Studies of Effects of Light on Growth Pattern and of Gibberellin Sensitivity in Relation to Age, Growth Rate, and Illumination in Intact Wheat Coleoptiles [1]

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Introduction

Although there have been many studies on effects of light on over-all elongation of various plant organs, relatively little is known concerning effects of light on the pattern of elongation within a given organ, i.e., the relative contributions of various portions of the organ to the total elongation. In this study, intact wheat coleoptiles were marked with India ink to permit an investigation of effects of various light treatments on the pattern, as well as the total extent, of elongation. These intact coleoptiles are also used to test the suggestion that actions of photomorphogenic radiation on elongation are closely related to gibberellin effects (4, 17, 25, 27, 30), and the generalization that gibberellin is more effective on young, rapidly growing tissues than on older, more slowly growing tissues (4, 12, 13, 22, 23, 27, 33).

Materials and Methods

General Description of Experiments. Coleoptiles of intact seedlings were marked with India ink into 3 portions of equal length to permit observation of the pattern of subsequent elongation. Coleoptiles of a standard size, long enough to mark accurately yet short enough to undergo large percentage increases in length, were used whenever the choice was possible. Elongation of the different portions was measured 24 hours after marking. In most experiments the seedlings were germinated and grown in darkness; light treatments, when given to these plants, were begun immediately after marking. In some cases these light treatments took up a significant portion of the 24-hour period for which elongation was studied. In some other experiments seedlings were germinated and grown in white light of 16-hour photoperiod. Coleoptiles of these and other light-grown plants were similarly marked and measured after 24 hours. In some experiments, half the plants were exposed to gibberellic acid (GA) during the 24-hour period between marking and measuring. Apical, middle, and basal refer to the 3 portions of the coleoptile delimited by the India ink markings. In different coleoptiles similarly labeled portions can be considered to correspond exactly when the coleoptiles received identical treatment up to the time of marking. Because of non-uniform elongation within different portions of the same coleoptile, similarly labeled portions of coleoptiles differing in age or in previous light treatments do not correspond exactly.

Plant Material and Growth Conditions. The wheat used was *Triticum vulgare* Vill. (*Triticum aestivum* L.) var. Fulcaster obtained from the D. R. Mayo Seed Company, Knoxville, Tennessee. The same batch, which had been treated with Ceresan, was used for all experiments. Grain was sown on 2 pieces of Whatman No. 1 filter paper in covered 15 × 1 cm petri dishes. The grains, embryos up, were placed about 5 mm apart and 20 ml of distilled water was added. In all cases germination and seedling growth took place with a thermoperiod consisting of 16 hours at 21 ± 2° and 8 hours at 17 ± 1°. Relative humidity was 55 ± 5 %. Unless otherwise indicated, dark-grown seedlings with average coleoptile length of 1.5 cm were selected and marked 72 hours after sowing. In all experiments marking was done after cell division had ceased in the coleoptiles. Absence of cell division was shown by absence of mitotic figures in Feulgen-squashes (see also refs 1, 32). Only seedlings with straight shoots and well-developed roots were used. All manipulations were performed in a darkroom under 2 small Sylvania fluorescent tubes (F4T5/D) covered with four layers of 300 MSC dark-green Du Pont cellophane. The marking of coleoptiles of the intact seedlings was done with a Rapidograph pen No. 1 filled with India ink. Marks were placed at the base of the coleoptile and at points dividing the coleoptile into 3 portions of equal length. The plants were handled carefully and as rapidly as possible to prevent injury to the roots and long exposures to the green safelight. After selection for uniformity and marking, 15 plants were placed in each of a number of 10 × 1-cm petri dishes containing 2 pieces of Whatman No. 1 filter paper moistened with 10 ml of distilled water. Each

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dish was covered and given the light (or dark) treatment indicated.

Illumination. The high-intensity white light (33,900 ergs $cm^{-2}sec^{-1}$) was from a mixture of GE Power-Groove cool-white fluorescent tubes (F96PG17–CW) and incandescent lamps. When given in daily 16 hour-exposures, the photoperiod coincided with the thermoperiod described in the preceding paragraph. Far-red irradiation was obtained by passing light from GE reflector flood lamps (31) through a Corning filter No. 2600. The transmission spectrum had a maximum near 8000 A. All other light, red, blue, and cool-white, was supplied from GE fluorescent tubes (F20T12) and was filtered through 5 cm of water. The blue light was a broad wavelength band with maximum near 4400 A; red was a broad wavelength band with maximum near 6600 A. In experiments in which it was important that blue light be uncontaminated with red, the blue fluorescent tubes were covered with 3 layers of 300 MSC dark-blue Du Pont cellophane. The dark-adapted eye could see no light whatever when this light source was covered with 2 layers of red cellophane in a darkroom. All intensities were measured with a thermopile that had been calibrated with a standard tungsten lamp. These measurements were taken at the level of treatment dishes. All plants, including those described in this paper as dark-grown and as controls that received no light, were exposed to the green safelight during marking.

