derived signal. The commitment of *Striga* to primary haustorial formation has been shown to be regulated by the host-derived molecule, 2,6-

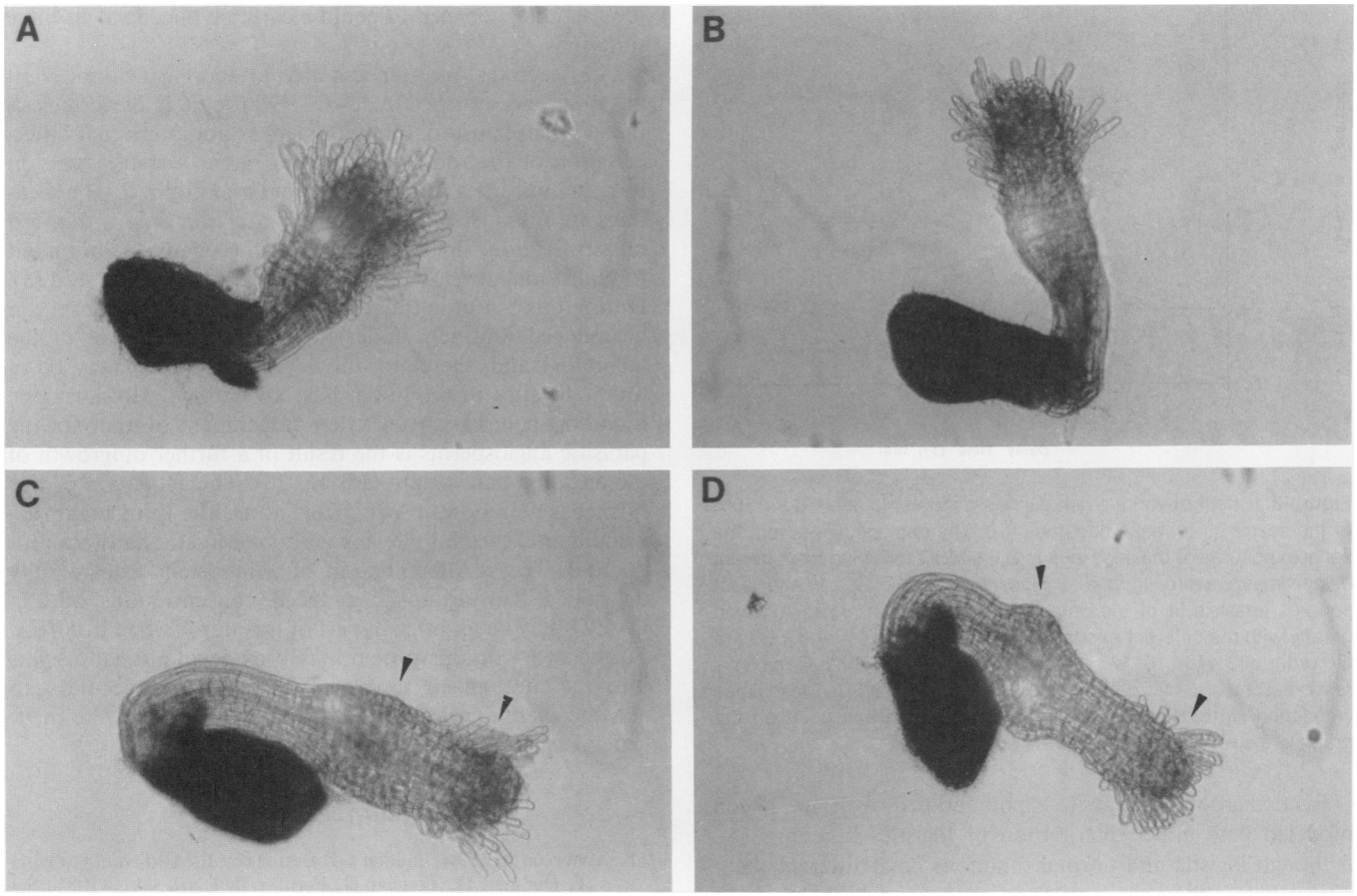

Figure 7. Effect of various delay times on the position of initial swelling and final haustoria formation. *S. asiatica* seeds were germinated as described. The seedlings (20–30) were placed in culture wells and incubated with 1 of mL 10^{-5} M 2,6-DMBQ for 2 h. The seedlings were washed with distilled water three times and allowed to stand in 900 μL of distilled water for various lengths of time. Every 2 h, 100 μL of 10^{-4} M 2,6-DMBQ was added to a different series of wells. Photographs were taken 48 h after the beginning of the assay. The delay times for the different photos are: A, 2 h; B, 4.5 h; C, 8.5 h; D, 10.5 h. Arrows indicate the distinctly swollen areas.

DMBQ (9). These experiments establish this to be an extremely rapid developmental process with morphological changes noticeable as early as 8 h after exposure to 2,6-DMBQ and completed approximately 12 h later.

The data in Figures 4 and 5 suggest that signal molecule concentration and exposure time were independent parameters. Both a micromolar quinone concentration and an exposure time of $\geq$6 h were required before haustorial development was induced. For example, no swelling was detected in seedlings exposed to low 2,6-DMBQ concentrations for extended periods of time (Fig. 5A), and seedlings initially exposed to 10^{-6} M 2,6-DMBQ for 2 h followed by long exposures to lower concentrations (Fig. 5B) did not develop haustoria. However, this 2-h exposure of the seedlings to micromolar levels of 2,6-DMBQ did induce meristem swelling. Longer exposures induced initial haustorial hair formation, but full development was terminated and the seedlings uniformly reverted to meristematic elongation without an exposure time of $\geq$6 h.

