ROLE OF GIBBERELLINS IN THE CONTROL OF INTERCALARY GROWTH AND CELLULAR DIFFERENTIATION IN DEVELOPING *AVENA* INTERNODES*

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Recently, it was found that exogenously supplied gibberellic acid causes a marked acceleration in the rate of internodal extension in excised *Avena* shoots and intercalary meristem (I.M.) segments (Kaufman, 1965b). The cellular basis for this response is an increase in rate of cell lengthening in the intercalary meristem cells of the elongating internode. Coupled with this is a rapid cessation of cell division activity within the intercalary meristem and a blocking of all further cellular differentiation within and above the intercalary meristem at the site of the internodal epidermis.

In this paper, new information is presented on (1) the effects of different concentrations of GA_3 and IAA on growth and cell elongation in *Avena* stem segments; (2) the effects of different gibberellins on growth in *Avena* intercalary meristem segments; and (3) the striking suppression of GA_3-promoted growth in these segments elicited by IAA.

Methods and Materials

Plants of *Avena sativa* cv. "Victory" were grown in the greenhouse with a mean night temperature of 22° C. and a mean day temperature of 26.5° C. After they were 40 days old, plants were placed in a growth chamber until ready for experimental use (7–10 days); here, they were kept on the following regime: 18 hr light at 21.2° C. and six hr dark at 15.5° C. in 24-hour cycles.

The portion of the plant used in these investigations was p-1 internode, which is the next to last internode in the shoot, located immediately below the peduncle and inflorescence (illustrated in Kaufman *et al.*, 1965). Shoots were carefully selected for p-1 internodes equal to 1.2 to 1.5 cm in length, a stage when cell division is dominant in the intercalary meristem of this internode and cell elongation is primarily occurring in the upper one-third of the internode.

One centimeter segments were excised from the bases of p-1 internodes at the locus of the intercalary meristem. In this paper, these segments will be referred to as I.M. segments. They were supported in perforated Plexiglas disks in plastic culture dishes as described in Kaufman, 1965b. Hormone (GA_3 or IAA) was supplied to tops of the segments via agar blocks. Several modifications of procedures cited in the above paper for culturing *Avena* I.M. segments have since been developed, including the following: (1) the nutrient solution that infiltrates the filter paper disk below the segments in Hoagland's we have found supports as satisfactory growth in *Avena* segments as the nutrient solution used earlier; (2) the 0.1 *M* fructose has been deleted from the nutrient solution as it is not necessary for expression of activity of GA_3 or of IAA in this system; and (3) the agar blocks are immersed in hormone solution for 24 hr at 4° C prior to their use on the segments rather than adding the hormone directly to hot agar solutions.

Dishes with I.M. segments were incubated in a growth chamber at 21.2° C. with 18 hr light at 7530 lux and six hr dark for the light experiments. Lights con-

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sisted of a bank of cool white fluorescent lamps (Sylvania Powertube) together with four incandescent lamps (60 watts each) to provide far-red irradiation. Dark experiments were run in an incubator at 22.5° C.; segments in these experiments were always observed and measured under green light (fluorescent lamp covered with one sheet amber and one sheet green cellulose acetate film), which does not suppress internodal extension in our excised I.M. segments. The procedure for obtaining cell widths and lengths is essentially the same as cited in Kaufman *et al.* (1965) except for the following change in staining procedure: substituted for acetocarmine was 2% tannic acid for 10 min followed by 3% $FeCl_3$ for five min (after Foster, 1934). This procedure is far more effective for staining cell walls and for measuring cell lengths and widths in fresh sections. Both epidermal and pith cells were measured at the locus of the intercalary meristem, ca. 0.5 cm above the node, using epidermal peels for the former and median longisections of the internode for the latter.

Gibberellic acid (GA_3) was obtained from Plant Protection, Ltd., England, GA_1, GA_4, GA_5, and GA_9 from Imperial Chemical Industries, Ltd., England, and indole-3-acetic acid from Hoffman LaRoche, Inc.

Results

1. *Comparison of Growth Responses of Avena I.M. Segments to Different Concentrations of GA_3 and IAA*

The curves in FIGURE 1 depict the growth responses of light-incubated *Avena* intercalary meristem segments to gibberellic acid at concentrations varying from 10^{-5} to 10^2 mg/l. Here, one observes a significant promotion of linear growth in these segments between 10^{-2} and 10^2 mg/l GA_3. The primary increase in amount of growth occurs between 10^{-1} and 1 mg/l GA_3. The lower limit of sensitivity, 10^{-2} mg/l, is equivalent to 0.29×10^{-7} *M* GA_3, which indicates that *Avena* I.M. segments are very sensitive to exogenously supplied GA_3. This is to be compared with exogenously supplied IAA, where the lower limit of sensitivity in these segments is 10 mg/l IAA (FIGURE 2). Thus, *Avena* I.M. segments are about 1000 times more sensitive to GA_3 than to IAA. Comparable responses to GA_3 are obtained with dark-incubated segments except that net growth promotion elicited by GA_3 is less in dark than in light (cf. section 2).

