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Time-dependent Changes in the Auxin Sensitivity of Coleoptile Segments

APPARENT SENSORY ADAPTATION[1]

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ABSTRACT

When segments are excised from corn (*Zea mays* L.) coleoptiles they exhibit a very low rate of elongation for about 3.5 hours. A strong increase in growth rate (the spontaneous growth response) then occurs and persists for many hours. During the latent period preceding the spontaneous growth response there is an apparent increase with time in the sensitivity of the segments to indoleacetic acid (IAA). This increase in sensitivity is expressed as a 2- to 3-fold increase in the magnitude of the growth response to low levels of IAA and a 3-fold decrease in the latent period of the response during the first 3 hours following excision. A similar increase in sensitivity to low levels of IAA is noted if application of IAA is timed from the point of termination of a previous exposure to the hormone. Since the increase in responsiveness to low levels of IAA is not paralleled by an increase in the rate of uptake of the hormone, the data may be interpreted as evidence for a type of time-dependent sensory adaptation to auxin. The IAA dose-response relationship also changes with time, and there is indirect evidence that an auxin-dependent inhibitor may influence the expression of the apparent sensory adaptation to auxin.

There are now several descriptions in the literature of spontaneously occurring changes in endogenous growth rates of isolated coleoptile segments (6, 11, 12, 16, 20). These endogenously controlled changes in growth rate occur within 5 hr which is well within the normal time span of short term growth experiments. In subapical corn coleoptile segments, a strong increase in the endogenous growth rate occurs about 3.5 to 4 hr after excision and has been identified as the spontaneous growth response by Evans and Schmitt (11). They observed that the SGR[2] rate in corn coleoptiles is 3 to 10 times greater than the very low growth rate which immediately precedes it. The SGR remains steady for at least 6 hr after it is initiated (11).

Previous attempts to uncover the nature of the SGR in corn coleoptile segments have indicated that the response may arise, in part, from an increased capacity for auxin biosynthesis throughout the subapical segments with increasing time after excision (11). The occurrence of the SGR appears not to be exactly the same as the phenomenon of regeneration of the physiological tip which occurs in decapitated coleoptiles (especially *Avena*) since the increase in production of auxin in corn coleoptile segments is apparently not limited to the apical portion of the segment (11). No single enzyme in the pathway from tryptophan to IAA has yet been found to be limiting during the period preceding the SGR (12).

Although an increase in auxin biosynthesis appears to accompany the SGR, here we present evidence that a time-dependent increase in sensitivity of the coleoptile tissue to endogenous auxin levels may also contribute to the SGR. Such a change in sensitivity to auxin might be viewed as a type of sensory adaptation to the lowered endogenous auxin level which occurs as a direct consequence of excision. Evidence is provided here that there is indeed a consistent increase in the magnitude and a decrease in the latent period of a response to IAA during the 3-hr period immediately following excision or following removal of 1 μM IAA.

MATERIALS AND METHODS

Plant Material. All experiments were done using subapical coleoptile segments from etiolated corn (*Zea mays* L., hybrid WF 9 × 38 from Bear Hybrid Corn Co., Decatur, Ill.) seedlings grown as previously described (9, 10). One-cm segments were cut beginning 3 mm from the tip of coleoptiles 3 to 3.5 cm long. The segments were deleafed and a column of 12 1-cm segments was mounted immediately after excision in a shadowgraphic growth-recording device as described previously (10, 12). Recording of growth of the segments began no longer than 10 min after excision of the first segment. The expression "time of excision" as used here refers to the time at which half of the segments were cut.

IAA Solutions. The pH of IAA solutions was adjusted to pH 6.5 to 6.8. Potassium phosphate buffer (3 mM) was used to maintain the pH of solutions containing high concentrations of IAA. This buffer has no effect on the occurrence of the SGR (11), or on auxin-induced growth responses.