Other systems have also been shown to require extended exposures to growth factors throughout a developmental program (11, 23, 28). For *Striga*, which is not immediately capable of radicle elongation after haustorial commitment, premature haustorial development would severely reduce the possibility of viable host attachment and successful progression toward seed set. This requirement for a specific signal over an extended period of time provides a mechanism for increasing the inherent resolution of the detection system. Such an increase in resolution would be expected to be beneficial for any irreversible differentiation event and may prove to be a feature of other developmental processes.

While our experiments have not further defined the mechanism of the detection system capable of processing such time-dependent information, they have added some perspective relative to the precision of the detection and the plasticity of the developmental commitment. The precise nature of the time requirement in *Striga* was most clearly demonstrated by the data shown in Figures 7 and 8. These experiments measured the time required for the *Striga* to 'forget' the initial incremental exposure to the quinone and revert back to the normal 6 h dependence. In each case, the demarcation between those seedlings which committed to haustorial formation and those which did not was very clear.

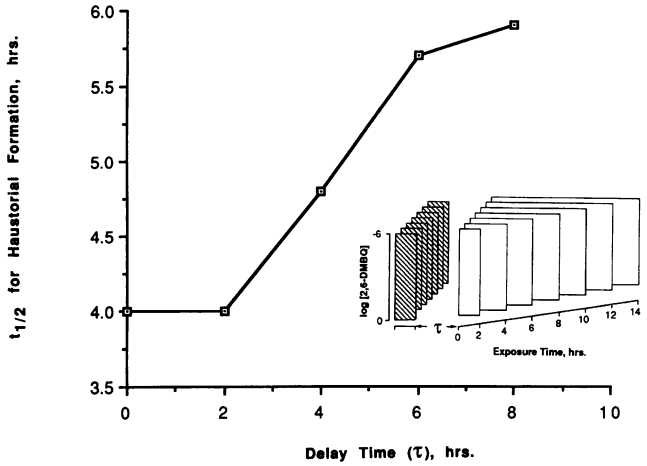

Figure 8. Effect of various delay times on the time needed for 50% of the seedlings to make haustoria ($t_{½}$). The data obtained from the serial exposures of the seedlings to 2,6-DMBQ following the different delay times τ were fit to a logistics sigmoid (3, 21). In the least squares analysis fit of the data, it was found that, while A varied greatly with the different exposure conditions, the rate term k was of the order of $3.44 \times 10^{-4} s^{-1}$ and varied only ±12%. The half-maximal response time, $t_{½}$, was calculated by setting $\%H = 0.5B$. These times were then plotted against the various τ times. Each point on the graph is the mean for two separate assays.

