THE EFFECT OF UNILATERAL ULTRAVIOLET LIGHT ON THE DEVELOPMENT OF THE FUCUS EGG*

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INTRODUCTION

Kniep (1907) and others observed many years ago that several species of Fucus eggs form rhizoids on the least illuminated sides when they are illuminated from one side by white light. The plane of the first cell division, and the developmental axis, are also determined. Winkler (1900) and Knapp (1931) have shown that Cystosira eggs respond in a similar manner. Hurd (1920) investigated the effects of different regions of the visible spectrum on the eggs of a species of Fucus, then known as F. inflatus, from San Francisco Bay. She used Wratten filters to obtain violet, blue, green, yellow, and red light from sunlight and from arc sources. A large proportion of the energy transmitted by these filters was contained in a fairly narrow span of wave-lengths. The intensity was measured, and in some experiments it was equal throughout. Hurd found that the place of rhizoid origin was determined only by the shorter wave-lengths; i.e., by the violet, blue, and probably by the shorter green (\( \lambda \)4000 to 5200 or perhaps somewhat more Ångstrom units). Some evidence that ultraviolet might be effective is referred to in the summary, but no results or information are given, and investigation of this region of the spectrum does not appear to have been pursued. The longer wave-lengths of the visible spectrum, 5800–7000 Å, had no effect even when the intensity was relatively high. The same wave-lengths that determined the place of rhizoid origin (4000–5200 Å) also caused negative geotropism of the growing rhizoid.

A number of other factors may also determine the place of rhizoid origin. These factors, and some of their interrelations, have recently been reviewed (Whitaker, 1940 a), and therefore at present they will merely be listed. They include the presence of neighboring eggs (Kniep, 1907; Hurd, 1920;...
Whitaker, 1931), especially in acidified medium (Whitaker, 1937 a; Whitaker and Lowrance, 1940); diffusion gradients resulting from development near one end in a capillary tube (Whitaker, 1937 b); electric current (Lund, 1923); pH gradients (Whitaker, 1938); temperature gradients (Lowrance, 1937); stratification by centrifuging (Whitaker, 1937 c, 1940); artificially imposed elongation (Whitaker, 1940 b); gradients of beta-indole acetic acid (Olson and Du Buy, 1937).

The experiments now to be reported were undertaken to test the effects of unilateral monochromatic ultraviolet light.

Material and Method

_Fucus furcatus_ was collected at Moss Beach and at Pescadero Point, California, and gametes were obtained by methods which have been described previously (Whitaker, 1936). The eggs are somewhat variable in size, ranging from 65 to 90 μ (average 75 μ) in diameter. Experiments were carried out from January to May, inclusive, 1940. This species of _Fucus_ is hermaphroditic and fertilization takes place when the capsules, each containing eight eggs, dissolve and liberate the eggs into sea water in which sperm are already swimming. The dissolution of the capsules can readily be observed under the microscope, and eggs were selected which had been fertilized during a span of 10 minutes. The midpoint of this span is the time of fertilization ± 5 minutes. Eggs were shed and fertilized in filtered sea water (specific gravity, 1.026-1.027), at pH 8.0-8.3, in the dark or in red light in a constant temperature room at 15 ± 3°C.

Eggs were reared in the constant temperature room approximately until the time of irradiation. After irradiation they were kept in a constant temperature cooled incubator, which was usually at about 15°C. During the irradiation the temperature approximated 15°C, although the system of control was not precise in this case. In all cases the eggs were constantly shielded from light which affects the rhizoid formation, except for the experimental exposure to ultraviolet, until the final results were observed. Immediately after fertilization the eggs secrete a pecten or cellulose-like jelly which gradually hardens to form a firm but sticky investing cell wall. By about 2 hours or somewhat longer this material attaches the eggs quite firmly to the bottom of the dish so that they do not roll or move if carefully handled. It was, of course, essential to minimize movement of the eggs after the irradiation, since there are no visible markers or points of reference on the spherical eggs. The culture vessels were handled with great care and were kept in the incubator in a levelled moist chamber mounted on sponge rubber to reduce vibration. The results were usually recorded at about 24 hours after fertilization, when well developed rhizoid protuberances are present. In certain cases after strong irradiation, however, the development was considerably delayed.