The time-course growth responses of *Avena* I.M. segments to GA_3 at 10^{-1}, 1, and 10 mg/l are also shown in the insert in FIGURE 1. The two highest concentrations of GA_3 cause a significant increase in the rate of linear extension in these segments between 24 and 48 hr after blocks are first placed on the segments. Interestingly, the rates of growth for GA_3 at 1 and 10 mg/l in these I.M. segments are approximately the same as in intact *Avena* internodes at the same stage of development (p-1 internode = 1.2–1.5 cm length), i.e., ca. 1.2 cm/24 hr. (Kaufman *et al.*, 1965).

At the cellular level, it was previously shown that the primary basis for GA_3-promoted linear extension in p-1 internodes of *Avena* is accelerated cell lengthening (Kaufman, 1965b). This is also true for I.M. segments (TABLE 1). The greatest promotion in cell lengthening occurs at the base of the internode, the next in the middle, and the least at the top, as would be expected. The greatest amount of increase in cell length occurs between 10^{-1} and 1 mg/l GA_3, concentrations which also elicit the greatest increase in segment extension (FIGURE 1). Concomitant with accelerated cell lengthening at the bases of these I.M. segments

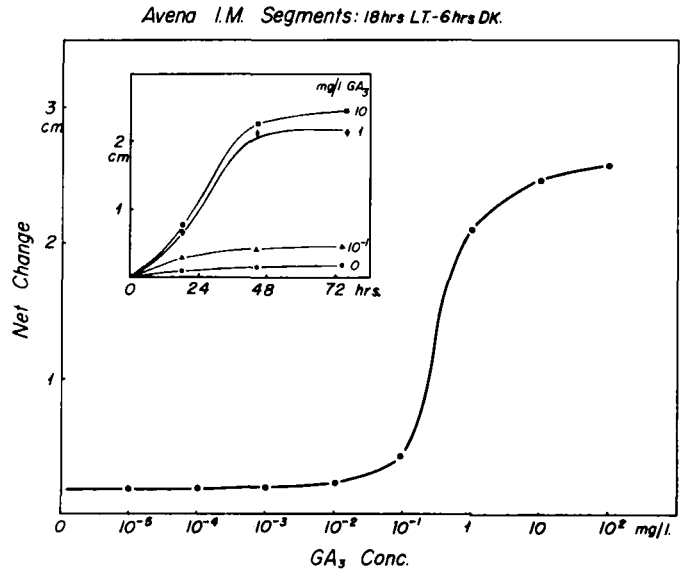


FIGURE 1. Growth responses of *Avena* I.M. segments to GA_3 at concentrations of 10^{-5} to 10^2 mg/l. Segments were incubated at 21.2° C in 18 hr light, six hr dark (24-hour cycles) for 72 hr. GA_3 was supplied via agar blocks as cited in METHODS. Insert shows time-course growth responses of these segments to GA_3 at 10^{-1}, 1, and 10 mg/l. Standard error for GA_3 at 10^2 mg/l = ± 0.08; for control it = ± 0.01.

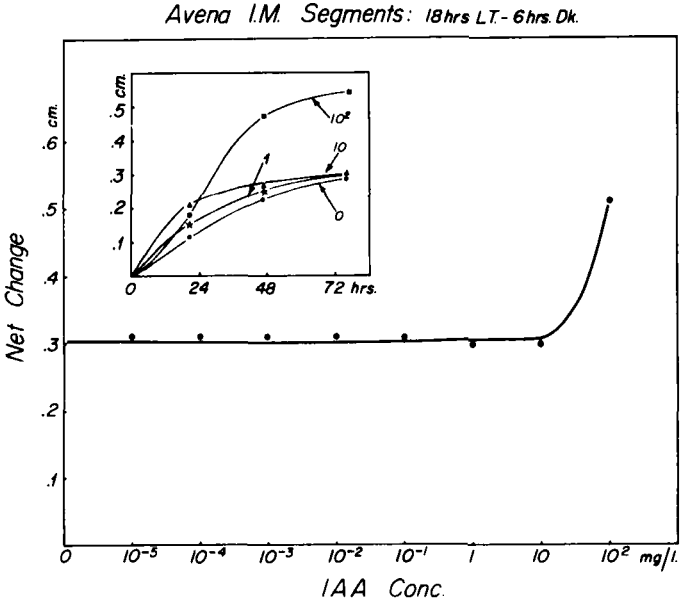


FIGURE 2. Same as FIGURE 1 except data are for IAA. Insert shows time-course growth responses for 1, 10, and 10^2 mg/l IAA. Standard error for IAA at 10^2 mg/l = ± 0.03; for control, it = ± 0.01.