Related growth changes (*e.g.* population growth) have been modeled with either distribution or logistics functions (5). Although logistic and normal functions have different theoretical bases, they are similar in shape and both have the property of only asymptotically approaching their limiting values. Since there is a logistics curve for any normal function where there is agreement to within 1.5% at all points (29), it was not possible to distinguish between the two treatments with these data. Nevertheless, the fit of the data to the logistics function and the constancy of the rate term (k varied ± 12%) were consistent with a precisely defined, and highly synchronous, response of the seedlings to the quinone.

The level of plasticity in *Striga*'s commitment to primary haustorial development during the 6-h detection period was quantified by the experiment shown in Figure 8. Following a 2 h exposure to 2,6-DMBQ, a 4-h period was required for reversion back to meristematic growth, and the normal 6-h exposure was required to induce haustorial development. The extent to which this plasticity provides a developmental advantage for *Striga* is not yet known. The parasitic members of the Scrophulariaceae form both primary as well as secondary haustoria (15) and, therefore, can establish multiple contacts with their hosts. The secondary haustoria develop laterally along the root and are not commitments from the meristematic tip. Therefore, primary haustorial attachment dictates the success or failure of *Striga*. Physical removal of the seedling from the host root surface, or initiation of attachment to a root too small to provide a local concentration of 10^{-6} M 2,6-DMBQ for at least 6 h, are two possibilities that would result in the redevelopment of a meristem. The ability of the seedling to revert rapidly to a growing meristem during the 6-h detection period could clearly be beneficial in these situations.

The seedlings were far less able to abort haustorial commitment once exposed to 2,6-DMBQ for ≥6 h. Nevertheless, the fact that haustorial development is not a terminal differentiation of the root meristem but rather a stable stage on route to host integration should not be minimized. The seedlings are responsive for haustorial induction only within 5 d of germination, presumably before the energy requirement for haustorial development exceeds the stores of the seed (8). During this 5-d time frame, only two primary haustoria can be induced routinely under the optimal conditions of the laboratory and, therefore, this level of plasticity may be of little relevance in the initial host attachment. However, the final host penetration for xylem attachment in many of the parasitic angiosperms is the result of a further outgrowth of the attached haustorium (15, 16, 25). The activation of this further penetration in *Striga* constitutes the third major developmental switch following germination and haustorial induction. The redifferentiation of a meristem from a fully developed haustorium in reduced concentrations of 2,6-DMBQ may be an integral part of this third switch in *Striga*. Further work on this system may provide additional insights into the mechanism through which signal molecules can activate these developmental changes and control the more general aspects of plant/pathogen interactions.

LITERATURE CITED

1. **Anderson MA, McFadden GI, Bernatzky R, Atkinson A, Orpin T, Dedman H, Tregear G, Fernley R, Clarke AE** (1989) Sequence variability of three alleles of the self-incompatability gene of *nicotiana alata*. Plant Cell **1:** 483–91
2. **Atsatt PR** (1977) The inset herbivore as a predictive model in parasitic seen plant biology. Am Nat **111:** 579–586
3. **Atsatt PR, Hearn TF, Nelson RL, Heineman RT** (1978) Chemical induction and repression of haustoria in *Orthocarpus purpurascens* (Scrophulariaceae). Ann Bot **42:** 1177–1184
4. **Berkson J** (1944) Application of the logistic function to bioassay. J Am Stat Assoc **39:** 357–365
5. **Bliss CI** (1935) The calculation of the dosage-mortality curve. Ann Appl Biol **22:** 134–168
6. **Bolker HI, Kung FL** (1969) Formation of 2,6-dimethoxy-1,4-benzoquinone by the action of nitrous acid on 1,2,3-trimethoxybenzene. J Chem Soc (C) 2298–2304
7. **Bolton GW, Nester EW, Gordon MP** (1986) Plant phenolic compounds induce expression of the *Agrobacterium tumefaciens* loci needed for virulence. Science **232:** 938–985
8. **Chang M** (1986) Isolation and characterization of semiochemicals involved in host recognition in *Striga asiatica*. PhD Thesis, University of Chicago, Department of Chemistry, 193pp
9. **Chang M, Lynn DG** (1986) The haustorium in the chemistry of host recognition in parasitic angiosperms. J Chem Ecol **12:** 561–579
10. **Chang M, Netzley DH, Butler LG, Lynn DG** (1986) Chemical regulation of distance: characterization of the first natural host germination stimulant for Striga asiatica. J Am Chem Soc **108:** 7858–7860
11. **Dicker P, Rozengurt E** (1981) Stimulation of DNA synthesis by transient exposure of cell cultures to TPA or polypeptide mitogens: induction of competence or incomplete removal? J Cell Physiol **109:** 99–109
12. **Edwards WGH** (1972) *Orobanche* and other plant parasite factors. *In* JB Harborne, ed, Phytochemical Ecology. New York: Academic Press, pp, 235–248
13. **Fate GD, Chang M, Lynn DG** (1990) Control of germination in