GA Treatment. The seedlings were first chosen for uniformity and then paired for identical coleoptile length at the time of marking. One of each pair was transferred immediately after marking to a 10 × 1-cm petri dish containing 2 pieces of Whatman No. 1 filter paper moistened with 10 ml of distilled water; the other member of the pair was transferred after marking to a similar dish containing a GA solution that was 8×10^{-4} M, the optimal concentration for coleoptile elongation determined in preliminary experiments. Light treatments were always identical for the paired dishes of GA-treated and water-control seedlings.

The GA was kindly supplied by Merck and Company, Inc. as Gibrel, the potassium salt of gibberellic acid. Molar concentration was calculated in terms of GA itself, taking into account the presence of inert material (Merck and Company, Inc., private communication).

Presentation of Data. The data presented in this paper refer to increases in length during 24 hours after marking the coleoptiles. Per cent increases in length, rather than absolute increases, are reported because not all coleoptiles were the same initial length. Data are from means from groups of 15 coleoptiles given identical treatment. In some instances the means of 3 experiments are averaged. Standard statistical analyses of the data are not presented, because they are meaningless in experiments in which original marking was done under very dim green light and final length was recorded only to the nearest 0.1 cm. All experiments, however, were qualitatively repeatable and there was consistency in observed patterns of differences.

Gibberellic acid sensitivity is reported as the relative GA effect, defined as

$$\frac{\text{increase in length (\%) with GA treatment}}{\text{increase in length (\%) of water controls}}.$$

As will be pointed out in the Discussion, the relative GA effect represents the elongation of GA-treated material properly corrected both for elongation of water controls and for any inequality in initial lengths of GA-treated and water-control material at the time GA treatment is begun.

Results

Elongation of Dark-Grown Coleoptiles. For 8 different age-height groups the over-all extent and the pattern of elongation during 24-hour periods were established. The results (fig 1) indicate that in dark-grown coleoptiles elongation ceases first in basal and last in apical portions.

Elongation of Dark-Grown Coleoptiles Exposed to Light. In all experiments involving illumination of dark-grown coleoptiles, coleoptiles with average length of 1.5 cm were selected 72 hours after sowing. Shorter (younger) coleoptiles are more difficult to mark accurately and longer (older) coleoptiles grow at slower rates (fig 1). Table I shows that although red light (1800 ergs $cm^{-2}sec^{-1}$) has no effect on over-all elongation, it greatly alters the pattern of elongation. Short exposures greatly inhibit elongation of basal portions while promoting elongation of apical portions. Elongation of the middle portions is practically unchanged.

Short exposures to blue light (5500 ergs cm^{-2} sec^{-1}) gave effects similar to those of red light. With longer exposures, however, this blue light was more effective than red light in inhibiting the basal portions, but less effective than red light in stimulating the apical portions, since for exposures greater than 300 minutes, apical elongation decreased with increasing exposure. The middle portions, which are not affected by red light, are inhibited by blue light. These effects thus result in less total elongation in the blue light than in either the red light or in total darkness. Since the intensity of the 5500 ergs $cm^{-2}sec^{-1}$ blue light is greater than that of the red light, another series of experiments was run with blue light intensity of 1650 ergs $cm^{-2}sec^{-1}$, which was somewhat lower than the intensity of the red light. The results with blue light of 1650 ergs cm^{-2} sec^{-1} are essentially the same as those with 5500 ergs $cm^{-2}sec^{-1}$. Consequently, the differences in response of dark-grown coleoptiles to red and blue light after comparable durations of exposure (table I) should be attributed to differences in light quality rather than to differences in intensity.

Illumination of dark-grown plants with white light produces effects similar to those of red and blue light. High-intensity (33,900 ergs $cm^{-2}sec^{-1}$)