TABLE 1

EFFECTS OF DIFFERENT CONCENTRATIONS OF GIBBERELLIC ACID ON MEAN CELL LENGTH OF PITH CELLS* AT THREE POSITIONS IN *Avena* I.M. SEGMENTS AFTER INCUBATION FOR 72 HRS IN LIGHT/DARK (18/6 HRS) AT 21.2° C

Treatment	Mean Cell Length (μ)**		
	Top	Middle	Base
Control	207	116	42
10^{-5} mg/l GA_3	221	143	39
10^{-4} "	228	141	57
10^{-3} "	248	129	35
10^{-2} "	260	144	50
10^{-1} "	269	174	45
1 "	269	294	140
10 "	269	342	143
100 "	222	300	152

* Based on 25 measurements at each position and for each treatment.

** Standard errors for GA_3 at 100 mg/l = $\pm$ 9.8μ (top), $\pm$ 13.1μ (middle), $\pm$ 6.0μ (base); for control cells = $\pm$ 12.1μ (top), $\pm$ 4.8μ (middle), and $\pm$ 2.3μ (base).

TABLE 2

NET GROWTH (CM) OF *Avena* INTERCALARY MERISTEM SEGMENTS* AFTER EXPOSURE TO GA_3 AT 10^2 MG/L IN AGAR BLOCKS FOR ½ TO 48 HR

Observation Period	Exposure Time to GA_3 (hr)								
	0	½	1	2	3	6	9	24	48
24 hr	0.15	1.16	1.28	1.09	1.24	1.34	1.32	1.24	1.30
48 hr	0.23	1.74	1.85	1.63	1.82	1.99	2.14	1.93	2.01

* 25 *Avena* I.M. segments were used for each treatment. Standard error (48-hr observation period) for control segments = $\pm$ 0.01 cm; for GA_3 (48-hr exposure time) = $\pm$ 0.07 cm.

TABLE 3

NET GROWTH (CM) OF *Avena* INTERCALARY MERISTEM SEGMENTS* AFTER EXPOSURE TO GA_3 AT 10^2 MG/L IN AGAR BLOCKS FOR 0 TO 30 MINUTES

Observation Period	Exposure Time to GA_3 (min)					
	0	5	10	15	20	30
24 hr	0.16	1.17	1.08	1.10	1.10	1.15
48 hr	0.25	2.18	1.97	2.15	2.07	2.18
72 hr	0.30	2.29	2.03	2.24	2.15	2.25

* 25 *Avena* I.M. segments were used for each treatment. Standard error (72-hr observation period) for control segments = $\pm$ 0.01 cm; for GA_3 (30-min exposure time) = $\pm$ 0.07 cm.

is the cessation of all cell division activity in the intercalary meristem and a blocking of any further cellular differentiation at the site of the epidermis above the I.M. This was also observed in p-1 internodes in excised shoots (Kaufman, 1965b).

We were next interested in how long it takes to obtain a saturation growth response to gibberellic acid. Therefore, agar blocks containing GA_3 at 10^2 mg/l

were removed from I.M. segments after 30 min and 1, 2, 3, 6, 9, 24, and 48 hr. Surprisingly, it was found that a saturation growth response was obtained in these segments after 30 min exposure time to GA_3 (TABLE 2). A comparable experiment was then run at shorter time intervals, namely, 5, 10, 15, 20, and 30 min. All GA_3 treatments at these time intervals showed the same amount of promoted growth (TABLE 3), so that even after as short an exposure time as five min, we get a saturation growth response to exogenously supplied GA_3. The same response was also obtained with 10^{-1} mg/l GA_3. This obviously means that GA_3 enters these segments very rapidly, the exposure time needed to elicit a maximal growth response being very short.