Striga asiatica: chemistry of spatial definition. Plant Physiol **93:** 201–207

14. **Firmin JL, Wilson KE, Rossen L, Johnston AWB** (1986) Flavonoid activation of nodulation genes in Rhizobium reversed by other compounds in plants. Nature **324:** 90
15. **Kuijt J** (1969) The Biology of Parasitic Flowering Plants. University of California Press, Berkeley, CA
16. **Kuijt J** (1977) Haustoria of phanerogamic parasites. Annu Rev Phytopathol **17:** 91–118
17. **Lynn DG** (1985) The involvement of allelochemicals in the host selection of parasitic angiosperms. *In* AC Thompson, ed, The Chemistry of Allelopathy: Biochemical Interactions Among Plants, ACS Symposium Series No. 268, American Chemical Society, Washington, DC, pp 55–81
18. **Nickrent DL, Musselman LJ, Riopel JL, Eplee RE** (1979) Haustorial initiation and non-host penetration in witchweed (*Striga asiatica*). Ann Bot **43:** 233–236
19. **Peters NK, Frost JW, Long SR** (1986) A plant flavone, luteolin, induces expression of *Rhizobium meliloti* nodulation genes. Science **233:** 977–979
20. **Redmond JW, Batley M, Djordjevic MA, Innes RW, Kuempel PL, Rolfe BG** (1986) Flavones induce gene expression of nodulation genes in *Rhizobium.* Nature **323:** 632–634
21. **Reed LJ, Berkson J** (1929) The application of the logistic function to experimental data. J Physiol Chem **33:** 760–779
22. **Riopel JL, Musselman LJ** (1979) Experimental initiation of haustoria in *Agalinis purpurea* (Scrophulariaceae). Am J Bot **66:** 570–575
23. **Roger PP, Servais P, Dumont JE** (1987) Regulation of dog thyroid epithelial cell cycle by forskolin an adenylate cyclase activator. Exp Cell Res **172:** 282–292
24. **Stachel SE, Messens E, Van Montagu M, Zambryski P** (1985) Identification of the signal molecules produced by wounded plant cells that activate T-DNA transfer in *Agrobacterium tumefaciens.* Nature **318:** 624–626
25. **Stephens EL** (1912) The structure and development of the haustorium of *Striga lutea.* Ann Bot **26:** 1067–1076
26. **Stephens JC, Lynn DG, Kamat VS, Riopel JL** (1982) Molecular specificity of haustorial induction in *Agalinis purpurea* (L) Raf. (Scrophulariaceae). Ann Bot **50:** 1–7
27. **Visser J** (1981) South African Parasitic Flowering Plants. Cape Town: Creda Press Ltd.
28. **Van Obberghen-Schilling E, Chambard JC, Paris S, I'Allemain G, Pouyssegur J** (1985) α-Thrombin-induced early mitogenic signalling events and GO to S-phase transition of fibroblasts require continual external stimulation. EMBO J **4:** 2927–2932
29. **Winsor CP** (1932) A comparison of certain symmetrical growth curves. Washington Acad Sci **22:** 73