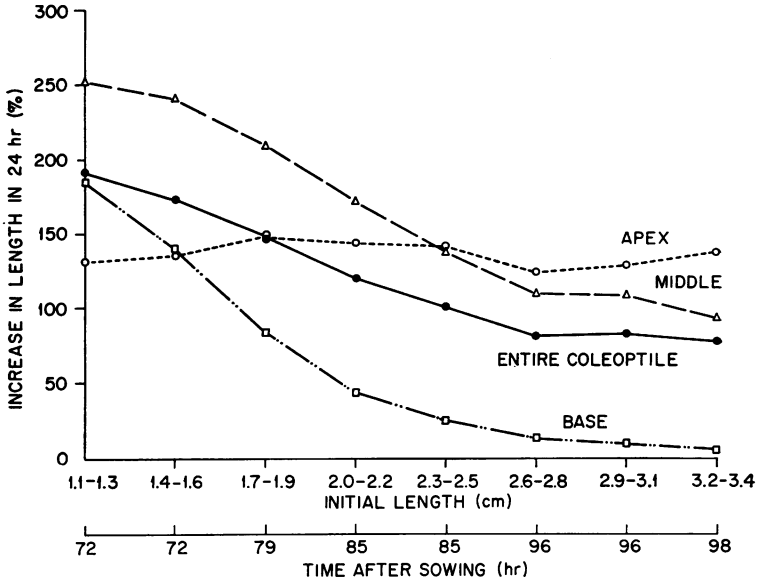

Fig. 1

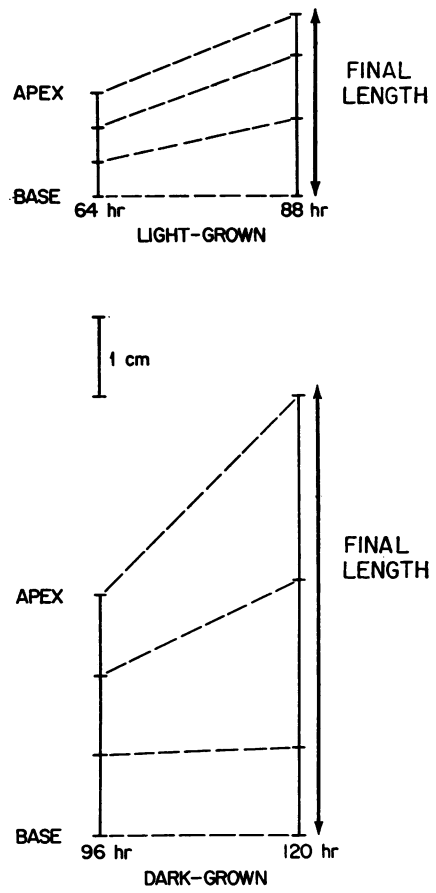

Fig. 2

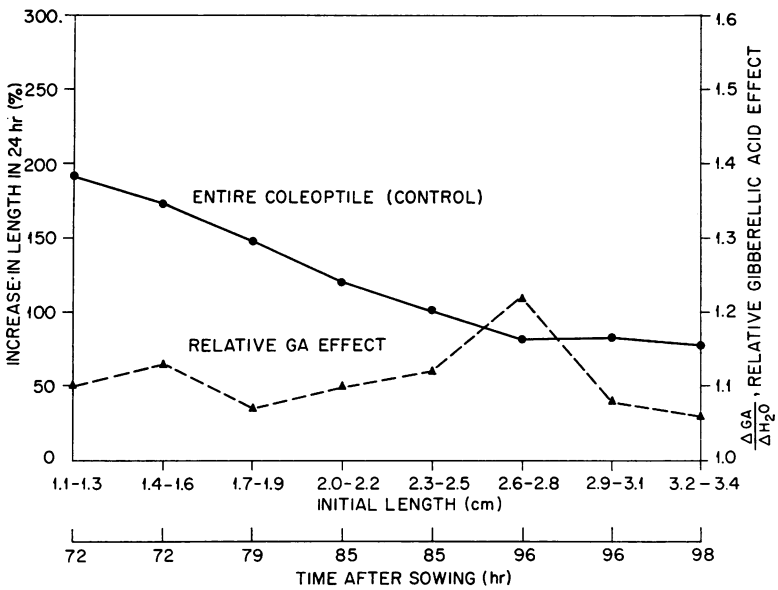

Fig. 3

FIG. 1. Growth pattern of dark-grown coleoptiles of various age-size groups. Each point represents mean increase in length of 15 coleoptiles. In all experiments, apical, middle, and basal portions were one-third of length of coleoptile when marked at beginning of 24 hour growth period.

FIG. 2. Comparison of growth patterns of light-grown and dark-grown coleoptiles. Times indicate hours after sowing when coleoptiles were marked and measured. Light-grown plants were given 16 hour photoperiods of white light (33,900 ergs cm^{-2} sec^{-1}) on the day of sowing and each day thereafter. All lengths are to same scale.

FIG. 3. Elongation and relative GA effect in dark-grown coleoptiles of different age-size groups. These plants received no light treatments after marking.

white light (mixed fluorescent and incandescent) was very effective in reducing total coleoptile elongation. With regard to the curve relating (a) elongation of the apical portion and (b) duration of illumination, this white light treatment considerably decreases the value of (b) corresponding to the maximum value of (a) and also increases the absolute value of the negative slope of (a) with respect to

Table I

Elongation and Relative GA Effects in Dark-grown Coleoptiles Exposed to Light

Each entry is an average from 45 coleoptiles for the red and 5500 ergs cm^{-2} sec^{-1} blue light experiments and 15 coleoptiles for the white and 1650 ergs cm^{-2} sec^{-1} blue light experiments.