The eggs were grown and irradiated in six culture vessels made of clear fused quartz 1 mm. thick. These vessels were made in the form of cubes, 1 cm. X 1 cm. X 1 cm., with open tops. Two opposite sides of each vessel were polished on the outside. The eggs were spaced thinly over the square centimeter of vessel bottom and were irradiated from the side so that the direction of rhizoid formation could be observed from above. No eggs were counted which were within 5 egg diameters of another egg, or of a vessel wall, and most eggs were considerably further apart. A lip pipette was used to space the eggs.
Although the quartz vessels were well made and the sides were quite well aligned, fused quartz is difficult to work and, as the results ultimately indicated, these dishes were not optically perfect nor did they all deliver identical doses to the eggs on the bottom. This was true even when the eggs were thinly and similarly spaced. There was inevitably a certain amount of eclipsing in the populations irradiated from the side, although the incident beam slanted downward approximately 3° to reduce the eclipsing. In a given set of experiments the eclipsing, like most other factors, was essentially similar throughout. It is hoped to obtain vessels of a different design for future work and to know precisely the dosage received by each egg. In the present experiments the absolute intensity of the beam reaching the face of the culture vessel is known quite precisely, but the dose actually reaching the eggs in the populations is known only relatively. It must also have varied somewhat for different individual eggs in a population, although differences in response in different regions of the bottom of the vessel were small. Some vessels consistently gave somewhat greater response than others. This was probably due largely to differences in dosage received by the eggs due to different optical properties in the region of junction of the bottom and side of the vessel. Such differences were not great compared with those resulting from the differences in applied dosage, and they tend to cancel out when the results of different experiments are averaged.

The total energy applied to the side of the culture vessel, and the loss in passing through 1 mm. of flat, polished quartz into sea water, are known quite precisely. The absorption of λ2804 Å by the sea water in the culture vessels was found by direct measurement to be negligible. If the sides of the culture vessels were optically perfect, and if there were no eclipsing, the unit of dosage used in this paper would represent 1.2 ergs per mm.² applied to the eggs. In view of these two undetermined correction factors, however, 1.2 ergs per mm.² must instead be regarded as the order of magnitude of the energy actually applied to the eggs.

Dr. Arthur Giese kindly permitted use of his ultraviolet equipment, which attains unusually high intensity and monochromatic precision. The source was a large mercury arc operated on 3-6 amperes of direct current supplied by a 220 volt generator. Special devices maintained a relatively constant current. After passing through a slit, the beam passed through a monochrometer with two large quartz crystal prisms, and lenses, which separated the bands of different frequency. To further purify, the selected band was admitted through another slit and passed through a second monochrometer with lenses and a single large fused quartz prism. At the site of irradiation the emerging monochromatic beam was elliptical in cross-section and large enough, with a convenient margin, to cover the entire side of a culture vessel with very nearly uniform intensity. The rays were nearly parallel but diverged slightly. The intensity of the ultraviolet light was measured by means of a sensitive thermopile and a high sensitivity galvanometer. The thermopile was made by Mr. Emerson Reed. It was blackened with zinc black, which absorbs all frequencies to the same high degree.

RESULTS

It has been shown earlier (Whitaker and Lowrance, 1936) that the response of a population of Fucus eggs to unilateral illumination by white light from a frosted 40 watt electric lamp at 1 meter depends on how long
The eggs have been fertilized. Thus exposure for 1 hour beginning 2 hours after fertilization (15°C.) had almost no effect, while a similar exposure beginning 7 hours after fertilization caused 97 per cent of the eggs in a population to form rhizoids on the side away from the light. The response was nearly maximal throughout the period 7–11 hours after fertilization. The rhizoid protuberances do not begin to form until some time later, 12–24 hours (average 18) after fertilization (Whitaker, 1936).

In view of the results with white light, the first exposures to ultraviolet were started between 7 and 10 hours after fertilization. After preliminary results had shown that high percentages of the eggs responded, the magnitude of the response was studied with respect to two variables: the amount of radiation, and the time after fertilization when it was applied.

The First Series of Experiments

The first series of experiments was carried out through most of January, 1940, using λ2804 Å. The dosage (total energy) applied to populations was 10, 100, 1000, 5000, 10,000, and 20,000 units.

