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II. INHIBITION OF MESOCOTYL ELONGATION IN VARIOUS GRASSES BY RED AND BY VIOLET LIGHT[1]

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INTRODUCTION

Inasmuch as close similarity between the action spectrum for a photobiological reaction and the absorption spectrum of the photoreceptor may ordinarily be expected, knowledge of the action curve may be of considerable value in elucidating the mechanism of the reaction.

The provisional action spectrum previously reported (Weintraub and McAlister, 1942) for inhibition of elongation of the oat mesocotyl by continuous illumination at low intensities showed a single peak at approximately 6600 A. and a suggested second maximum at somewhat shorter wave length. Additional data have been obtained from experiments with monochromatic light (4358 and 6234 A. mercury lines and 6678 A. helium line) which show clearly this second band and also a third, much weaker band at the extreme long-wave limit of the visible spectrum. The modified curve is shown in figure 1.[2] The finding of much greater effectiveness by red than by violet light is in agreement with all prior studies on *Avena* (duBuy and Nuernbergk, 1929; Johnston, 1937; Avery, Burkholder and Creighton, 1937, 1938; Goodwin, 1941).

Experiments with *Zea mays,* however, led Flint (1944) to directly opposite conclusions, namely, that elongation of the mesocotyl was retarded by blue but unaffected by red light, and he suggested that different species of grasses might exhibit diverse action spectra for this reaction. Such divergent behavior would imply the existence either of fundamentally different mechanisms of light perception for the

[1] Part I appeared in Smithsonian Miscellaneous Collections, vol. 101, No. 17, June 24, 1942.

[2] Further experiments, which are in progress, indicate the presence of a fourth, relatively weak band in the green, which has not been shown in figure 1.