Light treatment	Duration of exposure	Basal portion*		Middle portion*		Apical portion*	
		Increase in length of water controls	Relative GA effect	Increase in length of water controls	Relative GA effect	Increase in length of water controls	Relative GA effect
	(min)	(%)		(%)		(%)	
	0**	163	1.22	203	1.14	132	1.09
Red	10	103	1.19	187	1.22	169	1.19
	30	105	1.35	200	1.16	177	1.07
(1800 ergs	90	98	1.31	180	1.23	179	1.19
cm^{-2} sec^{-1})	150	88	1.21	176	1.22	209	1.15
	300	81	1.24	191	1.24	211	1.13
	1440	87	1.20	206	1.20	239	1.15
	0**	139	1.14	229	1.20	123	1.24
Blue	10	89	1.37	204	1.25	166	1.12
	30	89	1.16	204	1.26	173	1.11
(1650 ergs	90	83	1.21	195	1.18	179	1.13
cm^{-2} sec^{-1})	150	71	1.30	188	1.26	187	1.07
	300	52	1.33	173	1.30	203	1.14
	1440	39	1.26	140	1.31	177	1.27
	0**	155	1.21	212	1.18	145	1.08
Blue	10	120	1.34	218	1.19	155	1.10
	30	114	1.24	210	1.18	159	1.18
(5500 ergs	90	99	1.38	200	1.25	177	1.08
cm^{-2} sec^{-1})	150	87	1.21	191	1.28	179	1.20
	300	61	1.32	164	1.33	201	1.20
	1440	54	1.38	129	1.46	165	1.32
	0**	197	1.19	213	1.21	142	1.18
White	30	89	1.53	187	1.20	172	1.19
	150	59	1.44	177	1.24	204	1.25
(33,900 ergs	300	66	1.47	178	1.28	157	1.33
cm^{-2} sec^{-1})	960	43	1.53	116	1.44	127	1.50

* In all experiments, each portion was one-third of total coleoptile length when marked at beginning of 24 hour growth period. For the experiments in this table, illumination began immediately after marking, when the plants were 72 hours old and the coleoptiles had an average length of 1.5 cm.

** Dark controls.

Table II

Photoreversibility with Far-red Radiation of Red Light Effects on Dark-grown Coleoptiles

Each entry represents average from 30 coleoptiles (initial age, 72 hr; initial length 1.5 cm).

Light treatments*	Increase in length during 24 hr after beginning first light treatment	
	Basal portion**	Apical portion**
	(%)	(%)
None	160	133
10 min red	94	159
10 min far-red, 10 min red	86	165
10 min red, 10 min far-red, 10 min red	74	170
10 min far-red	140	141
10 min red, 10 min far-red	133	150
10 min far-red, 10 min red, 10 min far-red	119	157

* Intensities: red, 1800 ergs cm^{-2} sec^{-1}; far-red, 61,800 ergs cm^{-2} sec^{-1}.

** Each portion was one-third of total coleoptile length when marked at beginning of light treatment.

Table III

Photoreversibility with Far-red Radiation of Blue Light Effects on Dark-grown Coleoptiles

Each entry represents average from 30 coleoptiles (initial age, 72 hr; initial length, 1.5 cm).

Light treatments*	Increase in length during 24 hr after beginning first light treatment	
	Basal portion**	Apical portion**
	(%)	(%)
None	148	156
10 min blue	117	179
10 min far-red, 10 min blue	114	175
10 min blue, 10 min far-red, 10 min blue	107	172
10 min far-red	134	158
10 min blue, 10 min far-red	138	149
10 min far-red, 10 min blue, 10 min far-red	131	149
20 min blue	111	185
20 min far-red, 20 min blue	93	187
20 min far-red	129	167
20 min blue, 20 min far-red	127	151

* Blue fluorescent light was filtered through 3 layers of dark-blue cellophane to remove any red impurities. Intensity of this pure blue light was 990 ergs cm^{-2} sec^{-1}. Intensity of far-red was 61,800 ergs cm^{-2} sec^{-1}.

** Each portion was one-third of total coleoptile length when marked at beginning of light treatment.

(b) for superoptimal values of (b). Similar results were obtained with white light of slightly different quality (warm-white) at an intensity of 7200 ergs $cm^{-2}sec^{-1}$. (see also ref 24.)