2. *Effects of Different Gibberellins on the Growth of Avena I.M. Segments*

GA_1, GA_3, GA_4, GA_5, and GA_9 were supplied to *Avena* I.M. segments at 10^2 mg/l via agar blocks. Segments were cultured in both light and dark. Curves in FIGURE 3, showing the time-course growth responses of these segments in the light, indicate the following: (1) each of these gibberellins markedly accelerates linear extension in I.M. segments; (2) the order of promotion, from greatest to

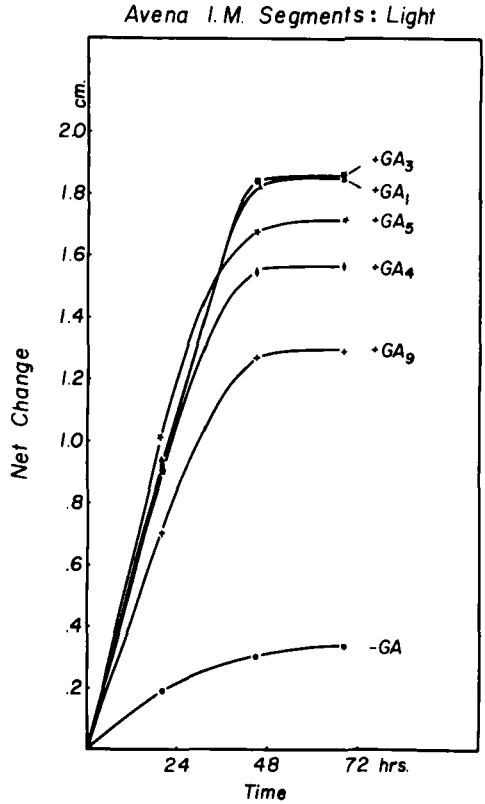


FIGURE 3. Time-course growth responses of *Avena* I.M. segments to five different gibberellins. Segments were incubated at 21.2° C in 18 hr light, six hr dark (24-hour cycles) for 72 hr. Twenty-five segments were used for each treatment. Mean standard error for gibberellin-treated segments at 72 hr was ± 0.02 cm.

least, is $GA_1 = GA_3 > GA_5 > GA_4 > GA_9$; (3) the increase in growth rate for each of the gibberellins occurs in linear fashion from time zero during the first 36 hr of incubation; (4) after 48 hr there is no further promotion in growth of the segments by the gibberellins. The net growth responses of these I.M. segments to the different gibberellins after 72 hr in the light are illustrated in FIGURE 4. In the dark, the same order of response occurs as that cited above; however, the amount of promotion elicited by these gibberellins is about 15–20 percent less in dark compared with that in light. This has also been observed in other systems (Vince, 1960).

Maximum rates of growth elicited by the different gibberellins in these segments are attained within the first 24 hr. (FIGURE 3). The rates are ca. 1.2 cm/24 hr for GA_1, GA_3, GA_4, and GA_5, and 0.9 cm/24 hr for GA_9. Growth rate of control segments during this same time period is 0.25 cm/24 hr. This is an acceleration in growth rate by the first four gibberellins of about five times that of the control rate. After 24 hr growth rates for all gibberellin treatments decline, most rapidly for GA_9, and least rapidly for GA_1 and GA_3. It is during the period 24–48 hr after time zero, that the differences in the effects of the different gibberellins on the rate of growth of I.M. segments become most pronounced.

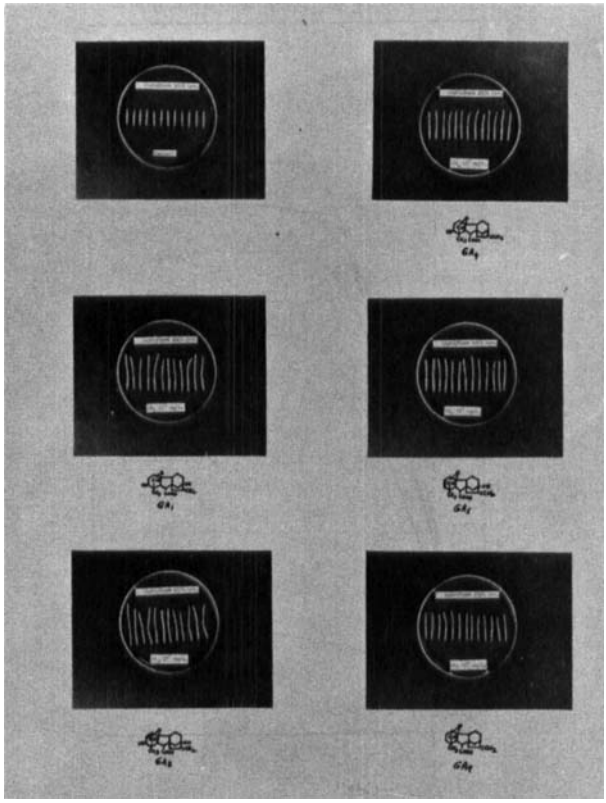


FIGURE 4. Comparison of the effect of five different gibberellins on net growth of *Avena* I.M. segments after 72 hr incubation as cited in FIGURE 3. Time-course growth responses of these same segments are shown in FIGURE 3.

