THE ACCELERATING ACTION OF ILLUMINATION IN RECOVERY OF ARBACIA EGGS FROM EXPOSURE TO ULTRAVIOLET RADIATION

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The recognition that recovery from the effects of ultraviolet radiation may, in some instances at least, be accelerated by exposure to "visible" light would seem to initiate a new era in the study of the effects of ultraviolet radiation on living systems, calling for the revision of ideas, and the repetition of a considerable amount of experimental work. Papers describing this effect in fungi and in bacteria appeared early last year; the first by Kelner (1949 *a*) was followed shortly by one by Dulbecco (1949). The studies described herein were prompted by the appearance of the first of these papers; preliminary reports have appeared elsewhere (Blum *et al.*, 1949 *a*, *b*). Studies paralleling ours in some aspects have been described by Marshak (1949 *a*, *b*).[1]

EXPERIMENTAL

The method used in these studies has already been described in an earlier paper in this journal (Blum and Price, 1950 *a*), in which were shown the continuous nature of the recovery from exposure to ultraviolet radiation, and the existence of a period during which the cell division process is refractory to the effects of this radiation. In the earlier experiments (summer of 1948), the eggs were continuously subjected to light from "fluorescent" lamps used for observation and photography. The first experiments performed during the past summer (1949) showed that this light markedly accelerated recovery after exposure to ultraviolet radiation.

For convenience the light which accelerates recovery will be referred to as "visible"; its spectral character and intensity will be discussed later on. For the moment, it is only necessary to say that no wave lengths longer than 0.50 μ

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[1] There are basic points at which these results seem at variance with ours. This we attribute to the inadequacy of the methods used by Marshak. A critical examination of such methods has been presented by Blum and Price (1950 *a*, *b*).

are included; hence it was possible to observe and to photograph the eggs in effective darkness by interposing a filter which cuts off wave lengths shorter than this limit (*e.g.*, No. 2424 in Fig. 8).

Acceleration of Recovery by Visible Light

Fig. 1 shows the results of an experiment in which the rates of recovery in visible light and in effective darkness are compared. A sample of eggs was exposed to ultraviolet radiation, and then divided into two samples, one being

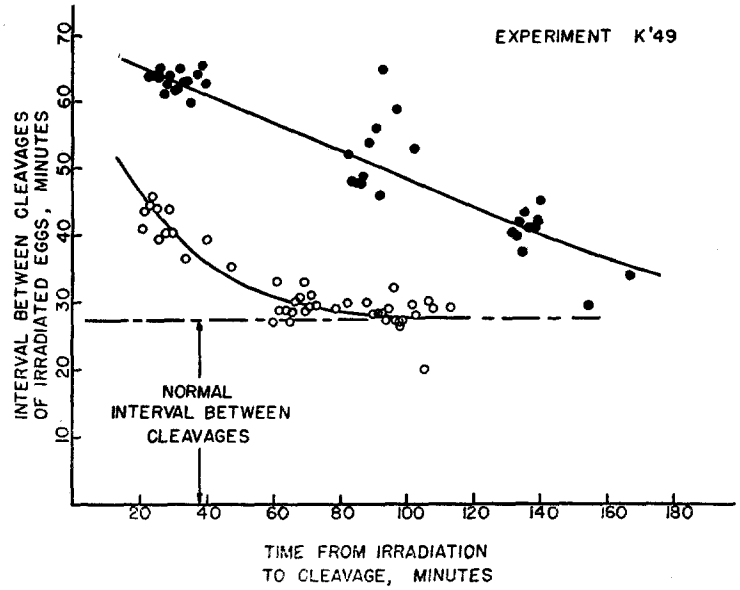

FIG. 1. Recovery of cell division rate after exposure to ultraviolet radiation ($\sim$ 100 ergs per egg of radiation of wave lengths 0.238 μ to 0.313 μ). Black disks, eggs maintained in effective darkness. Open circles, eggs in "visible" light. The points represent cleavage of one or more eggs; second, third, and fourth cleavages are included. Compare with Text-figs. 7 and 8 (Blum and Price (1950 *a*)).

placed in the light, the other in the dark. The results are plotted in the manner used by Blum and Price (1950 *a*). It is clear that the cleavage rate returned more rapidly toward normal in the illuminated eggs than in those maintained in darkness.