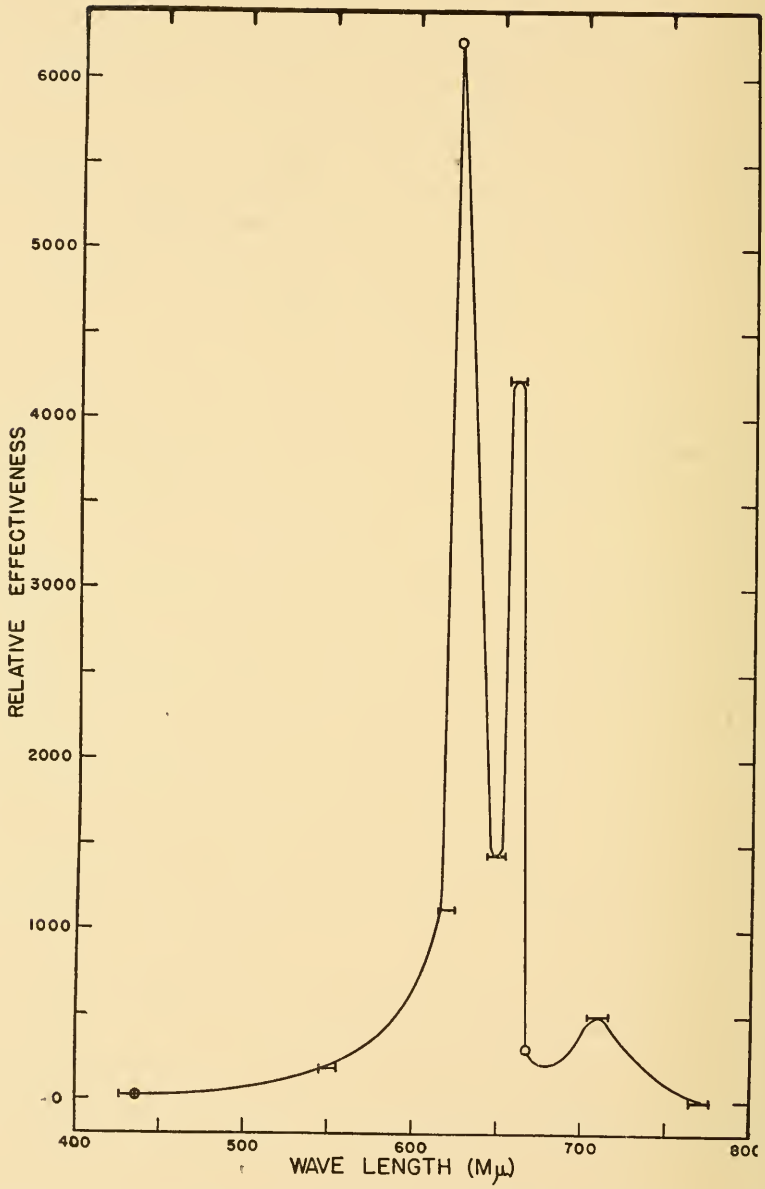

FIG. 1.—Action spectrum for inhibition of *Avena* mesocotyl by light of low intensity. Horizontal bars indicate positions of bands isolated by double monochromator. Points represent monochromatic lines. Ordinates are proportional to reciprocals of intensities required to produce a given degree of inhibition. Owing to the relatively great differences in effectiveness, the general shape of the curve is not appreciably altered by plotting on a quantum basis.

same end reaction or of some interfering factor, such as preponderance of a masking pigment, in certain species.

Further information being clearly desirable, we have made observations on the relative effectiveness of red and of violet light in suppressing the elongation of the mesocotyls of several species of grasses. Consideration has been given also to certain other factors (temperature, light intensity, and developmental stage of the seedling) which conceivably might influence the action spectrum.

EXPERIMENTATION AND RESULTS

The 6234 A. (red) and 4358 A. (violet) mercury lines were chosen for comparison. The source was a 400-watt General Electric type H-1 glass-enclosed mercury arc. The red line was isolated by a filter composed of 6.7 mm. H. R. Signal Red glass (Corning #2408), 5.0 mm. Dark Shade Aklo glass (#3961), and 6 cm. of water; the violet filter consisted of 6.6 mm. Violet glass (#511), 4.2 mm. Noviol A glass (#038), and 6 cm. of water.

The desired intensities were obtained by adjusting the distance between the arc and plants, and by the use of additional filters made of layers of "black" or green Cellophane sandwiched between sheets of glass; the transmissions of these filters were determined with a General Electric recording spectrophotometer by H. J. Keegan, of the National Bureau of Standards.

The intensities of the radiation incident on the seeds were measured, at the highest intensities, with a vacuum thermocouple in combination with a Leeds and Northrup type HS galvanometer which had been calibrated against a National Bureau of Standards carbon filament standard of radiation. At lower intensities, for which this instrument was not sufficiently sensitive, a Photovolt photoelectric photometer was used; this was calibrated against the thermocouple for individual mercury lines. No instrument of sufficient sensitivity was available for direct measurement of the lowest intensities studied; these were calculated from the transmissions of the Cellophane filters used as light screens.

In some experiments the "seeds" were planted individually on slants of 1.0 or 1.5 percent agar in tap water contained in test tubes; in others, they were planted on porous stone wicks which had been wrapped in filter paper and partially immersed in water. Glumes were removed from *Avena* and *Oryza* before planting. The plants were grown in a controlled-temperature room in galvanized iron boxes which admitted no radiation except that passing through the