3. *Suppression of GA_3-Promoted Growth in Avena I.M. Segments by IAA*

Both GA_3 and IAA were supplied simultaneously to I.M. segments, each at concentrations of 10^2 mg/l. Blocks containing IAA were placed directly on tops of the I.M. segments, and GA_3 blocks on top of the IAA blocks. The relative position of the IAA and GA_3 blocks makes essentially no difference in the growth responses of the segments to combinations of IAA and GA_3.

FIGURES 5 and 6 illustrate the time-course growth responses and the net growth responses after 30 hr incubation, respectively, of I.M. segments to IAA and GA_3, and IAA + GA_3 in the light. They indicate that (1) both IAA and GA_3 alone promote linear growth in the segments, that elicited by GA_3 being much greater than that due to IAA; (2) while both IAA and GA_3 alone promote growth in the segments, IAA causes approximately a 45 percent suppression of GA_3-promoted growth compared with control growth when the two hormones are supplied simultaneously; and (3) the suppressing action by IAA of GA_3-promoted growth starts from time zero and becomes most pronounced between 24 and 48 hr after time zero, where growth rate decreases most sharply for IAA + GA_3 compared with that for GA_3 alone.

In the dark, IAA also suppresses GA_3-promoted growth (TABLE 4), except that under these conditions, IAA suppresses GA_3-promoted growth completely, i.e., to the control level of growth. This is probably related to the fact that (1) we obtain suppression of segment growth by IAA alone in the dark (TABLE 4) and promotion in the light (FIGURES 5, 6) and (2) we do not obtain as much promotion of segment growth by GA_3 in the dark as in the light (cf. section 2).

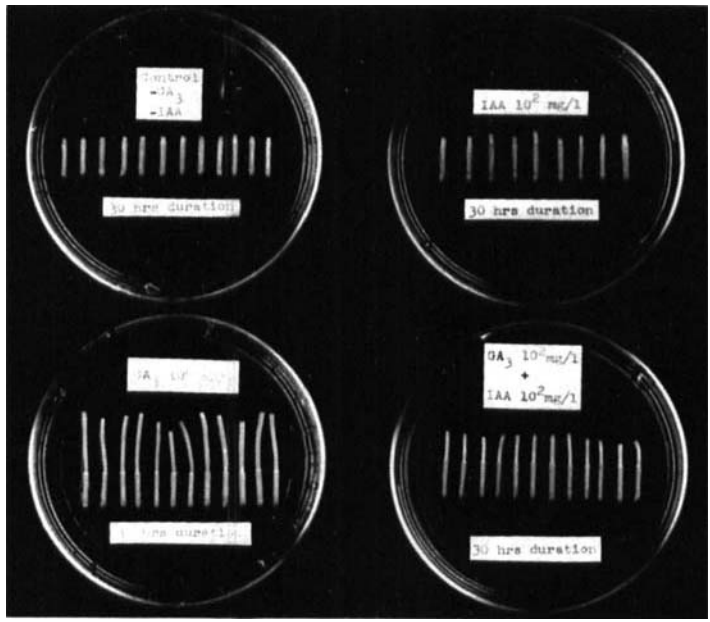


FIGURE 5. Time-course growth responses of *Avena* I.M. segments to IAA, GA_3, and IAA + GA_3, each at 10^2 mg/l. Segments were cultured in light/dark (18/6 hr) for 72 hr at 21.2° C, using 25 I.M. segments per treatment. Mean standard errors for 72-hour data are as follows: control = ± 0.03, IAA = ± 0.03, GA_3 = ± 0.10, IAA + GA_3 = ± 0.11.