The mercury arc used as the source of ultraviolet radiation emits considerable visible light. To reduce this, filter 9863 (Fig. 8) was interposed, which transmits somewhat more of the shorter wave lengths than does that used in the earlier experiments (Blum and Price, 1950 *a*). The eggs were placed at about 50 cm. from the arc, where they received $\sim 1.3 \times 10^4$ ergs per sq. cm. per second of wave lengths 0.238 to 0.313

μ. The total dose of these wave lengths ranged for individual experiments from 50 to 150 ergs per egg. The diameter of these eggs is 74 μ; the dose is calculated as the total amount striking a circular area having this diameter.

The results of a similar experiment are represented in a different way in Fig. 2. Here the percentage of eggs cleaved is plotted against the time after fertilization. Curves so plotted serve to illustrate semiquantitatively the mag-

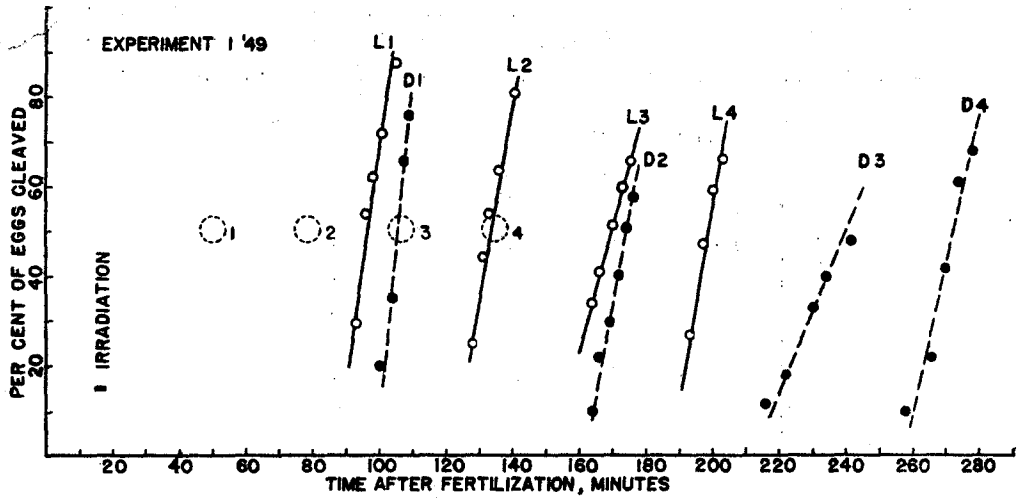

FIG. 2. Recovery of cell division rate after exposure to ultraviolet radiation. Large circles indicate times at which fifty per cent of normal eggs have reached the first, second, third, and fourth cleavage stage. Curves L1, L2, L3, L4, indicate the corresponding cleavages of eggs exposed to ultraviolet radiation and subsequently illuminated with visible light. Curves D1, D2, D3, D4, indicate the corresponding cleavages of ultraviolet-irradiated eggs maintained in effective darkness.

Dosage of ultraviolet radiation $\sim$ 150 ergs per egg of wave lengths 0.238 μ to 0.313 μ.

nitude of the effects studied, although for reasons discussed earlier they are not interpretable in a strictly quantitative manner. Such plotting is convenient, however, and will be used herein for illustrative purposes. For simplicity only the middle portion of each curve is drawn; comparisons may be made at, say, 50 per cent cleavage. The large dotted circles labeled 1, 2, 3, and 4 represent the times of the first four cleavages in a sample of normal eggs. The two sets of curves represent the four cleavages after a dose of ultraviolet radiation was applied; L1, L2, L3, L4, when the eggs were illuminated with visible light; and D1, D2, D3, D4, when they were maintained in effective darkness. Again it is clear that recovery is much slower in the absence of visible light. It is to be noted that the action of the light is apparently progresssive. For example, there is

very little difference in the times of the first cleavages in light and dark; but the difference is greatly increased in the case of the second and third cleavages. By the time the fourth cleavage occurs the rate has returned in both cases to near the normal, that is, the interval between the third and fourth cleavages is about 30 minutes, a normal value at the temperatures of these experiments (see Blum and Price, 1950 *b*).