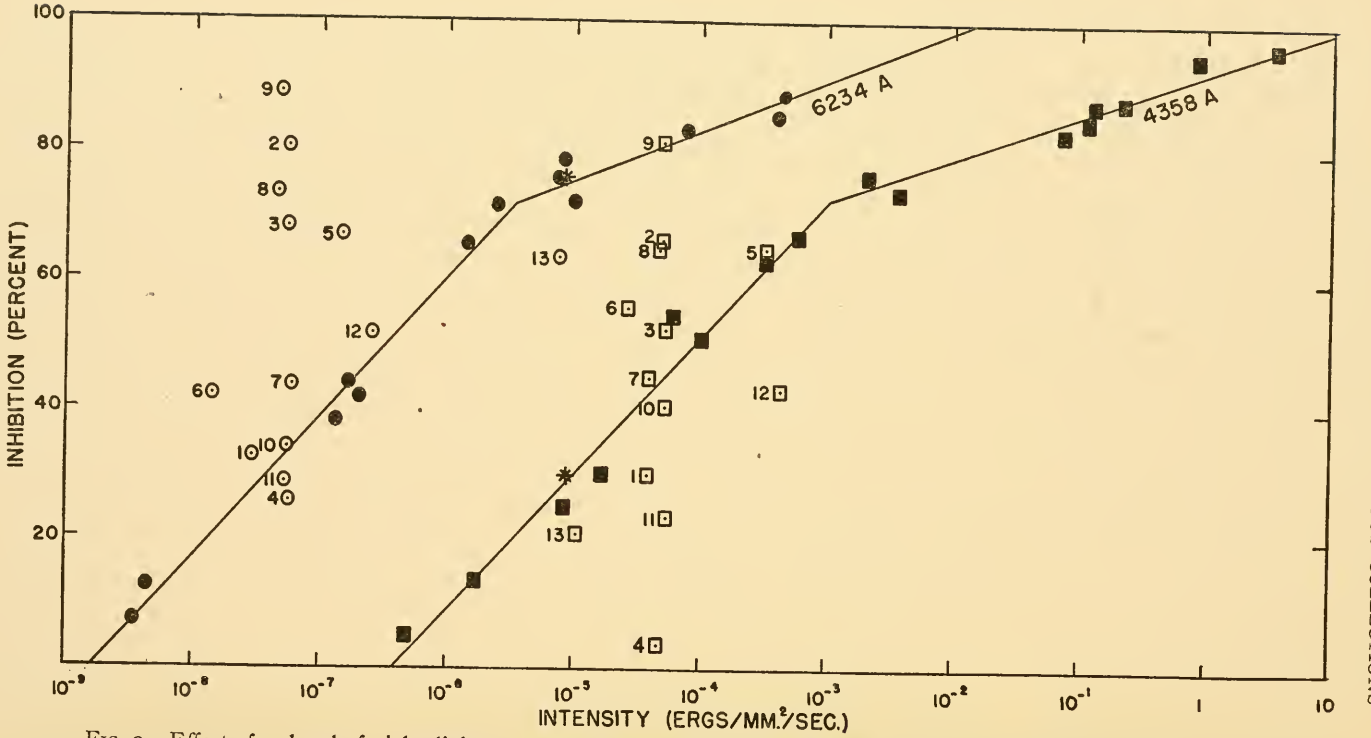

FIG. 2.—Effect of red and of violet light on mesocotyl growth in various grasses. Circles, illumination by 6234 A.; squares, illumination by 4358 A.

1, *Aeluropus littoralis;* 2, *Festuca elatior;* 3, *Festuca ovina;* 4, *Phleum pratense;* 5, *Buchloë dactyloides;* 6, *Chloris gayana;* 7, *Phalaris arundinacea;* 8, *Phalaris tuberosa;* 9, *Oryza sativa,* var. Tajai-77; 10, *Panicum virgatum;* 11, *Sorghum vulgare,* var. Colby Milo; 12, *Zea mays,* var. Ioana; 13, *Zea mays,* var. Funk's 176A.

Curves, *Avena sativa,* var. Markton (solid points, 27° C.; stars, 17.5° C.).

TABLE 1.—*Inhibition of mesocotyl elongation in several species of grasses by continuous exposure to red and to violet light*