The intensity of the beam did not vary greatly in the different experiments and the dosage was varied principally by varying the duration of exposure. The time required to apply the various dosages was usually approximately as follows: 10 units, 7–7.5 seconds; 100 units, 70–90 seconds; 1000 units, 11½–15 minutes; 5000 units, 55–62 minutes; 10,000 units, 1 hour 55 minutes–2 hours 8 minutes; 20,000 units, 4–5 hours.
The results of this first series of experiments are shown graphically in Fig. 1, curve a. Each point is the average of either six or seven experiments involving a total of 354 to 461 eggs. When no radiation at all is applied, the rhizoids form in random directions so that 50 per cent form on the halves of the eggs away from either side of the vessel. The effect of the radiation is therefore indicated by the excess above 50 per cent which form rhizoids on the halves away from the source of radiation. The total energy applied is shown on the horizontal axis on a logarithmic scale. It is clear that the curve is approximately a straight line over most of the range of response, from low to near maximal. At both 5000 and 10,000 units the response was maximal; slightly more than 98 per cent of the eggs formed rhizoids away from the source of radiation. The percentage was 100 in half of the populations irradiated with 5000 and 10,000 units. After strong irradiation, especially after 10,000 units, the rhizoids of most of the eggs formed very nearly opposite the source of the ultraviolet light, as shown in Fig. 2.

In three experiments of the first series, cultures were irradiated with 20,000 units. The irradiation began at approximately 8 hours after fertilization and lasted 5 hours in two cases and 4 hours in the other. In the first two cases no rhizoids whatsoever developed, while in the third case 22 out of 165 eggs formed rhizoids, mostly delayed, and the remainder formed no rhizoids. None of the eggs which failed to form rhizoids were cytolized. It appears, however, that this dosage is almost completely inhibitory to rhizoid formation.

Visible Contamination of the Monochromatic Beam

Although the monochromatic beam of λ2804 Å which emerged from the second monochrometer was of an unusually high degree of purity, the dark-adapted human eye could detect a slight content of bluish or violet visible light. This was presumably the result of a small amount of scattering within the prisms, and it was perhaps even more due to fluorescence of the quartz prisms. Since no information exists as to the minimum dosage of visible light which will affect a population of Fucus eggs, a collateral series of experiments was designed to show conclusively whether the observed results are attributable to the ultraviolet and not to the minute amount of visible light. Two plates of clear glass each 6.4 mm. thick were interposed to absorb the ultraviolet while permitting the visible (as well as long ultraviolet, if any) to pass. The radiation which passed through the glass was

2 The wave-length 2537 Å caused a considerably more marked fluorescence of the fused quartz prism.
Fig. 2. Photomicrograph of a small area of the bottom of a quartz culture vessel after rhizoids have formed. The culture was irradiated (λ2804 Å) unilaterally from the left hand side during the period 7-9 hours after fertilization with 10,000 units (1 unit representing 1.2 ergs per mm.² applied to the side of the culture (see text)). The rhizoids have formed on the halves of the eggs away from the source of radiation.

tested on seven populations of Fucus eggs at 7–8 hours after fertilization. The dosage applied would have been 1000 units were it not for the inter-
ception of ultraviolet by the glass. In these seven experiments 52.3 per cent of 652 eggs formed rhizoids away from the light. Since six of the seven dishes showed a slight increase above 50 per cent, a small response appears to exist. An inspection of curve a, Fig. 1, shows that if the glass had not been present, 1000 units would have caused 93 per cent of the rhizoids to form away from the light. If curve a, Fig. 1, is extrapolated to 52.3 per cent, it is found that this response would be expected from a dosage of 2 units, which is 0.2 per cent of 1000 units. It is clear therefore that almost all of the response in the experiments represented by curve a, Fig. 1, is due to ultraviolet light. The small response when the glass is interposed may be due to the visible light, but even it is probably due more to ultraviolet since nearly 0.2 per cent of \( \lambda 2804 \) Å may reasonably be expected to pass through the glass.