The recovery of the eggs from the effects of the ultraviolet radiation seems to be complete, this being true whether they are maintained in the dark or in the light. The completeness of recovery is shown by the development of the eggs to the ciliated free swiming blastula stage and eventually into normal

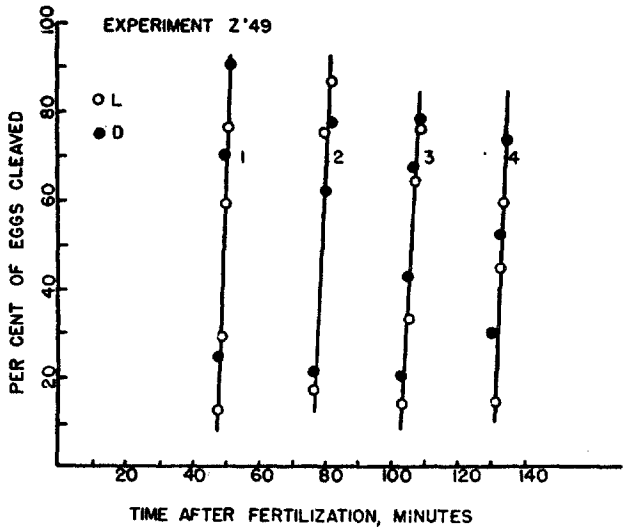

FIG. 3. Absence of effect of visible light on normal fertilized eggs. Open circles, eggs exposed to visible light ($\sim 4.3 \times 10^{-2}$ erg per egg, $\lambda = 0.40\,\mu$ to $0.50\,\mu$). Black disks, eggs in effective darkness.

plutei. Upon reaching the blastula stage the egg, which up to this time has remained at the bottom of the vessel, rises and swims away. Virtually all the fertilized eggs reached this free swimming stage, indicating complete recovery. Thus, in this instance the only apparent effect of visible light is to accelerate the rate of recovery, which would seem to go on just as completely, though more slowly, in darkness.

Visible Radiation Does Not Affect Normal Eggs

Visible radiation does not alter the cleavage rate of cells that have not been exposed to ultraviolet radiation, as is clearly shown by the experiment described in Fig. 3. One sample of eggs was exposed to visible light, the other maintained

in effective darkness; cleavages occurred at the same times in both samples. Such an experiment was carried out in 1948, when the method was first employed, to make sure that the light used for photography had no effect on the experiment; a good example of a control that was not truly a control.

Recovery before Fertilization

When the eggs are irradiated prior to fertilization, recovery under comparable conditions of illumination occurs at about the same rate as when the

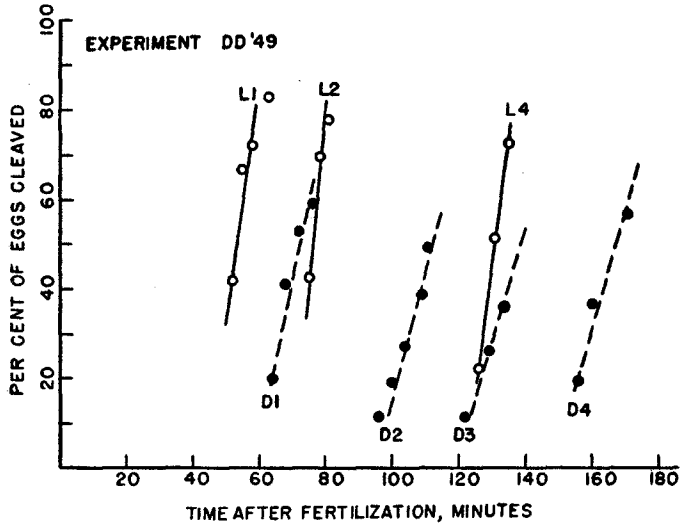

FIG. 4. Effect of visible light on recovery of eggs exposed to ultraviolet radiation 93 minutes before fertilization. Eggs exposed to visible light until fertilization (curves L1, L2, L4—the photographic record failed for the third cleavage in this experiment) underwent cleavage at about the same time as normal eggs, indicating virtually complete recovery. In effective darkness (curves D1, D2, D3, D4) the cleavages are much delayed, indicating that recovery has been much slower than in the light. Both samples were in effective darkness after fertilization.

Dosage of ultraviolet radiation $\sim$ 100 ergs per egg of wave lengths 0.238 μ to 0.313 μ.

radiation is applied after fertilization (Blum and Price, 1950 *a*). Light accelerates the recovery process under these conditions just as it does after fertilization, as is shown by the experiment described in Fig. 4. The eggs were exposed to ultraviolet radiation 1½ hours before fertilization. Immediately afterwards one sample of the eggs was exposed to visible light where it remained until fertilization, after which it was placed in effective darkness. The other sample was maintained throughout in effective darkness. The eggs exposed to visible

light underwent first cleavage at approximately the same time required by normal untreated eggs, indicating that recovery was complete, or nearly so, at the time of fertilization, that is, after 1½ hours' exposure to visible light. The later cleavages also occurred at times expected for normal eggs. The eggs kept in effective darkness, on the other hand, were considerably delayed in first and in subsequent cleavages. This experiment shows that recovery, whether in light or darkness, goes on independently of cell division.