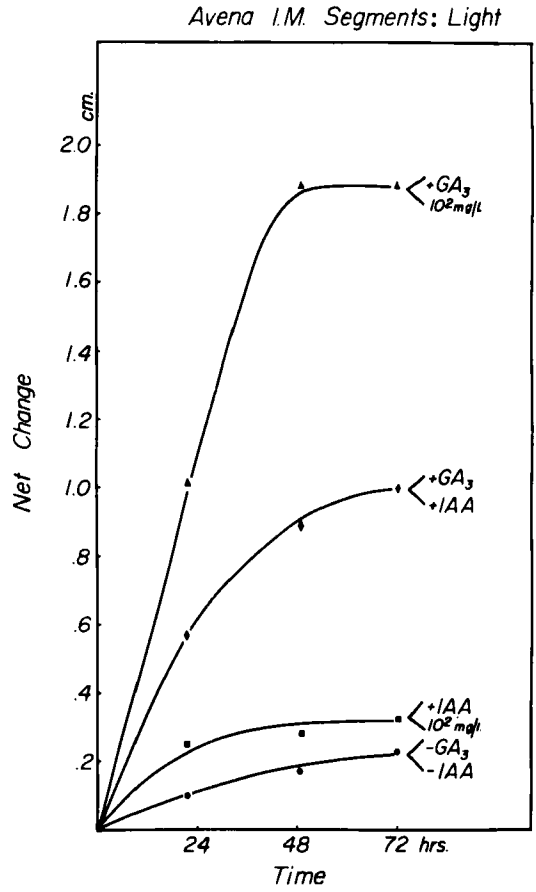


FIGURE 6. Illustration of growth responses of I.M. segments to same treatments as cited in FIGURE 5. Segments were incubated as above for 30 hr.

One further point is that in separate experiments, we have found that IAA suppresses GA_3-promoted growth significantly in *Avena* I.M. segments at concentrations down to 1 mg/l IAA. At this concentration, suppression is 55 percent in the light and 10 percent in the dark. This means that IAA at lower concentrations exerts a rather strong braking action on GA_3-induced growth acceleration in intercalary meristem segments in the light. One of the questions posed here is whether IAA at physiological concentrations (< 1 mg/l) exerts this same action and whether this might not be one of the actions of IAA in the intact developing internode.

The cellular basis for the suppressing action of IAA on GA_3-promoted growth in *Avena* I.M. segments is one of decreased cell elongation. This was found to be true in both pith and epidermal systems at the site of the intercalary meristem, and is especially obvious after segments have been incubated for 72-hour periods. This is revealed by the following data for mean cell lengths of epidermal cells

TABLE 4

EFFECT OF IAA, GA_3, AND IAA + GA_3 (EACH AT 10^2 MG/L) ON NET GROWTH (CM) OF *Avena* I.M. SEGMENTS* CULTURED IN THE DARK AT 21.2° C FOR 72 HR

Observation Period	Treatment			
	Control	IAA	GA_3	IAA + GA_3
21 hr	0.79 ± 0.05	0.52 ± 0.02	1.31 ± 0.06	0.75 ± 0.02
44 hr	0.89 ± 0.06	0.57 ± 0.02	1.35 ± 0.07	0.96 ± 0.03
70 hr	0.97 ± 0.07	0.70 ± 0.03	1.51 ± 0.06	0.98 ± 0.04

* 25 *Avena* I.M. segments were used for each treatment.

in segments cultured in the light: control = 39.3 μ; IAA = 43.3 μ; GA_3 = 208.8 μ; IAA + GA_3 = 44.7 μ. There was no significant difference in epidermal cell widths in these I.M. segments. The results of these experiments on IAA + GA_3 clearly show that IAA exerts a braking action on the rate of GA_3-accelerated linear growth in *Avena* I.M. segments, and that the cellular basis for this action of IAA is one of suppressed cell lengthening in the I.M. cells which have been shown to undergo a striking acceleration in their rate of cell elongation in response to GA_3 alone (Kaufman, 1965b).

DISCUSSION

This investigation poses three primary questions in connection with roles that gibberellins might play in the control of intercalary growth in *Avena* internodes. These include the following: (1) What are the physiological implications of the striking growth responses elicited in *Avena* I.M. segments by exogenously supplied GA_3? (2) How do *Avena* I.M. segments compare with other systems in their responses to different gibberellins? (3) What might be the mechanism(s) by which GA_3 accelerates linear growth in I.M. segments, and how does IAA act to suppress the action of GA_3? These questions will constitute the focal points for the discussion which follows.

Physiological Implications of Growth Responses of Avena I.M. Segments to GA_3

In the present investigations, *Avena* I.M. segments are shown to be very sensitive to exogenously supplied gibberellic acid, i.e., linear growth rate is significantly accelerated down to 0.3×10^{-7} *M* GA_3 (FIGURE 1). By contrast, these segments are relatively insensitive to exogenously supplied IAA, where growth is only promoted by extremely high concentrations of IAA between 1.8×10^{-3} and 1.8×10^{-4} *M* (FIGURE 2). In this sense, *Avena* I.M. segments constitute a rather favorable system with which to test native gibberellins derived from different portions of the same plant. In addition, it is suggested that *Avena* I.M. segments might be used as a bioassay system along with the lettuce hypocotyl test (Frankland & Wareing, 1960), the dwarf corn test (Phinney & West, 1960), or the barley endosperm test (Nichols & Paleg, 1963) to test for gibberellin activity in other plants. Obviously, it is not a desirable system to test for auxin activity because of the extreme insensitivity of I.M. segments to exogenously supplied IAA.