Far-Red Reversals of Effects of Red and Blue Light on Dark-Grown Plants. In order to characterize further the effects of red and blue light on dark-grown plants, experiments were designed to see whether these effects are reversed by far-red radiation. Table II shows that both red light-inhibition of basal and red light-stimulation of apical portions are reversed by far-red radiation. Table III similarly shows far-red reversal of effects of blue light from which all red contamination had been removed. In all cases, the last light treatment given was the effective one. This indicates reciprocal reversibility of the blue and far-red-light effects as well as reciprocal reversibility of the red and far-red-light effects.

Elongation in Light-Grown Coleoptiles. The growth pattern of light-grown (16-hour photoperiod, 33,900 ergs $cm^{-2}sec^{-1}$ white) coleoptiles is distinctly different from the pattern of elongation in dark-grown coleoptiles. In contrast to elongation in dark-grown coleoptiles, elongation in light-grown coleoptiles ceases first in apical and last in basal portions. Figure 2 illustrates that during a 24-hour period when light-grown coleoptiles approach their final size the apical region has ceased to contribute to over-all elongation. Also shown in figure 2 are data from etiolated coleoptiles similarly presented to emphasize the opposite patterns of elongation in light-grown and dark-grown coleoptiles during a 24-hour period when they approach their final size. The white light treatments given in the experiments depicted in table I and figure 2 are identical with respect to light quality and intensity. This light given in 16-hour photoperiods from the first day of planting appears to reverse the pattern of elongation compared to the pattern in dark-grown controls that receive no light (fig 2). However, as previously stated, the same quality and intensity given in shorter exposures to dark-grown plants do not reverse but in fact exaggerate the pattern found in dark-grown controls that receive no light (fig 1, table I).

GA Sensitivity in Dark-Grown Plants Exposed to Light. In this subsection, comparisons are made among corresponding portions (apical with apical, middle with middle, and basal with basal) of coleoptiles given different treatments after marking. Table I reveals 2 important features of our results with the effects of GA applied at the beginning of red light exposure of dark-grown plants: (a) GA promotes coleoptile elongation irrespective of whether red light promotes elongation or reduces elongation, and (b) within any portion of the coleoptile, the exposures to red light which affect elongation have little or no effect on GA sensitivity. Table I also shows similar results concerning GA sensitivity of dark-grown plants treated with blue and white light. GA promotes elongation both in portions where blue or white light promote elongation and in portions where blue or white light inhibit elongation. With the blue light of 5500 ergs $cm^{-2}sec^{-1}$ intensity and with this high intensity white light, however, there is a tendency for increasing exposures to increase the relative GA effect.

GA Sensitivity in Light-Grown Plants. To complement the studies described on GA sensitivity of dark-grown plants, the GA sensitivity of light-grown plants was also studied (table IV). The re-

Table IV

Elongation and Relative GA Effect in Light-grown Coleoptiles

Light treatment	Intensity	Age of plants when marked	Mean length of coleoptiles when marked	Increase in length of water controls*	Relative GA effect*	Mean length of coleoptiles at maturity
	(ergs cm^{-2} sec^{-1})	(hr)	(cm)	(%)		(cm)
None	...	72	1.5	175	1.17	5.6
Red fluorescent**	1800	64	1.5	157	1.16	4.9
Blue fluorescent**	1650	68	1.5	143	1.13	4.4
Warm-white fluorescent**	7200	72	1.5	107	1.07	3.5
White fluorescent + incandescent***	33,900	64	1.3	86	1.14	2.5

* During 24 hour period after marking and beginning of exposure to GA.
** Continuous illumination.
*** 16 hour photoperiod.

sults in table IV, in contrast to those in table I, refer to plants in which the coleoptiles were not comparable at the time of treatment with GA, since the prior light conditions were different. The data do suggest, however, that GA sensitivity in all light-grown plants is no greater than in dark controls. This seems to contrast with the results obtained after the relatively short (i.e., less than 1 day) exposures to 5500 ergs $cm^{-2}sec^{-1}$ blue or 33,900 ergs cm^{-2} sec^{-1} white light given to dark-grown plants.

GA Sensitivity in Different Portions of the Same Coleoptile. In this subsection comparisons are made among the apical, middle, and basal portions within coleoptiles given the same treatment throughout the experiment. The 4 sets of dark controls in the experiments presented in table I indicate that in the same dark-grown coleoptile, different portions, which elongate to different extents, do not have significantly different relative GA effects. Similar results are obtained for light-grown plants given any 1 of 4 different light regimes (table V). As shown in table I, the relative GA effect is also the same in different portions of the same dark-grown coleoptile exposed to red light, even though the different portions elongate to very different extents. There were no instances in which GA sensitivity appeared to be positively correlated with the extent of elongation within different portions of the same coleoptile.