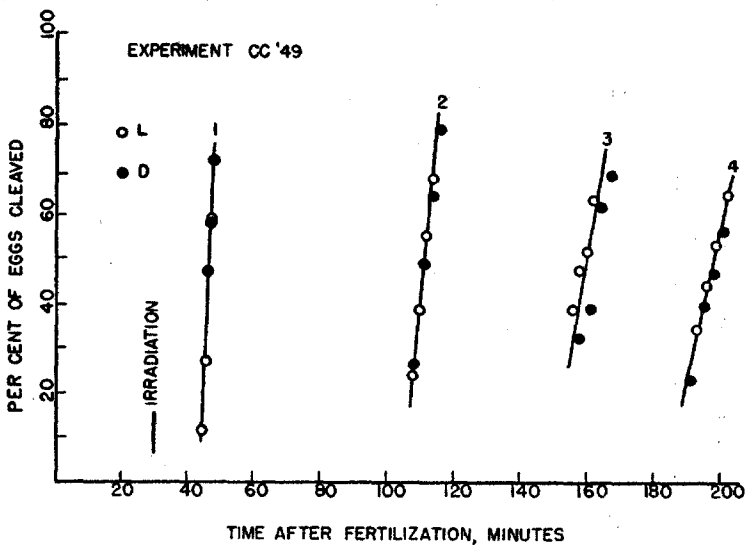

FIG. 5. Effect of illumination with visible light prior to exposure to ultraviolet radiation. Open circles, eggs in visible light for 126 minutes before exposure to ultraviolet radiation (97 minutes before, 29 minutes after fertilization). Black disks, eggs in effective darkness. Both samples in effective darkness after exposure to ultraviolet radiation.

Dosage of ultraviolet radiation $\sim$ 100 ergs per egg of wave lengths 0.238 μ to 0.313 μ.

Preillumination Does Not Affect Recovery

Illumination with visible light prior to the application of ultraviolet radiation does not affect the recovery rate. An experiment demonstrating this is described in Fig. 5. Two samples of eggs were placed, one in light, the other in darkness, for 2 hours, toward the end of which time they were fertilized. They were then exposed to ultraviolet radiation, and both samples placed in effective darkness. In this particular experiment the ultraviolet radiation was applied within the "refractory" stage for the first cleavage, so that this cleavage is not affected. Subsequent cleavages are delayed however, and since the eggs of

both samples go through these cleavages at the same time, it is evident that the preillumination has had no effect on recovery. Other experiments of the same general type failed, likewise, to show any clear cut effect of preillumination; in some of these there was a slight suggestion of acceleration of recovery, but this was always within the limits of experimental error (see Blum and Price, 1950 *b*).

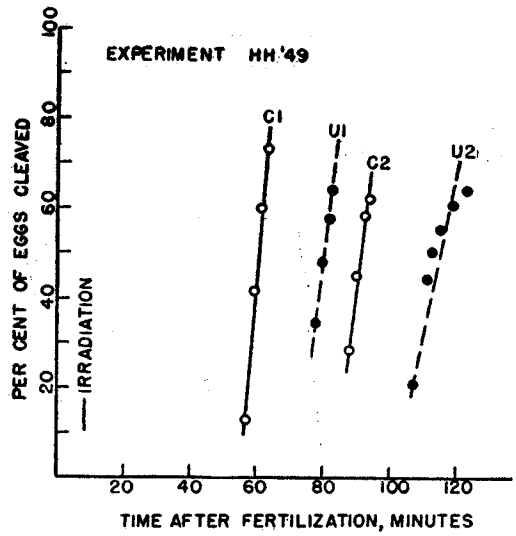

FIG. 6. Effect of ultraviolet radiation on cleavage of "white halves" of *Arbacia* eggs. Curves C1 and C2, first and second cleavages in halves which were not irradiated. Curves U1 and U2, first and second cleavages in halves which were irradiated 8 minutes after fertilization. Both samples illuminated with visible light.