**Fluorescence of the Vessels**

During irradiation with \( \lambda 2804 \) Å, the walls of the quartz culture vessels emit a very dim visible light as a result of fluorescence. To test the effect of this fluorescent light four culture vessels containing populations of eggs which had been fertilized 7 hours were placed beside similar vessels and eggs which were directly in the ultraviolet beam. The vessels not in the beam were separated from those in the beam by 6.4 mm. of plate glass to stop any reflected ultraviolet while permitting the visible fluorescent light to pass. The vessels in the beam were irradiated with 10,000 units over a period of 2 hours. The eggs in these vessels responded as in curve a, Fig. 1 (98 per cent). Of 257 eggs which were subjected only to the fluorescent light coming from one side, 50.2 per cent formed rhizoids away from the light. Two of the populations formed slightly more and two slightly less than 50 per cent away. The dim fluorescent light from the walls of the vessels is thus seen to be ineffective.

**The Second Series of Experiments**

A second series of experiments was carried out, principally in February, in which a constant dosage (5000 units) was applied at a variable time after fertilization. Throughout the whole series the variation in intensity of the beam was such that the time required to apply 5000 units ranged from 45 to 62 minutes. With a few exceptions, the irradiating was started exactly at the beginning of each hour from 3 to 10 hours after fertilization. The results are shown in Fig. 3, in which the points are located on the time (horizontal) axis at the midpoint of the period of irradiation. Each point represents the average of the results of five to seven experiments involving a total of 410 to 665 eggs, except that the last two points are based on four
experiments. It is seen in Fig. 3 that the response of the eggs is not great until some time after fertilization. It does not become maximal until the interval 7–8 hours after fertilization, but it remains maximal for some time thereafter. In these respects, and in general, the increase in response with age resembles the response to white light (Whitaker and Lowrance, 1936).

Eggs were not irradiated earlier than 3 hours after fertilization because they do not become firmly attached to the bottom of the dish until nearly this time.

The Third Series of Experiments

In March, in the course of some other experiments, it was found that the responsiveness of the eggs had apparently increased. The Fucus had also come into full ripeness. Gametes were shed copiously, in contrast to the condition in January, and the vegetative spring growth of the plants had begun. In the January experiments (curve a, Fig. 1) the six quartz culture vessels had been used at random, without mark or distinction, and either polished side had faced the beam. By March one of the six vessels had been broken and the remainder had been numbered. It had been found that some of the vessels consistently gave higher percentages than others, and that the two polished sides of some of the vessels also differed significantly. In view of the apparent increase in sensitivity of the eggs, a third series of experiments, in general similar to the first, was carried out in March to test again the logarithmic relation of response and dosage which was found in the first series. An equal number of experiments with each vessel was carried out at each dosage so that differences in the vessels would cancel out with equal weighting in the averages. The same side of each
vessel faced the beam. Twenty experiments, in the course of which each vessel was used four times, were carried out at each of the following dosages: 1, 5, 10, 100 units. At each dosage 1529 to 2200 eggs were counted. In all cases the eggs were irradiated within the period 8–9 hours after fertilization, and the duration of the irradiation was approximately as follows: 1 unit, 0.7–0.8 seconds; 5 units, 3.2–3.6 seconds; 10 units, 5.8–7.0 seconds; 100 units, 60–71 seconds.

The results are shown in Fig. 1, curve b. It is seen that the eggs responded with greater sensitivity than they did in January (curve a). Since the quartz vessels were used differently, it is not certain how much of this increased sensitivity is due to a difference in the eggs and how much is only apparent, due to the eggs having actually received a greater amount of ultraviolet per unit applied to the vessel. A somewhat greater number of eggs was placed in each vessel in the March series, due to improved technique, but the population density was quite uniform throughout the series. The greater number of eggs would tend to increase the eclipsing and reduce the average amount of energy received by the eggs. Curve b, Fig. 1, is very nearly parallel to curve a, and it is also essentially a straight line over the range covered, confirming the logarithmic relation of dosage and response.

**Other Wave-Lengths**

Four shorter wave-lengths, 2654, 2537, 2482, and 2345 Å, were tested in an exploratory way in a number of similar experiments to see if they also could determine the place of rhizoid origin. All of these wave-lengths were highly effective, and in sufficient dosage caused 100 per cent of the rhizoids in some of the vessels to form away from the source of radiation. While the results are inadequate to permit an exact comparison of the effectiveness of these wave-lengths with each other and with λ2804 Å, it can safely be said that their effectiveness is of the same order of magnitude. Some of them are probably more effective than λ2804 Å.