No.	Species and tribe	Temp. (° C.)	Culture period (days)	Length mesocotyl in dark (mm.)	4358A. Intensity (ergs/mm.^{2}/sec.)	4358A. Inhibition (%[a])	6234A. Intensity (ergs/mm.^{2}/sec.)	6234A. Inhibition (%[a])	Ratio of intensities $\left(\frac{4358}{6234}\right)$	Ratio of inhibitions $\left(\frac{4358}{6234}\right)$
1	*Aeluropus littoralis* (Gouan) Parl. (Festuceae)	25.3±0.2	14	49.2[b]	$3{,}920.\times10^{-8}$	30.3	2.93×10^{-8}	32.5	1340.	.91
2	*Festuca elatior* L. (Festuceae)	25.3±0.2	14	44.0	5,020.	66.1	5.56	80.5	903.	.82
3	*Festuca ovina* L. (Festuceae)	25.3±0.2	14	8.8	5,120.	54.5	5.49	68.2	932.	.80
4	*Phleum pratense* L. (Agrostideae)	25.3±0.2	14	7.8	4,740.	3.8	5.56	25.6	852.	.15
5	*Buchloë dactyloides* (Nutt.) Engelm. (Chlorideae)	26.0±0.5	13	35.8	32,800.	64.8	14.7	66.8	2230.	.97
6	*Chloris gayana* Kunth (Chlorideae)	26.4±0.1	19	5.2	2,650.	55.8	1.41	42.3	1880.	1.32
7	*Phalaris arundinacea* L. (Phalarideae)	25.3±0.2	14	36.5	3,970.	44.9	5.96	43.6	666.	1.03
8	*Phalaris tuberosa* L. (Phalarideae)	25.3±0.2	14	34.5	4,740.	64.9	4.46	73.3	1060.	.89
9	*Oryza sativa* L., var. Tajai-77 (Oryzeae)	25.3±0.2	14	46.9	5,020.	81.6	4.73	88.9	1060.	.92
10	*Panicum virgatum* L. (Paniceae)	25.3±0.2	14	13.6[b]	5,300.	40.6[b]	5.41	34.0[b]	980.	1.19
11	*Sorghum vulgare* Pers., var. Colby Milo (Andropogoneae)	25.3±0.2	14	130.2	5,580.	23.4	5.27	28.7	1060.	.82
12	*Zea mays* L., var. Ioana (Tripsaceae)	26.0±0.5	13	146.9	44,100.	43.0	25.5	51.7	1730.	.83
13	*Zea mays* L., var. Funk's 176A (Tripsaceae)	17.5±0.5	23	133.8[b]	1,070.	20.9[b]	760.	63.5[b]	1.41	.33

[a] $\%\ \text{inhibition} = 100\ \frac{\text{length dark mesocotyl} - \text{length illuminated mesocotyl}}{\text{length dark mesocotyl}}$.

[b] Leaves not emerged from coleoptiles by end of culture period.

filters in the top. The dark controls were grown in a similar light-tight box situated nearby. Large water surfaces were provided in the growth chambers in order to maintain the humidity at saturation.

For the determination of growth curves, samples were withdrawn at the desired ages; in the light experiments, the arc was extinguished during the few minutes required for removing the samples so that the remainder of the population was not exposed to the unfiltered radiation.

Influence of red and violet light on final mesocotyl length.—The sharp inflection in the intensity-inhibition curves for *Avena* (fig. 2) suggests that two processes are involved in inhibition of mesocotyl elongation by light.[3] The effectiveness of the two spectral lines relative to each other is about the same, however, over the entire intensity range. Owing to the greater slopes of the curves, comparisons can be made more accurately at the lower intensities.

In the present experiments comparison was made between intensities of the two wave lengths which would be expected, from the *Avena* results, to cause approximately equal inhibitions. Table 1 and figure 2 summarize the results obtained with 12 species of grasses representing 8 tribes of Gramineae exclusive of the Aveneae.[4]

With due regard for uncertainty of the magnitude of the actual intensity incident on the plants owing to possible mutual shading by the seedlings, and for the individual variability to be expected among genetically impure populations, it may be concluded that, although there are considerable differences in the absolute intensities required for inhibition, the relative effectiveness of the 6234 and 4358 A. lines is of the same order of magnitude for all the species studied. Insofar as it may be justifiable to extrapolate from two points, this relation indicates that the action spectra are similar for all these species.

Influence of temperature.—The growth rate and ultimate length of the mesocotyl grown in darkness is influenced by temperature, the precise relationship apparently depending upon the species or variety (Hamada, 1931; Weintraub and McAlister, 1942; Baumann, 1911; Silberschmidt, 1928; Flint, 1944; Kempton, 1943; Terao and

[3] For other evidence see Goodwin (1941).

[4] For most of the seeds used we are greatly indebted to M. M. Hoover, M. A. Hein, J. W. Jones, T. R. Stanton, and R. W. Leukel, of the U. S. Department of Agriculture. *Phleum pratense* and Ioana corn were purchased from a commercial seedsman. Funk's 176A corn was obtained through the courtesy of the Funk Bros. Seed Company and presumably is the same as variety Funk's Disease Free used by Flint (1944).