Dosage of ultraviolet radiation $\sim$ 50 ergs per egg of wave lengths 0.238 μ to 0.313 μ.

Recovery in "White Halves"

It is possible by centrifugation at high gravity to separate the eggs into white and red halves (Harvey, 1932, 1940). The red half contains all the echinochrome pigment. The white half contains the nucleus; after fertilization it develops in the same way as the intact egg. Ultraviolet radiation affects the white nucleated halves as it does the whole eggs, as is shown in the experiment represented in Fig. 6. One sample of such halves was irradiated 8 minutes after fertilization, another sample, fertilized but not irradiated, serving as control. Both control and irradiated eggs were illuminated with visible light. The halves which were not irradiated underwent the first and second cleavages at times characteristic of normal eggs. Both first and second cleavages were de-

layed in the irradiated eggs, cleavages beyond the second not having been followed. Fig. 7 describes an experiment in which after exposure to ultraviolet radiation one sample of "white halves" was maintained in the light and another in the dark. Only the first and second cleavages were followed, but it is obvious that the recovery of cleavage rate was much slower in the dark than in the light. Although the white halves appear susceptible to somewhat smaller incident dosages of ultraviolet radiation than the whole eggs, there seems to be no qualitative difference in the behavior of nucleated halves from that of whole eggs. The same is true for the acceleration of recovery by visible light.

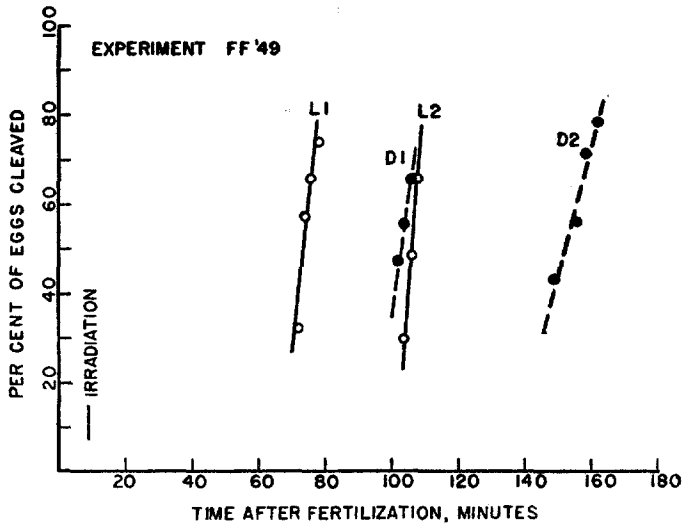

FIG. 7. Acceleration by visible light of recovery in "white halves" after exposure to ultraviolet radiation. L1 and L2, halves subjected to visible light; D1 and D2, halves in effective darkness.

Dosage of ultraviolet radiation $\sim$ 50 ergs per egg of wave lengths 0.238 μ to 0.313 μ.

The Spectral Range for Acceleration of Recovery

Experiments were carried out which locate the spectral range of the radiation that accelerates recovery (referred to above as visible) in the blue, violet, and very near ultraviolet.

Eggs were exposed to ultraviolet radiation after fertilization. Samples of these were then placed in small vessels covered with glass color filters of various known spectral transmissions. In some experiments the vessels were exposed to light from fluorescent lamps, in some to sunlight. Precautions were taken to eliminate stray light that had not passed through the filters, and to maintain all vessels at nearly the same tempera-