^{3}H-IAA Uptake. Uptake of IAA was measured by incubating segments in 0.5 μM IAA (plus 3 mM K-phosphate buffer, pH 6.5) containing ^{3}H-IAA at a specific radioactivity of 500 μCi/μmol. Coleoptile segments were mounted as for recording of elongation and uptake was monitored over a 30-min period beginning either 0.5 or 2.5 hr after excision. At prescribed intervals, the uptake of ^{3}H-IAA was terminated by removing the segments from the uptake medium and immediately rinsing them in three changes of distilled H_2O. Each 1-cm segment was flushed with a stream of deionized water for 10 sec. The segments were blotted briefly before each was placed into a test tube containing 2 ml of 80% ethanol. The segments were extracted overnight and 1 ml of the ethanolic extract was added to a scintillation vial containing 9 ml of Bray's scintillation cocktail. Determinations of radioactivity were made with a Beckman model LS-230 scintillation spectrometer. An external standard was used to correct for sample quenching. Counting efficiency was about 26%.

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[2] Abbreviation: SGR: spontaneous growth response.

Chemicals. IAA was obtained from Eastman Kodak Co. and ^{3}H-IAA (17,000 mCi/mmol) was purchased from Schwarz/Mann.

RESULTS

Dependence of Auxin Response on Time from Excision or Time after Withdrawal of Exogenous IAA. The possible existence of a time-dependent increase in sensitivity to auxin in corn coleoptile segments was tested using two experimental protocols: (*a*) a low concentration of IAA (0.5 μM) was applied at increasing times from excision; (*b*) 0.3 μM IAA was applied at increasing times from the withdrawal of a higher auxin concentration (1 μM). In each case, the effect of the time of IAA application was discerned by measuring the magnitude of the IAA response and the duration of the latent period associated with the response. The latent period is defined here as the period following application of auxin during which there is no measurable increase in growth rate.

In the intact seedling, the coleoptile tip is considered a source of growth-promoting auxin for the remainder of the coleoptile (1, 20). Therefore, excision of a subapical segment results in its removal from an immediate active auxin supply. In corn coleoptiles there is a period of rapid elongation which follows excision and persists for about 35 to 40 min. This initial period of rapid growth in *Avena* has been attributed largely to residual auxin. Therefore, by 30 min after excision the level of endogenous active hormone in the corn segments is probably very low.

Growth curves of segments exposed to a low concentration of IAA at increasing times after excision are shown in Figure 1. There is a dramatic increase in the magnitude of the response to IAA and a dramatic decrease in the latent period of the response with increasing time from excision. The average growth rate induced by IAA given 0.5 hr after excision is about 0.17 mm/hr·segment, and the latent period is about 60 min. However, when IAA is applied 2.5 hr after excision, the auxin-enhanced growth rate is about 0.52 mm/hr·segment and the latent period is reduced to 14 min.

In other experiments, the coleoptile segments were placed in 1 μM IAA immediately after excision and left there for 45 to 60 min. They were then rinsed thoroughly and transferred to water. A low concentration of IAA (0.3 μM) was then applied at increasing times from withdrawal of the 1 μM auxin and the time-dependent changes in the magnitude and latent period of the auxin response were measured. Again there was strong evidence for enhanced sensitivity to auxin with time, as measured by the increased magnitude and decreased latent period of the response to 0.3 μM IAA. Figure 2 shows the relationship of both the auxin-induced growth rate and the latent period of the auxin response to time of application of IAA following termination of the 1 μM IAA pulse.

The increase in sensitivity is strongest (as measured by the magnitude of the response) during the period 1.5 to 2.5 hr following withdrawal of 1 μM IAA. This differs somewhat from the time course of change in auxin sensitivity after excision where the greatest change in sensitivity appears between 1 and 1.5 hr (Fig. 1). In either case, the period of strongest increase in magnitude of the response to IAA does not correspond to the period of strongest decrease in latent period.

Uptake of ^{3}H-IAA. ^{3}H-IAA uptake was followed for 30 min beginning either 0.5 hr after excision or 2.5 hr after excision. The uptake kinetics for these periods is shown in Figure 3. There appears to be no significant difference in the capacity for IAA uptake measured shortly after excision as compared to 2.5 hr after excision. Therefore, differential hormone uptake cannot explain the 2- to 3-fold increase in auxin responsiveness that occurs during this same time span.