GA Sensitivity and Age. The relative GA effect during 24 hours after treatment of dark-grown coleoptiles of different age-size groups is presented in figure 3. There seems to be no general correlation between GA sensitivity and coleoptile age. It is especially clear that younger coleoptiles are not more sensitive to GA than older ones.

Discussion

Dual Effects of Light on Dark-Grown Plants. It is known that illumination of dark-grown plants in some instances increases and in some instances decreases elongation. Our results demonstrate that illumination of dark-grown plants with red, blue, or white light can simultaneously increase and decrease elongation in different portions of the same organ.

Table V

Elongation and Relative GA Effect in Different Portions of Light-grown Coleoptiles

Data taken from same coleoptiles represented in table IV.

Light treatment	Basal portion*		Middle portion*		Apical portion*	
	Increase in length of water controls	Relative GA effect	Increase in length of water controls	Relative GA effect	Increase in length of water controls	Relative GA effect
	(%)		(%)		(%)	
Red fluorescent	167	1.14	203	1.18	100	1.16
Blue fluorescent	131	1.10	215	1.14	87	1.14
Warm-white fluorescent	104	1.12	169	1.04	58	1.05
White fluorescent + incandescent	124	1.15	79	1.13	19	1.11

* Because of non-uniform elongation in different portions of the same coleoptile and because light treatment itself alters growth pattern, similarly labeled portions of coleoptiles grown under the different light conditions do not correspond exactly.

These results seem most easily interpreted by a theory very similar to that advanced by Thomson (28) to explain her results on the time-course of over-all elongation of illuminated and dark-grown oat coleoptiles. By this interpretation there are 2 results of light given to our dark-grown coleoptiles: (a) stimulation of elongation in relatively immature tissues, and (b) acceleration of differentiation in less immature tissues. Whereas (a) tends to increase coleoptile length in immature portions of the coleoptile, (b) tends to reduce coleoptile length due to an earlier cessation of growth in portions nearing maturity. Thomson has developed the suggestion that a light-induced inhibition of elongation ". . . can be looked upon as a stimulation of the maturing process rather than an inhibition of enlargement" (28). We do not suggest that our results necessarily prove her theory that light affects elongation by hastening the transition from one phase to another in a postulated ". . . sequence of cell division, cell enlargement, and cell maturation or differentiation" (29). In our experiments all light treatments given to dark-grown plants exaggerated the change in growth pattern that occurs in dark-grown plants that received no light. Since apical portions of dark-grown coleoptiles are the last to cease elongating, the tendency of light to promote elongation, (a), is not obscured by light-acceleration of maturation, (b). In middle portions the tendency of light to promote elongation, (a), is approximately offset by the acceleration of maturation, (b); elongation of middle portions is thus relatively little affected by light. In the basal portions, which are the first to cease elongating, acceleration of maturation by light, (b), gives little opportunity for light to stimulate elongation, (a), and thereby results in great inhibition of elongation. Each of these 2 light effects, (a) and (b), appears to be controlled by the well-known red, far-red pigment system, since both the red-light-induced stimulation of elongation of apical portions and the red-light-induced inhibition of basal portions are reversed by far-red radiation. These results are consistent with recent findings of Fujii (6) and of Thomson (29). Our findings with coleoptiles illustrate that the different types of response to red light are not determined by age per se, but by the closeness of the tissues to maturity at the time of illumination.

Comparison of Effects of Red and Blue Light on Dark-Grown Plants. The effects of blue and red light on coleoptiles of dark-grown plants are remarkably similar in a number of respects: elongation of the apical portion is increased; elongation of the basal portion is decreased; and in each case the effect of blue or red light is reciprocally reversible with the effect of far-red radiation. These results are consistent with those of Bertsch (2) who found far-red reversal of effects of uncontaminated blue light given to stem sections cut from dark-grown peas. Other blue photomorphogenic effects have been variously interpreted (14, 19). For relatively long exposures, blue light produces less elongation in all portions of the dark-grown coleoptile than red light of comparable intensity (table I). Thus, despite the similarities, these red and blue light effects should not be considered identical in all respects. Our results might suggest that blue light has 2 effects on dark-grown wheat coleoptiles: a relatively low-energy one similar or identical to that of red light, and a higher-energy one inhibitory to elongation in all portions of the coleoptile.

Importance of Growth Pattern in Photobiological Studies. Since a given light treatment can have different effects on elongation of different portions of the same organ, it is obvious that the action of light on elongation can be described adequately only when changes in pattern, as well as changes in over-all extent of elongation, are considered. If only entire coleoptile length had been measured, one might have come to the erroneous conclusion that the red light in the experiment in table I had no effect on elongation. The 2 very striking effects, promotion of elongation in apical and inhibition in basal portions, are evident only when the pattern of elongation is also considered.