Midusima, 1939; Ocfemia, 1924). Flint implied that temperature might influence also the action spectrum of inhibition, and as the temperature of his experiments (18° C.) was somewhat lower than those of previous investigations it was desirable to test this possibility. The results of experiments with corn and oats at 17-18° C., which are included in table 1 and figure 2, are in agreement with those at the higher temperatures and offer no support for the suggestion of an effect of temperature upon the action curve.

Influence of red and violet light on growth curves.—As the experiments of Flint were terminated before the completion of mesocotyl growth (at least in the dark controls) it became of interest to compare the relative inhibitory effects of red and of violet light at early stages of development. The results of such an experiment with *Avena* are shown in figure 3 and table 2. With the exception of the earliest measurement, which is of relatively low accuracy owing to the short mesocotyls, the ratio of inhibitions caused by the two wave lengths is substantially constant throughout the growth period. The experiments with *Aeluropus littoralis, Panicum virgatum,* and *Zea mays* var. Funk's 176A, which were terminated prior to cessation of mesocotyl growth, also gainsay the likelihood of any appreciable influence of the developmental stage of the seedling upon the action spectrum.

Interrelations among mesocotyl, coleoptile, and leaf.—Flint's interpretation of his results is that blue light decreases the growth rate of the coleoptile but not of the first leaf and hence shortens the time to leaf emergence which he regards as the cause of stoppage of mesocotyl elongation. It is hoped to present our data on the relationships among the various seedling organs in greater detail in a future report, but figures 4 and 5 are included here to show that elongation of the mesocotyl is nearly or quite ended by the time the first leaf emerges through the coleoptile tip. This is true whether the mesocotyl is allowed to complete its development in darkness (fig. 4), or if its growth is terminated abruptly by illumination following an initial dark period (fig. 5), or if the plant is exposed throughout the growth period to light of intensity such as to cause only partial inhibition of the mesocotyl.

These results indicate that termination of mesocotyl elongation is not initiated by the act of leaf emergence per se.

Relation of light inhibition to pigmentation.—As mentioned above it is to be expected that the seedling contains a pigment with absorption spectrum corresponding to the inhibition action spectrum. However, the converse line of reasoning advanced by Flint, namely,

that the action spectrum should resemble the absorption spectrum of the predominant pigment present, is not necessarily valid. While

TABLE 2.—*Inhibition of mesocotyl of* Avena sativa *var. Markton at various ages. Seeds planted on slants of 1.5-percent agar and illuminated continuously by red or violet light*

Age (hrs.)	Length mesocotyl (mm.)			Percent inhibition	
	Dark	6234 A.	4358 A.	6234 A.	4358 A.
48	4.3	3.2	3.7	25.6	14.0
69	27.0	9.4	15.3	65.2	43.4
95	60.4	21.8	31.6	63.8	47.7
140	70.1	24.9	37.3	64.5	46.8