Differential IAA uptake has been shown by Macdowall and Sirois (17) to be largely responsible for variation with time from excision in the IAA growth response in wheat coleoptile segments. As additional support of the controlling effect of uptake, these workers have presented evidence that as the number of transverse cuts per unit length of coleoptile tissue increases, the latent period in response to IAA decreases. However, in our corn coleoptile material, subsectioning of the 1-cm segments was found to cause no change in the latent period of the response to either 0.5 μM or 1 μM IAA in

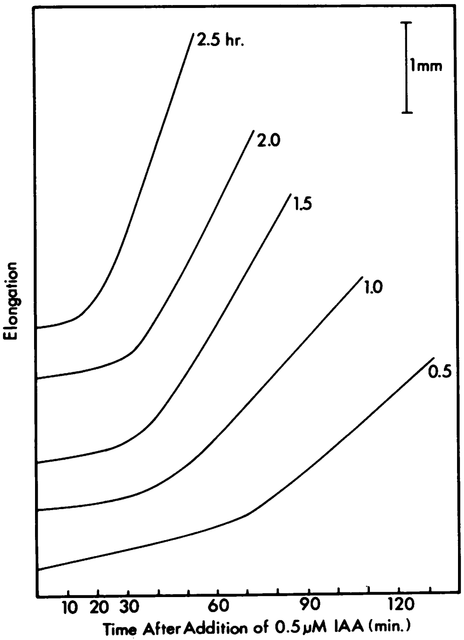

Fig. 1. Dependence of the growth response to IAA on time after excision. Segments were held in water prior to exposure to auxin. The time in hr by each curve indicates the time after excision at which IAA (0.5 μM) was applied to that set of segments. Each experiment was repeated at least four times with representative curves displayed.

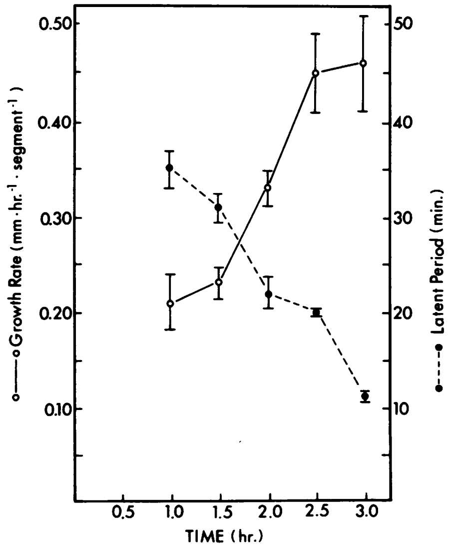

Fig. 2. Dependence of the growth response to IAA on time after prior exposure to IAA. The time on the abscissa is time from withdrawal of 1 μM IAA. Following withdrawal of IAA the segments were thoroughly rinsed and placed in water until 0.3 μM IAA was added. Left ordinate: growth rate in response to 0.3 μM IAA. Right ordinate: latent period of response to 0.3 μM IAA. Standard deviations are given for each point. Experiments were performed a minimum of four times each. (SGR had begun just prior to addition of IAA at 3 hr; growth rate expressed at 3 hr is total rate.)

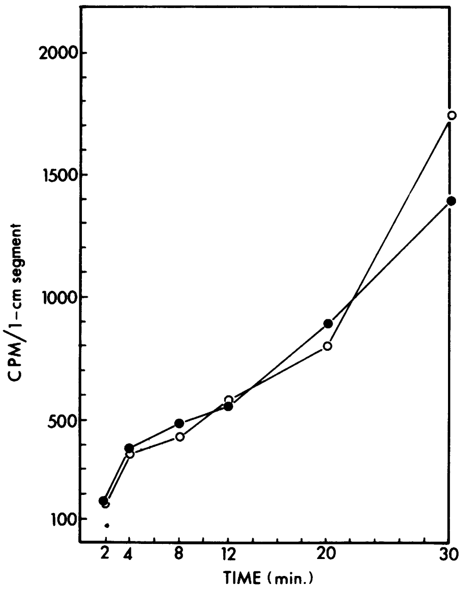

FIG. 3. Uptake of ^{3}H-IAA from 0.5 μM IAA was followed over a 30-min period using segments placed in uptake medium either 0.5 hr (○——○) or 2.5 hr (●——●) after excision. Each point represents the average of at least eight segments. Variation between segments was not larger than 25%.