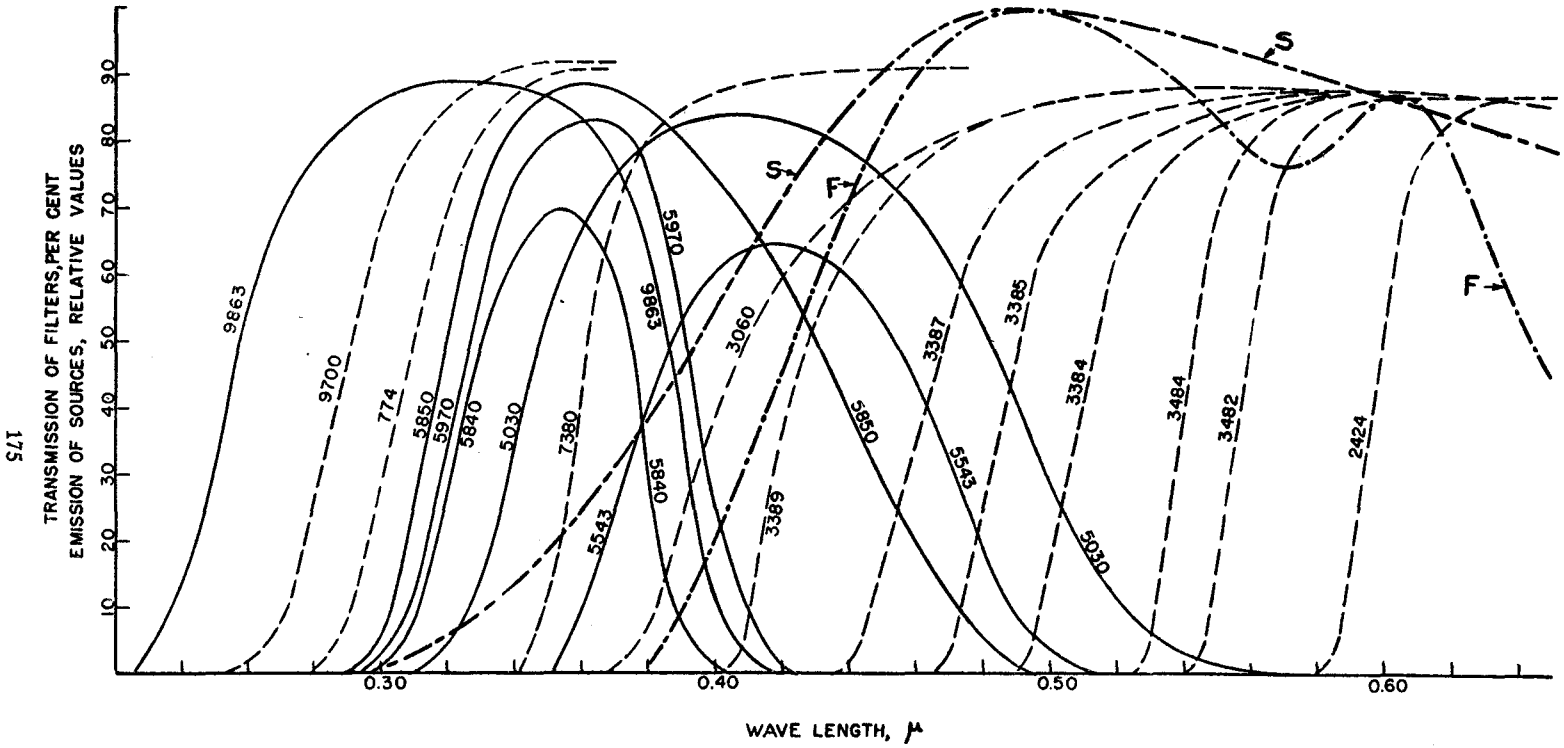

FIG. 8. Spectral emission of sources and transmission of filters used to determine the spectral range which accelerates recovery from ultraviolet radiation.

The "sunlight" and "fluorescent" light curves are brought to a common maximum, and hence the intensities are not comparable (sunlight spectrum after Moon, 1940, that of fluorescent lamp after manufacturer's description).

Transmission of "short wave length cut-off" filters shown as broken lines, "long wave length cut-off" filters as solid lines.

ture by surrounding them with running water. In each experiment one of the vessels was exposed directly without any filter interposed, and one was covered with an opaque screen. At appropriate times, usually between first and second cleavages, samples were removed from all vessels and fixed in order to determine the percentage of eggs cleaved. By comparison of the percentage cleaved under a given filter with the percentage cleaved in the sample maintained in full illumination and that in complete darkness, estimates could be made as to whether the light through the given filter had accelerated recovery. This is a rough measure but is adequate, considering other uncertainties pointed out below. The results are summarized in Fig. 8 and Table I.

TABLE I

Wave Length Range of Light Accelerating Recovery from Exposure to Ultraviolet Radiation

Filter	Wave lengths in μ	Results*						
		"Fluorescent" lamp				Sunlight		
Short wave length cut-offs								
2424	>0.58				−			
3482	>0.54	−			−	−		
3484	>0.52	−				−		
3384	>0.49	−	±	+		−	−	±
3385	>0.46						−	+
3387	>0.44	+	+			+		+
3389	>0.40		+		+	+		
3060	>0.37						+	+
7380	>0.34		+	+		+	+	+
774	>0.28			+				
9700	>0.26						+	+
Long wave length cut-offs								
5030	0.31–0.56			+		+		
5843	0.34–0.51			+		+		
5850	0.29–0.49						+	+
5970	0.30–0.42						+	+
9863	0.23–0.42	−	−			+	−	+
5840	0.30–0.40						+	+

* + indicates accleration of recovery; − indicates no acceleration; ± indicates acclera-tion in one sample not in another.