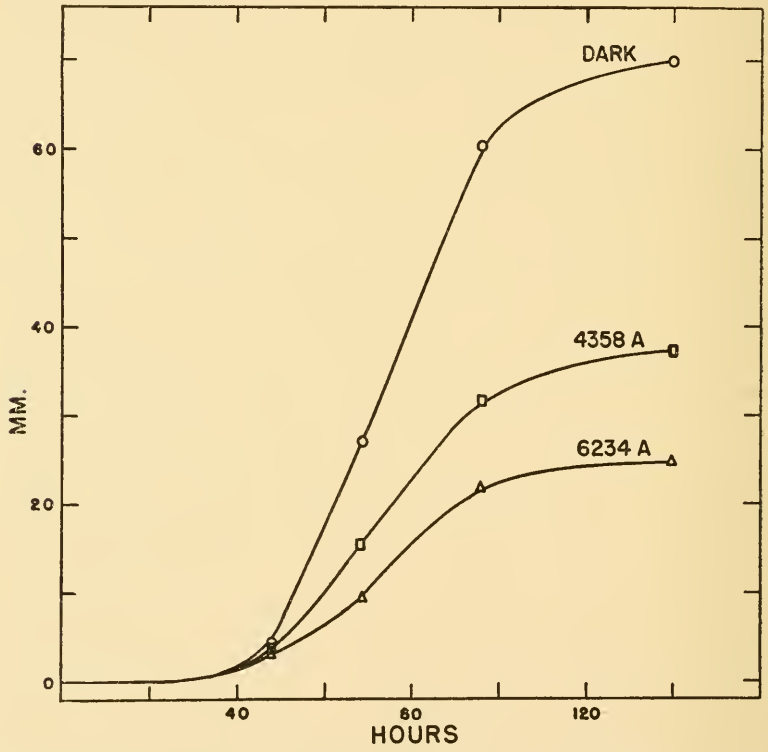

FIG. 3.—Growth curves of *Avena* mesocotyl at 28° C. in darkness, in red light, and in violet light.

carotenoid pigments are present in all the organs of the seedling shoot: coleoptile (Wald and duBuy, 1936; Brunner, 1936; Bünning, 1937a, b), mesocotyl (Weintraub, unpublished data), and leaf, the preponderance of these pigments is not evidence that they function

as photoreceptors for the mesocotyl-inhibition process. Furthermore, the region of greatest photosensitivity for mesocotyl inhibition is in the vicinity of the coleoptilar node (Araki and Hamada, 1937; Goodwin, 1941, Weintraub, unpublished) although the concentration of carotenoids is much greater in the apical portion of the coleoptile (Bünning, 1937a, b). A similar distribution has been reported for chlorophyll in the illuminated coleoptile (Clark, 1937). This is not to deny that the coleoptile apex is involved in the

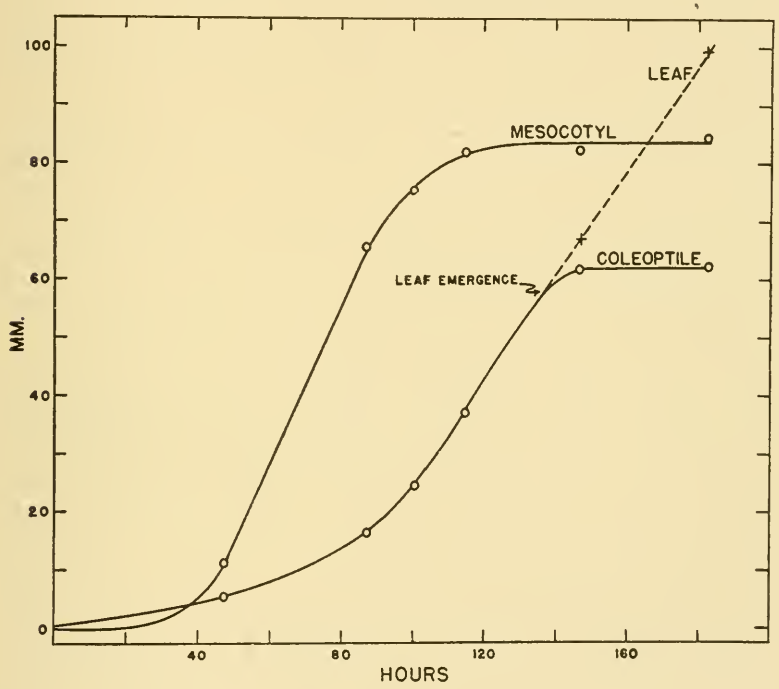

FIG. 4.—Growth curves of *Avena* mesocotyl, coleoptile, and leaf in darkness at approximately 25° C.

growth reactions of the mesocotyl for there is indeed evidence that such is the case. Participation of carotenoids in these reactions does not appear to have been demonstrated as yet, however.

On the other hand, etiolated oat and maize seedlings do contain small amounts of pigments with absorption bands in the orange and red region of the spectrum (Weintraub and McAlister, 1942) where we have found the greatest sensitivitiy to light; the quantitative distribution of these pigments in the various organs has not yet been studied. The nature of the pigments is thus far unknown but from

the available information of the absorption spectra it may be hazarded that they belong to the class of porphyrins and possibly are related to chlorophyll genetically as well as structurally.