segments measured either at 0.5 hr or 2.5 hr after excision (data not shown). A similar lack of dependence of the latent period of the auxin response on segment length in corn coleoptiles was demonstrated by dela Fuente and Leopold (7). Also in contrast to wheat coleoptiles in which there was an inverse relationship between segment length and magnitude of the auxin response, increasing the number of cut ends per unit length of corn coleoptile tissue led to no increase in the IAA-induced growth rate and, in some cases there was a measurable decrease relative to the auxin-induced growth rate of control segments. Likewise, the response of peeled coleoptiles to IAA did not deviate from that observed in nonpeeled segments.

Changes in IAA Dose-Response Relationship with Time from Excision. The shape of the dose-response curve differs significantly in segments used 0.5 hr after excision compared to segments used 2.5 hr after excision (Fig. 4). Segments used shortly after excision display a definite sigmoidal pattern in their response to increasing IAA concentrations over the lower end of the range of concentrations used. A similar dose-response relationship has been described for *Avena* (5, 18). The maximum rate of elongation in our corn material measured 0.5 hr after excision was not attained until the IAA concentration had been raised to 5 μM (Fig. 4, curve A). In *Avena*, the maximum rate of elongation was obtained at 0.3 μM IAA (5).

When the IAA dose-response curve for corn coleoptiles is determined using segments 2.5 hr after excision, the curve is not sigmoidal (Fig. 4, curve B). Instead, over the low range of auxin concentrations, there is a linear rise in response to increasing concentrations of IAA. A plateau of maximum rate begins at 0.5 μM and extends to about 5 μM. Further increases in concentration from this point result in decreased auxin responses. The shape of the curve generated with segments 2.5 hr from excision could be called a modified bell curve. Dose-response curves for wheat coleoptiles show no evidence of a sigmoid-shaped curve at low IAA concentrations (17).

It has been shown in *Avena* that the shape of the dose-response curve changes with time, but that a bell curve is only obtained in the presence of sucrose (5), or after about 24 hr (18). Our evidence indicates that the IAA dose-response curve in corn also changes with time, but that the changes occur between 0.5 hr and 2.5 hr after excision, that is, within the latent period of a normal SGR in this tissue.

Concentration Dependence of Latent Period as a Function of Time from Excision. The latent period of the response to IAA decreases with increasing concentrations of IAA whether the auxin is applied to segments 0.5 hr or 2.5 hr after excision (Fig. 5). This is true up to 50 μM in segments used 2.5 hr after excision and up to 0.5 mM in segments used 0.5 hr after excision. As higher concentrations are applied, the latent period again increases, but the point of inflection differs in segments tested at 0.5 hr and segments tested at 2.5 hr (Fig. 5). The shortest latent period (16.7 min) in segments tested at 0.5 hr from excision is associated with the response to 0.5 mM IAA, while the shortest latent period (8.5 min) in segments tested 2.5 hr after excision occurs in response to 50 μM. The latent period in response to a given concentration of IAA is always longer in segments used 0.5 hr as compared to 2.5 hr after excision.

Using wheat coleoptile segments, Macdowall and Sirois (17) have recently shown that a plot of the inverse of the intercept

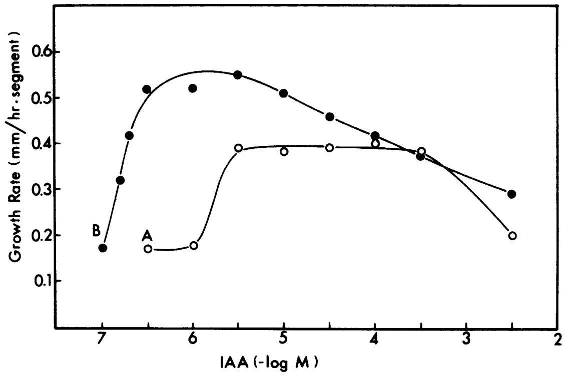

FIG. 4. IAA dose response curves for segments 0.5 hr and 2.5 hr after excision. Curve A: IAA applied 0.5 hr after excision; curve B: IAA applied 2.5 hr after excision. In controls the SGR rate ranged from 0.12 to 0.17 mm/hr·segment. Each concentration of IAA was tested at least three times in both cases.