Role of Cell Division in Photomorphogenesis. The many effects of light on elongation of dark-grown coleoptiles reported here are caused by exposures given after cell division has ceased in the coleoptiles. Similar findings are the absence of cell division in red-light-induced opening of the etiolated bean hypocotyl (16) and opening of the lettuce plumular hook (21) and the nonessentiality of cell division for stimulation of germination of photoblastic lettuce seed (9). These studies showing effectiveness of red and far-red light on growth without cell division complement studies showing ineffectiveness of red and far-red light on cell division without growth (10). This supports the suggestion that many effects of light on cell division are consequences, and not causes, of initial actions on expansion (10). According to this point of view, although cell division in many instances is necessary for the structural expression of photomorphogenesis, cell division plays no immediate role in the mechanism(s) by which the photoreaction regulates development. Such a point of view is consistent with recent findings concerning the roles of cell division in morphogenesis (8).

Growth Pattern of Light-Grown Coleoptiles. As shown in figure 2, the growth pattern of light-grown coleoptiles approaching maturity seems the opposite of the growth pattern of dark-grown coleoptiles approaching maturity. It remains for future studies to determine whether there is such a fundamental difference in pattern throughout the entire period of coleoptile growth or only as the coleoptiles approach maturity. It should be emphasized that, compared to controls that receive no light, the manner in which light given as several consecutive 16-hour days beginning with sowing alters growth pattern seems to be the opposite of the manner in

which short exposure of dark-grown plants with light of the same quality and intensity alters growth pattern (table I and fig 2).

Wuhrmann-Meyer and Wuhrmann-Meyer (34) found deposition of cellulose in secondary cell walls in basal earlier than in apical portions of dark-grown, but in apical earlier than in basal portions of light-grown coleoptiles. Thus, in comparing light-grown and dark-grown plants, there are similarities between effects of light on maturation by the anatomic criterion of cell-wall thickening in oat coleoptiles (34) and the effects of light on maturation by the physiological criterion of cessation of elongation in wheat coleoptiles (fig 2). This parallel is consistent with the general correlation between light-induced inhibition of growth and cell-wall thickening (7, 26).

GA Sensitivity and Endogenous Growth: The generalization that GA is more effective in young, rapidly growing than in older, more slowly growing tissues probably arose from considering absolute, rather than relative, increases in length resulting from GA treatment (see ref 33). In the special case in which the initial lengths of the GA-treated and water control material are equal, the relative GA effect, defined under Materials and Methods, reduces to: (mm increase in length in GA) per (mm increase in length of water control). Perhaps this last consideration may make it easier to see that the transformation of absolute differences in length of GA-treated and water-control material into relative GA effect is tantamount to correcting the elongation in GA for the elongation of the water controls. In the more general case in which initial lengths of GA-treated and water-control material are unequal at the time of first exposure to GA, the relative GA effect thus represents the elongation of GA-treated material corrected both for elongation of water controls and for any inequality in initial lengths. In studies of this type, plant physiologists in general do correct for water controls and for inequalities in length of starting material. The essential difference between the usual treatment of data and our treatment here is in the manner in which the corrections are made. The use of ratios, both in relating final length to initial length and in relating elongation of GA-treated to water-control material, takes into account the principle that growth is ". . . multiplicative in style, and not accretionary or additive" (18). Our conclusion, that GA sensitivity is not dependent upon endogenous growth rate, thus does not arise from studies with exceptional biological material, but rather from a different manner of interpreting data. Thus, for example, the data of Purves and Hillman (fig 4 of ref 22) also demonstrate that the relative GA effect is independent of endogenous growth rate.

That relative GA effect is not positively correlated with growth rate suggests that the processes underlying gibberellin response are not necessarily more effective in more rapidly growing tissues. Thus we believe that the distinction between absolute and relative formulations of growth data is of more than purely semantic interest. [The advisability of considering the percentage increase in length in GA-treated material relative to the percentage increase in length of water controls has been discussed previously with reference to another aspect of gibberellin action (11).]

Light Does Not Affect Elongation by Regulating Endogenous Gibberellin Levels. It has been suggested that in some systems the mechanism by which light influences elongation is the regulation of endogenous gibberellin levels (17). Red, blue, or white light does not regulate elongation of dark-grown plants by regulating endogenous gibberellin levels in this system because in the same organ GA (a) mimics light, in stimulating elongation of apical portions and (b) acts in apparent opposition to light, in stimulating elongation of basal portions. The finding that there is less elongation but not greater GA sensitivity in light-grown than in dark-grown coleoptiles (table IV) suggests that, in this instance also, the effects of light on elongation can not be attributed simply to differences in endogenous gibberellin levels. The hypothesis that light reduces elongation by lowering endogenous gibberellin levels is not, however, disproved as conclusively for light-grown plants as for dark-grown plants.