It was thought that pertinent information might be obtained from the mesocotyl response of seedlings deficient in the ability to syn-

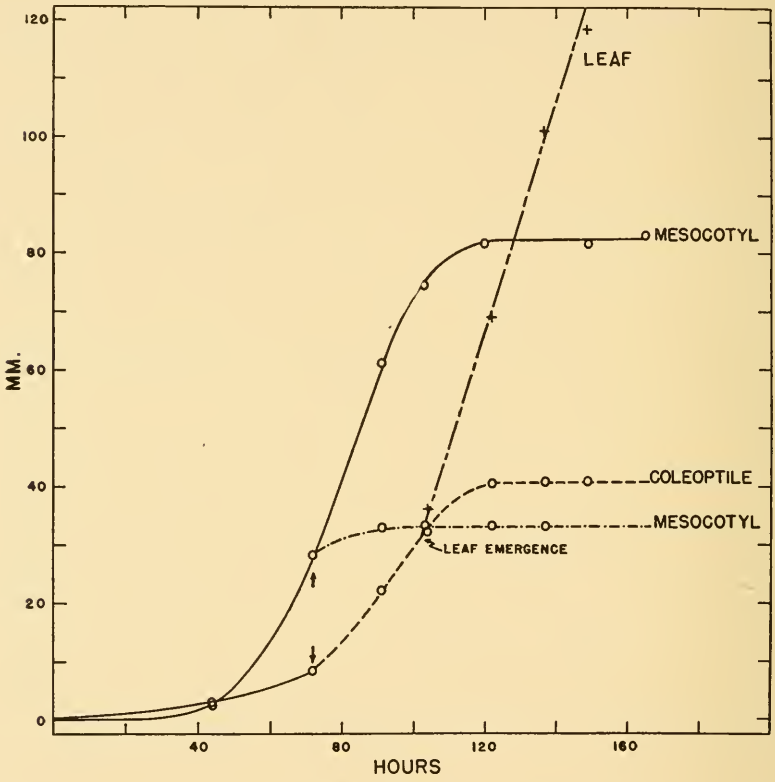

FIG. 5.—Growth curves of *Avena* mesocotyl, coleoptile, and leaf. All plants in darkness during first 72 hours, after which a portion of the population (broken curves) was illuminated by a tungsten filament lamp through a Wratten Safelight Series O filter ($\lambda > 575 m\mu$). General Electric light meter reading = approximately 2 foot-candles. Intensity in visible estimated to be of order of 3 ergs/mm.^{2}/sec.

thesize chlorophyll. Maize seedlings[5] of the strain Sh 303(4)$_{(x)}$ were grown at 26-27° C. under exposure to low intensities of violet light for 10 days and the degree of mesocotyl inhibition determined. The plants were then exposed for several days to sunlight so that

[5] Seeds kindly furnished by the Maize Genetics Cooperation, Department of Plant Breeding, Cornell University.

the chorophyll-deficient plants might be distinguished. This strain is reported to produce plants in the proportions 75 percent normal (containing both chlorophyll and carotenoids in the leaves) to 18.75 percent white (neither chlorophyll nor carotenoids) to 6.25 percent yellow (carotenoids only). Under the conditions of the experiment, however, we were unable to identify all these types with certainty. The green, normal plants could be clearly recognized but the others ranged from very pale yellow through deep yellow to a greenish yellow. In addition a few plants with very nonuniform pigmentation were classified as doubtful.

The results of the experiment are given in table 3. The mesocotyls of the dark controls showed no significant differences in length among the various classes of segregates. In view of the small number of

TABLE 3.—*Inhibition of mesocotyls of normal and chlorophyll-deficient maize seedlings by λ4358A. Average mesocotyl length of dark controls of all classes (23 plants) = 73.6 mm.*

Classification according to pigmentation of leaves after exposure to daylight	Intensity = 0.00037 ergs/mm.²/sec.			Intensity = 0.013 ergs/mm.²/sec.		
	No. plants	Percent of population	Percent inhibition of mesocotyl	No. plants	Percent of population	Percent inhibition of mesocotyl
Green	20	77	28.0	19	70	44.4
Pale yellow, yellow, and greenish-yellow	5	19	7.3	7	26	39.0
Doubtful	1	4	15.8	1	4	44.3

seeds available and the uncertainty of classification, relatively little significance can be attached to this experiment. However, the potentially chlorophyll-deficient seedlings tend to show less inhibition than the normal. This is the result to be expected if the photoreceptor were also deficient in such plants.