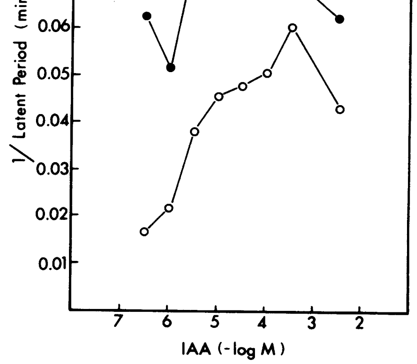

FIG. 5. Concentration dependence of latent period of IAA response in segments 0.5 hr and 2.5 hr after excision. Data shown were taken from the same experiments used to generate dose-response curves of Figure 4.

time *versus* the negative log of the IAA concentration gave a linear curve. This observation indicated to them that the intercept time is a good reflection of the rate-limiting penetration of IAA in media containing low concentrations of IAA. A similar plot for corn coleoptiles (using inverse of the latent period instead of inverse of the intercept time) is not linear whether determined using segments 0.5 hr or 2.5 hr after excision (Fig. 5).

Resetting SGR by Low Levels of IAA. Results previously reported from our laboratory have shown that the SGR can be delayed by the application of IAA during the normal latent period preceding the SGR (11, 12). A pulse of 1 μM IAA longer than 10 min, if given during the 3-hr period preceding the SGR, results in the resetting of the SGR, *i.e.* the SGR is delayed until a fixed time after removal of exogenous auxin. The SGR usually occurs about 2.5 hr after withdrawal of auxin. Since the concentrations of IAA used to suppress the SGR in these experiments were themselves sufficient to stimulate growth, it seemed possible that the resetting of the SGR may involve the depletion of some substrate pool within the tissue during the IAA-induced growth. If this were the case, one would expect that a pulse of IAA of a concentration insufficient to stimulate growth should be ineffective in suppressing or delaying the SGR. This was tested by measuring the effect of a 1.5-hr pulse of 0.3 μM IAA on the SGR. When this concentration is applied to segments during the period 0.5 to 2 hr after excision, there is no enhancement of elongation. As shown in curve B of Figure 6 this treatment does result in a delayed and weakened SGR as compared to the control. This indicates that auxin can cause at least a partial resetting of the SGR even at a concentration insufficient to induce a growth response. The coleoptile tissue is apparently able to recognize a level of IAA too low to result in the usual expression of auxin "recognition," *i.e.* an increased growth rate.

If the 0.3 μM IAA is allowed to remain on the segments (replenished hourly) beyond the 1.5-hr pulse, an increased growth rate becomes apparent after about 2 hr 20 min (Fig. 6, curve C). The induced rate is very similar to the control SGR rate (Fig. 6, curve A). However, this response differs from a true SGR in at least two ways: (*a*) the response appears earlier than the control SGR; and (*b*) removal of the IAA after the response is established results in a gradual slowing of elongation to a low rate, followed by an increased growth rate beginning about 1.5 hr after IAA removal. A true SGR on the other hand is long lived and independent of the manipulations associated with solution changes.