In the figure are shown the spectral emissions of the two sources used in the experiments—fluorescent light and sunlight—and the transmissions of the filters used. The table indicates which of the filters pass wave lengths that accelerate recovery. Comparison of the table and figure indicates that no wave lengths longer than about 0.50μ are effective. As regards the short wave length

limit, it is seen that all the "long wave length cut-off" filters that transmit wave lengths longer than 0.40μ permit the acceleration of recovery. The "fluorescent" light does not include shorter wave lengths, so the experiment with sunlight must be consulted in estimating the lower wave length limit. In the latter there is indication that wave lengths shorter than 0.40μ are effective. The results are somewhat uncertain, but they indicate that the wave length range extends into the near ultraviolet, but not very far. Tentatively, then, the wave length range for the acceleration of recovery may be set at about 0.30 μ to 0.50μ with the long wave length limit more certain than the short wave length limit. The action spectrum determined by Dulbecco (1950) for reactivation of bacteriophage in the presence of *E. coli* has this range.

These results are admittedly rough and do not give a very exact idea of the action spectrum for the acceleration of recovery from ultraviolet radiation, but it seems unlikely that a more careful analysis would be of great value considering the nature of the material studied. For close matching of absorption spectrum and action spectrum rather ideal conditions are required (*e.g.* see Blum, 1950) which are not met in the present case. A complicating factor is the presence of the pigment, echinochrome, which absorbs in this spectral region (see Ball and Cooper, 1949). When the eggs are split by centrifugation, this pigment remains entirely in the red halves. Since the recovery of white halves is accelerated by light the echinochrome obviously is not the light absorber for that reaction, but behaves as an inner filter with nuisance value in rendering the action spectrum uncertain. An action spectrum obtained with the white halves might give a more accurate picture of the absorption spectrum of whatever material is the light absorber for acceleration of recovery.

Intensity of the Visible Radiation

The source of visible light in the principal experiments was a bank of two 15 watt "fluorescent" lamps, focused upon the eggs by means of a concave mirror in the arrangement described by Blum and Price (1950 *a*). The intensity of this radiation incident upon the eggs was estimated by means of a radiation thermopile placed at a position corresponding to that of the eggs; the values obtained should be correct to better than an order of magnitude. The total radiation from the fluorescent lamp was about 2,000 ergs per sq. cm. per second; the interposition of short-wave cut-off filters which remove the wave lengths not active in producing acceleration reduces this to about one-half, or 1,000 ergs per sq. cm. per second, which is 4.3×10^{-2} ergs per second per egg. This amount of energy would not raise the temperature of the eggs appreciably, when in a chamber adequately cooled by running water as in these experiments. The definite long wave length limit of the action spectrum also indicates that the acceleration of recovery is not due to an increase in temperature; as does the finding that illumination does not affect the rate of cleavage of normal eggs.

DISCUSSION

The spectral range for the acceleration of recovery of the *Arbacia* egg after exposure to ultraviolet radiation is approximately the same as that measured by Dulbecco (1950) for the photoreactivation of *Escherichia coli* bacteriophage under similar conditions ($\sim 0.30\mu$ to 0.50μ). Kelner (1949 *b*) indicates the same long wave length limit for his experiments with *Streptomyces griseus* and with *E. coli*. This apparent agreement of the action spectra, indicates that the same or a similar light absorber is concerned in all three instances, and that the phenomena are basically related. Striking similarity in other regards, which appear on comparing these three papers, bears out this relationship. The demonstration of the phenomenon in forms as widely divergent as the echinoderms, bacteria, and fungi is sufficient to indicate its widespread distribution among living organisms, and no doubt many other instances will be discovered in the animal and plant kingdoms. Although the phenomenon is easily observable in the instances mentioned, it may, however, be difficult or impossible to demonstrate in others (*e.g.*, Blum *et al.* (1949 *a*), and Johnson, Flagler, and Blum (1950)).[2] This may be due in some instances to the difficulty of finding a proper biological criterion for demonstrating the effect, in others to its absence or its small magnitude. The variability in occurrence may account in part for the phenomenon not having been recognized earlier, although the lack of any theoretical reason for suspecting such an effect, and its confusion with other phenomena must have contributed in great part.