One of the more interesting findings from the present studies is that exogenous GA_3, supplied via agar blocks, enters *Avena* I.M. segments very rapidly. Only five min exposure time to GA_3 at 10^2 and 10^{-1} mg/l is necessary to obtain a

saturation growth response in the light (TABLE 3), and the necessary time might even be less. In this connection, one might ask, (1) how fast is GA_3 actually transported to I.M. cells once it enters the I.M. segment? and, (2) just how much GA_3 is necessary to evoke a significant acceleration in the rate of elongation in *Avena* I.M. cells? It would be extremely interesting to explore these questions by using even shorter exposure times to GA_3 in agar blocks and to use ^{14}C-labeled GA_3 to determine the amount of residual GA_3 in the agar blocks, how rapidly it is transported, and how much GA_3 arrives at the I.M. with short exposure times (similar to techniques employed by Thimann & Wardlaw (1963) with ^{14}C-IAA in pea-stem segments). Perhaps the internodal I.M. is a site where gibberellins are selectively accumulated, particularly during stages when cell elongation is dominant (latter two-thirds of intercalary growth in p-1 internode-Kaufman *et al.*, 1965). Certainly, gibberellic acid's effect on cell elongation in the I.M. suggests that GA_3 or other gibberellins may be among the primary hormones controlling intercalary growth during later stages in the development of *Avena* internodes.

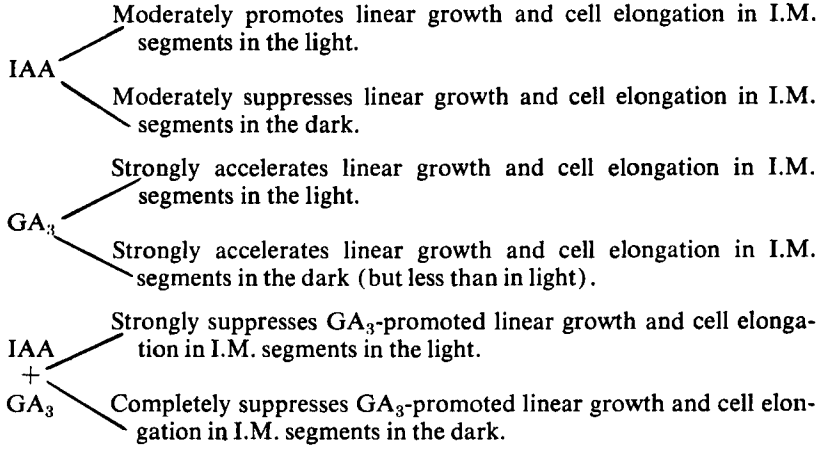
Comparison of Avena I.M. Segments with Other Systems in Response to Different Gibberellins

The present experiments clearly show that there is significant variation in the growth responses of *Avena* I.M. segments to the five different gibberellins tested in this system (FIGURES 3 & 4). GA_1 and GA_3 evoke maximal acceleration in linear growth rate, GA_4 and GA_5, intermediate growth promotion, and GA_9, the least. However, all five gibberellins show significant growth acceleration activity in comparison with control growth in both light and dark in these segments. Even though there are only slight differences in molecular structure, the physiological responses to different gibberellins are rather divergent as shown by the present work and as pointed out by Michniewicz and Lang (1962), Paleg (1964), and van Overbeek (1966) for other systems.

The other point worth emphasizing here is that in comparing the responses of five species of plants to a series of nine gibberellins, Michniewicz and Lang (1962) found that the relative order of promotion is *not* the same, either when comparing stem elongation with flowering, or when comparing elongation and flowering responses of the different plant species. The order of growth promotion elicited by GA_1, GA_3, GA_4, GA_5, and GA_9 in *Avena* stem segments is not the same as with any of the species tested by the above workers. The only consistent pattern that can be detected between the results with *Avena* stem segments and those of Michniewicz and Lang (1962) is with GA_9, where the latter workers found it to be among those gibberellins which evoked the lowest activity or were inactive with respect to flower formation, and in our system, where it was the least active as far as promotion of stem elongation was concerned. A second point is that we obtain essentially the same order of growth promotion by these gibberellins in both light and dark, whereas Sembdner and Schreiber (1965) find that in d-1 dwarf mutant of *Zea mays,* they obtain no differences in response to GA_3, GA_5, and GA_6 in the dark but very striking differences in the light. One cannot help drawing the conclusion that (1) the kinds of endogenous gibberellins operating in the control of stem elongation are probably not the same in different plants and (2) there must be profound differences in sensitivity of stem tissues to different gibberellins as recently suggested by Kende and Lang (1965).