Independence of GA and Red Light Effects on Dark-Grown Plants. Illumination of dark-grown plants with red light in our experiments did not alter the relative GA effect even though the light simultaneously increased greatly elongation of apical and decreased greatly elongation of basal portions of the same coleoptile. It is conceivable that red light of higher energy than that used in these experiments might alter GA sensitivity, perhaps as in coleoptiles exposed to high-energy blue and white light (table I). Our results nevertheless demonstrate clearly that striking photomorphogenic effects on elongation, both stimulatory and inhibitory, can occur without change in GA sensitivity. Instead of considering the relative GA effect as influenced by red light, we might just as readily have considered the relative red effect (i.e., the ratio of the percentage increase in length of red light treated to the percentage increase in length of dark-control material) as affected by GA treatment. It can be shown that if the relative GA effect is not altered by red light, then the relative red effect is not altered by GA and vice versa[4]. Thus, in this system the action of red light, whether increasing or decreasing elongation, and the action of GA appear to be independent of each other. From studies of other plant material, similar conclu-

[4] Let the percentage increase in length of water controls in darkness be c; in GA in darkness, g; in water-controls with red light, r; and in GA with red light, t. By definitions, the relative GA effect is g/c in darkness and t/r in red light; and the relative red effect is r/c in absence and t/g in presence of added GA. Since the relative GA effect is not altered by red light, $g/c = t/r$. Therefore, $r/c = t/g$. Q.E.D. Conversely, $r/c = t/g$ implies that $g/c = t/r$.

sions have been reached (3, 5, 15). Recently, Mohr and Appuhn (20) have concluded that in mustard seedlings "The relative inhibitory influence of red light on hypocotyl lengthening via the phytochrome system is about the same in seedlings saturated with externally applied gibberellin A_3 and in seedlings without gibberellin A_3 treatment". One need assume only that the initial length of the mustard hypocotyl is negligible (see figs 2 and 3 ref 20) to show that Mohr and Appuhn's "Hemmung durch Hellrot" expressed as "relativ (%)" (see table 2 ref 20) equals $1 - x$, where x is the relative red effect. Thus (a) independence from GA treatment of their "Hemmung durch Hellrot" expressed as "relativ (%)" would imply (b) independence from GA treatment of the relative red effect and vice versa. Furthermore, both (a) and (b) imply, and are implied by, independence from red light exposure of the relative GA effect (see footnote 4).

Summary

As dark-grown wheat coleoptiles approach maturity, elongation ceases first in basal and last in apical portions. Illumination of dark-grown coleoptiles with red, blue, or white light increases elongation of apical and decreases elongation of basal portions. These light treatments thus exaggerate the growth pattern of dark-grown coleoptiles approaching maturity. These results suggest that there are 2 effects of light on dark-grown wheat coleoptiles: (a) stimulation of elongation in relatively immature tissues, and (b) acceleration of differentiation in less immature tissues. Reciprocal photoreversibility with far-red radiation was established for both the promotion of elongation of apical and the inhibition of basal portions by red light and also for both the promotion of elongation of apical and inhibition of basal portions by blue light. Since all the light treatments given to dark-grown plants were given after cell division had ceased in the coleoptiles, the results demonstrate the nonessentiality of cell division for these photomorphogenic effects.

In light-grown coleoptiles elongation ceases first in apical and last in basal portions. Thus, with reference to controls that receive no light, the light which light-grown plants received decreases the ratio of apical to basal elongation, in contrast to the light given to dark-grown plants, which increases this ratio.

Gibberellin sensitivity, measured as percentage increase in length of gibberellic acid-treated material relative to water controls, does not decrease with increasing age of dark-grown wheat coleoptiles. Although in the same time interval different portions of the same coleoptile elongate to different extents, gibberellin sensitivity is not positively correlated with elongation in different portions of the same coleoptile. Gibberellin sensitivity is thus not greater in young, rapidly growing tissues than in older, more slowly growing tissues.

Although illumination of dark-grown plants with red, blue, or white light promotes elongation of apical and inhibits elongation of basal portions of the coleoptile, gibberellic acid promotes elongation of all portions. Thus the effects of these light treatments on elongation can not be attributed to the regulation of endogenous gibberellin levels. Gibberellin sensitivity in all portions of the dark-grown coleoptile was unaffected by red light that greatly stimulated elongation of apical and greatly inhibited elongation of basal portions. Thus in dark-grown coleoptiles the action of red light, whether increasing elongation or decreasing elongation, and the action of gibberellic acid appear to be independent of each other.

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