There has been a certain confusion in the literature regarding phenomena rather unfortunately described collectively under the term "antagonisms";[3] that is, effects in which one part of the spectrum seems to oppose effects induced by another part. For example, this occurs in some germinating seeds (*e.g.* Flint and McAlister (1935), Weintraub (1948)); but the wave length ranges as well as the phenomenon itself are widely different from those concerned in the present study and there seems no reason to suspect a basic relationship thereto. Again, the action of infrared radiation on recovery from x-rays (Hollaender and Swanson (1947) belongs in an entirely different category from the phenomenon herein discussed. The experiments of Whitaker (1942) on the alga *Fucus* may represent the present phenomenon, but that investigator's suggestion that his observation was a manifestation of photosynthesis is also plausible. It can hardly be overemphasized that careful distinction of such effects is important if confusion is to be avoided. The determination of spectral limits is particularly important, even where it is difficult or not particularly meaningful to measure action spectra in detail.

It is to be emphasized that in the present instance a particular biological

[2] Such variability is also being encountered in studies on other organisms, which are now going on in this laboratory.

[3] *E.g.* in the extensive review by Prát (1936) a wide variety of effects which probably have little in common in a fundamental sense are grouped under that term.

phenomenon is studied, namely, the slowing of cell division and its recovery to the normal rate; this process is completely reversible. The eggs are not killed, virtually 100 per cent surviving under the experimental conditions we have used. Shorter wave lengths of the ultraviolet spectrum induce parthenogenesis of *Arbacia* eggs, which is biologically irreversible. Thus, unless the spectrum is appropriately limited, one studies a mixed effect, with a reversible and an irreversible component. Dulbecco (1950) has suggested such an explanation for some of his results, which finds here some support. Wave length 0.2537μ which is so commonly used in such experiments (the emission of low pressure mercury arcs is principally in this line) produces both the reversible and irreversible effects in sea urchin eggs (see Fig. 1, Blum and Price 1950 *a*), and if this applies elsewhere, it may be a source of error in the interpretation of experimental results. Other interpretational errors may enter when the growth of populations of cells is studied rather than the reproduction of individual cells, as has been pointed out by Blum and Price (1950 *a*). It would seem wise to be cautious for the present in our interpretations, particularly our quantitative analyses.

Little can be said as yet about how visible light accelerates recovery from the effects of ultraviolet radiation. Dulbecco (1950) has made a number of suggestions regarding the general process, which our data give us no basis to dispute; but we remain without much knowledge of the intimate mechanism. It is clear that the recovery process depends primarily upon a photochemical reaction which is essentially different from that which produces the original changes in the cell. The distinctly different spectral ranges for the two effects, indicate two characteristically different light absorbers. Presumably these are two different kinds of molecules, but it is possible that they represent different absorbing structures in the same molecule,[4] and the second may be an ultraviolet-induced product of the first. So long as we remain without exact knowledge of the light absorbers we are critically limited as to the conclusions we may draw. In the meantime, one is free to make hypotheses, and the solution of the problem must depend ultimately upon the elimination of the untenable ones. One possibility that now seems to be eliminated is that photodynamic action (photosensitized oxidation) plays a role in the recovery process. Both Dulbecco (1950) and Johnson, Flagler, and Blum (1950) find that the elimination of O_2 does not inhibit that process, whereas photodynamic action is dependent upon this factor (*e.g.* see Blum, 1941).

SUMMARY

Light of wave lengths 0.30μ to 0.50μ, accelerates return of the cleavage rate of *Arbacia* eggs to normal, after delay by exposure to ultraviolet radiation (wave lengths 0.238μ to 0.31μ). Recovery is apparently complete. Wave lengths

[4] This seems unlikely since bacteriophage inactivated with ultraviolet radiation cannot be reactivated by light except in association with the host cell (Dulbecco, 1950).

0.30μ to 0.50μ have no effect on the cleavage rate of normal eggs, nor does such illumination previous to dosage with ultraviolet radiation influence subsequent recovery. Acceleration of recovery of the egg occurs before fertilization as well as after.

The effects of ultraviolet radiation and recovery therefrom are essentially the same in nucleated "white halves" as in the intact eggs.

This phenomenon in the *Arbacia* egg seems basically comparable to photoreactivation of bacteria and fungi.

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