Inhibitions at higher intensities.—The action curve for oats shown in figure 1 is derived from experiments at low intensities (i. e., those which result in inhibitions less than 75 percent). Data for intensities causing greater inhibition, although available for only a few wave lengths, do not yield any evidence that the action spectrum for this species is markedly influenced by the intensity. Nevertheless there exists the possibility that such an influence might be found in maize.

In testing this possibility it was attempted to duplicate closely the technique employed by Flint. "Red" and "blue" light was obtained by filtering the radiation from a Daylight Mazda lamp through red or

blue Cellophane, respectively. The intensity in each case was adjusted to give a reading of 3 foot-candles on a Weston Illumination Meter. Seeds of *Zea mays* var. Funk's 176A were planted on agar slants and allowed to develop for 21 days at 18±0.5° C., a period sufficient for completion of mesocotyl growth in the illuminated seedlings and in most of the dark controls. The results, presented in table 4, show approximately equal inhibitions by the two treatments.

Although this finding, at first glance, might seem in disagreement with the results obtained with monochromatic light it should be emphasized that the two experiments cannot be directly compared. The sample of blue Cellophane employed exhibited a rather high transmission in the red region of the spectrum, while the tungsten filament source is richer in the red than in the blue. An additional complication is introduced by the spectral response of the photocell which extends to about 9000 A.; although the cell sensitivity is rela-

TABLE 4.—*Inhibition of corn mesocotyls by light transmitted by red and blue Cellophane. Intensity, 3 foot-candles. Temperature, 18 ± 0.5° C.*

	Dark	Red	Blue
Number of seedlings	37	51	55
Average length of mesocotyl	169.3 mm.	28.3 mm.	35.3 mm.
Inhibition	—	83.3%	79.2%

tively low in the infrared, the lamp emission is very high in this region where both colors of Cellophane have high transmission. Consequently the larger portion of the incident radiation in both cases consists of wave lengths which are relatively ineffective for mesocotyl inhibition.

From the transmission curves of the Cellophanes (determined with a Beckman spectrophotometer), the energy distribution of the lamp (Taylor, 1943), and the photocell sensitivity (Weston Electric Instrument Corporation spectral response curve for the photronic cell), it was calculated that, in the region most effective for mesocotyl inhibition (6200-6600 A.), the energy transmitted by the blue Cellophane is somewhat more than one-fourth as great as that transmitted by the red Cellophane. Hence, owing to the flatness of the intensity-inhibition curve at higher intensities, the mesocotyls illuminated through the blue Cellophane would be expected to show nearly as much inhibition as under the red Cellophane, as was indeed observed.

DISCUSSION

In contrast to Markton oats, maize seeds of the varieties employed show very marked variability in rate of germination; at temperatures as low as 18°, at which germination is relatively slow, the nonuniformity is accentuated. For this reason there is considerable uncertainty in average values for mesocotyl length which are derived from small population samples prior to completion of elongation. We believe that this circumstance accounts for the apparent discrepancy between the results of Flint and those of other investigators, as his estimates of inhibition were made by comparison with dark controls which had made only a small fraction of their ultimate growth. The longest average length recorded by Flint for mesocotyls developed in darkness at 18° is 59 mm., and although it is not specified whether growth had ended in these plants, if they are compared with the illuminated mesocotyls in the same experiment, the inhibition by red light at 3 foot-candles is 72 percent, and by blue light 84 percent. Hence Flint's experimental data appear to be in fair agreement with our own (table 4).

SUMMARY

Comparison has been made of the relative effectiveness of monochromatic red (6234 A.) and violet (4358 A.) light in suppressing mesocotyl development in 12 species of grasses representing 8 tribes of the Gramineae. The intensity required to effect a given degree of inhibition is, for all these species, of the order of a thousand times as great for violet as for red light. The uniformity of these responses, which are similar to that of *Avena sativa,* suggests that the action spectrum determined for the latter is applicable to all the species investigated.

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