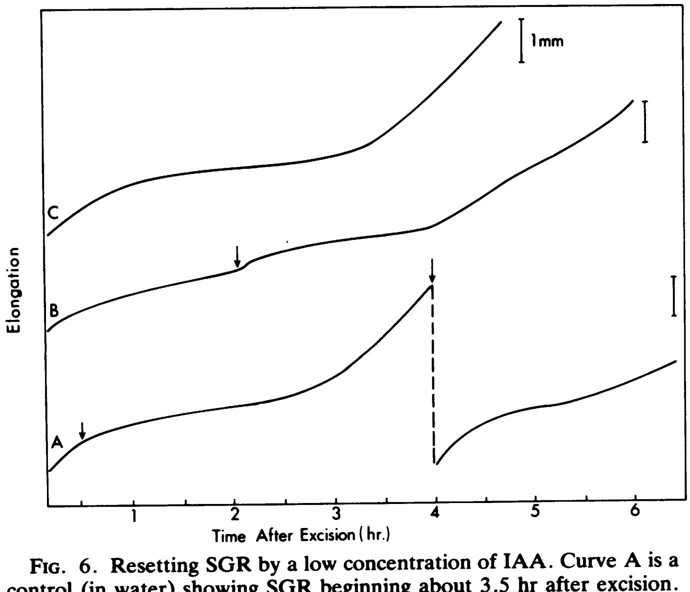

FIG. 6. Resetting SGR by a low concentration of IAA. Curve A is a control (in water) showing SGR beginning about 3.5 hr after excision. IAA (0.3 μM) was applied at first arrow and removed at second arrow in curves B and C. Segments removed from IAA were placed in water following thorough rinsing.

DISCUSSION

The experimental evidence presented here that indicates a time-dependent increase in sensitivity of corn coleoptile segments to auxin includes: (*a*) the 2- to 3-fold increase in the magnitude of the response to IAA with increasing time from excision or time from withdrawal of exogenous IAA accompanied by a 3-fold decrease in the latent period of the response to auxin; (*b*) the fact that changes in the response to auxin cannot be attributed to time-dependent changes in the IAA uptake ability of the segments; and (*c*) the occurrence of a time-dependent change in the dose-response relationship of corn coleoptile segments between 0.5 and 2.5 hr after excision. This measurable increase in sensitivity to exogenous auxin may reflect a type of sensory adaptation and may contribute to the development of the SGR.

There are reports of other adaptation phenomena in plants. List (15) has studied the ability of intact primary roots of corn to adapt to growth-inhibiting levels of IAA. He noted that roots inhibited by 0.1 μM IAA begin to adapt after a period of 1 hr and resume growth. Sporangiophores of *Phycomyces* show adaptation in their light-induced growth response. The growth response is dependent on the intensity to which the specimen is adapted before a new light stimulus is given (3). Hild and Hertel (13) followed sensory adaptation of corn coleoptiles to a geostimulus. They found that repeated brief exposures of the coleoptiles to a horizontal position (prestimulation) prior to the final geostimulus resulted in an alteration of the normal pattern of geotropic curvature in the coleoptiles. In both the *Phycomyces* and the corn coleoptile systems a time constant was determined which characterized the half-time of sensory adaptation. Experiments to derive this value in the study of coleoptile geostimulus adaptation involved the monitoring of the level of adaptation over time, the level of adaptation being set by prescribed increments of prestimulation.

In our corn coleoptile system the stimulus is the application of IAA and the response to this stimulus indicates the level of adaptation. If the level of adaptation is set by the intensity of prestimulation (in this case, the amount of endogenous active auxin), then there should be a time constant which is associated with the adaptation. One would have to assume that the level of endogenous active auxin does not change with time, at least from 0.5 to 2.5 hr after excision, in order to arrive at a valid time constant for adaptation. It is known that IAA-synthetase and IAA-oxidase increase in activity between 1 and 5 hr after excision in corn coleoptiles (11), but the relative amount of active auxin in the tissue during this period was not determined. In an earlier study of corn coleoptiles, van Overbeek (20) found that active (diffusible) auxin is very low in subapical segments until about 2 hr after excision. Therefore, we cannot assume that prestimulation is constant during the time course of the experiments, and an estimate of a time constant for adaptation is not warranted. That the prestimulation level of endogenous active auxin may itself be changing is indicated by the observation that the growth rate in response to low IAA does not increase linearly with time (Fig. 2). The latent period of the response to 0.3 μM IAA may appear to be a better indicator of the level of adaptation since the change in the latent period is linear during at least the first three-fourths of the prestimulation period. It may be inappropriate to use the change in latent period as a measure of adaptation since the latent period may reflect factors other than a change in sensitivity to auxin. The shortest latent period obtained in response to a given concentration of IAA did not correspond with the maximum growth rate obtained in the IAA concentration series (compare Figs. 4 and 5). That the latent period of a hormone response may be a significant indicator of conditions in the tissue is illustrated, however, by the data of Chang and Ruddat (4) in their study of the response of dwarf corn coleoptiles to GA_3. It was shown in this study that the growth response to applied GA_3 is accompanied by a decrease in the latent period as the hormone is given later after the time of excision.