Possible Mechanisms of GA_3-Induced Acceleration of Growth in Avena I.M. Segments and IAA Quenching of GA_3 Action

The diagram below summarizes the effects of IAA, GA_3, and IAA + GA_3 on linear growth and cell elongation at the site of the intercalary meristem in *Avena* I.M. segments under conditions of light and dark:



These growth responses in *Avena* I.M. segments to IAA + GA_3, where IAA at high concentrations strongly suppresses GA_3-promoted growth, have also been observed by other investigators using different experimental systems (Hillman & Purves, 1961; Kato, 1961; Katsumi *et al.*, 1965; Palmer, 1964; Purves & Hillman, 1951; and van Overbeek & Dowding, 1961). The primary difference in responses of *Avena* I.M. segments and those reported by the above investigators is that we obtain a consistent suppression of GA_3-induced growth by IAA in light and dark even when IAA alone promotes growth at high concentrations, as in the light; at comparable concentrations, IAA alone usually suppresses growth in other plants or excised portions cultured in the light or the dark. This discrepancy may be related to the fact that *Avena* I.M. segments are extremely insensitive to exogenous IAA except at very high concentrations (FIGURE 2).

The central question here is how does GA_3 so strongly accelerate linear growth rate in *Avena* I.M. segments and IAA suppress this GA_3-promoted growth? Palmer (1964) has proposed that auxin itself may reduce the level of natural gibberellins in the stem to suboptimal values; or it may act as an antigibberellin as suggested by van Overbeek and Dowding (1961). The third possibility is that gibberellin alone may control the synthesis of certain hydrolytic enzymes, e.g., promotion of synthesis of α-amylase (Varner 1964) in barley endosperm, or increase invertase activity (Sacher *et al.*, 1963) in sugarcane internodal intercalary meristem disks. Coupled with this might be IAA suppression of GA_3-induced synthesis of these enzymes. In preliminary work with *Avena* I.M. segments, we find the following values (in Klett units) for acid invertase activity (using procedures of Sacher *et al.*, 1963) after segments have been incubated with IAA, GA_3, and IAA + GA_3 (10^2 mg/l) in agar blocks in the light for 72 hr; control = 7.0; IAA = 5.7; GA_3 = 13.3; IAA + GA_3 = 10.7. These results have been obtained in duplicate experiments. They suggest that GA_3 promotes acid

invertase activity while IAA partially quenches the GA_3-promoted invertase activity in *Avena* I.M. segments. However, it is premature to relate these results causally to the effects of GA_3 alone on linear growth or of IAA on GA_3-promoted growth. GA_3 may also be promoting the synthesis of other enzymes such as α-amylase or enzymes concerned with carbohydrate biosynthesis, which have not yet been tested in our system.

The final point is that with *Avena* internodes, it is highly probable that we have several hormones, such as auxins, gibberellins and phytokinins, operating in unison to control intercalary growth; and that one of these, the gibberellins, must be isolated and their mechanism of action elucidated before we can understand how they may be participating with other hormones in the control of intercalary growth by cell division and cell elongation and in the process of cellular differentiation in the developing internode.

Summary

1. Linear growth and cell lengthening in *Avena* intercalary meristem segments are significantly accelerated by GA_3 at concentrations as low as 0.29×10^{-7} M in both light and dark. IAA, in contrast, promotes growth only in the light at concentrations above 1.8×10^{-4} M. In the dark IAA suppresses internodal extension in these segments.

2. A saturation growth response to GA_3 at 10^2 and 10^{-1} mg/l is obtained in *Avena* I.M. segments after only five min exposure to GA_3 in the light. This means that exogenously supplied GA_3 enters these segments very rapidly.

3. The order of acceleration of linear growth in *Avena* I.M. segments, from greatest to least, to five different gibberellins (10^2 mg/l) was as follows: $GA_1 = GA_3 > GA_5 > GA_4 > GA_9$ in light and dark.

4. IAA at $1–10^2$ mg/l quenches GA_3-accelerated growth in *Avena* I.M. segments in both light and dark as much as 45 percent. Several mechanisms for GA_3-accelerated growth in I.M. segments and IAA suppression of GA_3 action are discussed.

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