We have considered the possibility that the apparent increase in sensitivity to auxin with time from excision may be an indication of a change in the level of some "inhibitor" or inhibitory state within the coleoptile tissue. There is evidence that a sustained level of IAA can counteract the normal decrease of an ABA-like inhibitor in excised stem sections (8). It has been shown previously that apical (tip intact) corn coleoptile segments exhibit a lower endogenous growth rate than comparable subapical segments (12, 20). Therefore, there is cause to suspect that growth in the intact coleoptile may be controlled in part by some inhibitor and that this inhibitor or its effects may persist for some time following excision. This inhibitor could influence the response to exogenous IAA and also the ability of subapical segments to exhibit the SGR. Libbert (14) has presented evidence for an exogenously occurring inhibitor of auxin biosynthesis in shoots of pea seedlings. The putative inhibitor in corn coleoptiles is not likely to be ABA, however. Even though treatment of *Avena* coleoptile segments with ABA results in both a diminished IAA response (2, 19) and a reduced SGR (2), ABA does not alter the latent period associated with either response.

There is some evidence indicating the involvement of an auxin-dependent inhibitor in the apparent time-dependent changes in auxin sensitivity. Such an inhibitor might be maintained in the tissue as long as a certain minimal level of auxin is present. As the level of auxin drops, the inhibitory state would not be maintained with the result that the tissue becomes more sensitive to exogenous IAA. The lower endogenous growth rate (and reduced response to exogenous IAA) in apical coleoptile segments compared to subapical segments (12) might be viewed as evidence for the action of an inhibitor whose level is controlled by the auxin content of the tissue.

A subapical coleoptile segment probably remains under the influence of the auxin supply provided by the coleoptile tip for a time after excision. The inhibitor may remain in the segment after much of the endogenous auxin has dissipated. There is indirect evidence that a level of endogenous auxin too low to promote growth may still be sufficient to support the persistence of such an inhibitor. Exposure to a non-growth-promoting pulse of IAA (Fig. 6) was shown to cause a delay in the initiation of the SGR. As noted earlier, there is a sharp increase in the sensitivity to 0.5 μM IAA about 1.5 hr after tissue excision. This could be an indication of the effective lifetime of such an auxin-dependent inhibitor.

In order for an auxin-dependent inhibitor to be an integral part of the mechanism of adaptation to low concentrations of auxin, the inhibitor must influence both the magnitude of a response to IAA and the latent period of the response. The timing of an endogenous growth response, the SGR, can be affected by a prior exposure to IAA, whether the exposure results in increased growth (12) or not (Fig. 6). Furthermore, prior exposure to exogenous IAA results in a weaker SGR compared to controls receiving no exogenous IAA (Fig. 3 in ref. 12, and Fig. 6). In a study using corn coleoptile segments, dela Fuente and Leopold (7) noted that a 5-min pulse of 10 μM IAA given about 30 min after excision resulted in a lower growth rate than did a second 5-min pulse given about 65 min after the first pulse. Their results, which were consistent and reproducible but for which no explanation was found, may be accounted for by an increased sensitivity to auxin at the time of the second IAA pulse (65 min after a previous exposure to auxin) compared to the time of the first pulse (30 min after excision). Similarly, List (15) observed that the inhibitory effect of a second pulse (1 hr in duration) of 0.1 μM IAA on intact corn root elongation was substantially weaker than that of an initial pulse of the same concentration. Therefore, there is evidence for the existence of some inhibitory state which is dependent on, or induced by, the presence of auxin.

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