Two longer wave-lengths were also tested: λ3130 and 3660 Å. These were effective, but only when more total energy was applied. A great increase of total energy was necessary to give high percentage response. Very much larger doses were also received by the eggs without inhibition of rhizoid formation. 96 per cent of the eggs formed rhizoids away from the source of radiation when 577,000 units of λ3130 Å were applied, and 1,000,000 units of λ3660 Å caused 100 per cent of the eggs to respond in a similar manner. These large dosages were applied at a rapid rate. It may be recalled that 20,000 units of λ2804 Å inhibited rhizoid formation.
Absorption

Five measurements were made of the extent to which a beam of λ2804 Å is extinguished in passing through a single layer of Fucus eggs. Fertilized eggs were packed tightly on the bottom of a cylindrical depression in a quartz slide by means of a lip pipette. Unusually large and small eggs were discarded. The average diameter of the eggs in these measurements was 76 μ. The slide had been painted black except over the bottom of the depression containing the eggs. The intensity of the beam from a constant source was measured after passing through the slide with sea water in the depression, and again when a single layer of packed eggs was on the bottom of the depression. In the first two measurements, one on eggs fertilized 2 hours and the other on eggs fertilized 6 hours, the total area of the eggs was estimated by calculating the average projected area of the eggs from measurements of diameter, and counting the total number of eggs in the depression (approximately 3800). From the intensity measurements and the percentage of the total area covered by eggs it was calculated that in both cases 100 per cent of the radiation incident on the eggs was extinguished. In three other measurements eggs were used which had been fertilized 3, 3½, and 6½ hours and another method of calculation was employed. Perfectly packed spheres of the same diameter cover in projection 90.7 per cent of the total area. Assuming that Fucus eggs do so, it was calculated from the intensity measurements, with and without eggs in the depression, that 96, 95, and 97 per cent of the radiation incident on the eggs was extinguished in the three cases. Actually the geometric fit of the eggs was not perfect and the total space between eggs was probably somewhat more than assumed. If so, the percentage extinction would be slightly greater than calculated. It therefore appears that very nearly if not all of the beam incident on the eggs is extinguished whether the eggs have been fertilized 2, 3, 3½, 6, or 6½ hours. Extinction results from the combined effects of absorption and scatter.

Three similar measurements of extinction of a beam of λ3660 Å indicated 86, 84, and 87 per cent extinction. The second method of calculation mentioned above was used, and the eggs had been fertilized 7, 3½, and 6½ hours. The extinction of λ3660 Å is thus definitely less than the extinction of λ2804 Å. Although it is not known what part of the extinction is due to absorption and what part to scattering, it appears that λ3660 Å is less absorbed than λ2804 Å. However, the difference in proportion of energy absorbed by the eggs in the two cases is not nearly so great as the difference in effectiveness of the two wave-lengths. While 100 units of λ2804 Å
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caused more than 90 per cent of the eggs to form rhizoids away from the source of radiation, 50,000 units of λ3660 Å caused slightly less than 90 per cent to do so. 20,000 units of λ2804 Å inhibited rhizoid formation, while 1,000,000 units of λ3660 Å did not. It is quite possible that λ2804 Å and shorter wave-lengths are absorbed largely in the cortex of the egg so that the effect may be very concentrated locally, and conducive to a sharp gradient.

DISCUSSION

Heilbrunn (1937) and Heilbrunn and Mazia (1936) review some of the general effects of ultraviolet radiation on protoplasm and cite original sources. It appears probable that cell membrane permeability is locally increased, and that the surface charge, at least of certain bacteria, is decreased. The viscosity of the interior of many cells is increased, after a transitory decrease. The increase begins at the cortex and spreads inward. The viscosity increase is dependent upon calcium, and Heilbrunn (1937) attributes the internal increase of viscosity, as well as other effects of ultraviolet, to a release of protein-bound calcium from the cell surface to the interior.

Some of the effects of ultraviolet light are of a type tending to result from visible light as well, or from radiation in general. Other effects, especially those of a destructive nature which are caused by the middle and shorter ultraviolet, do not result from visible light. Some of these effects may have pronounced physiological consequences without killing the cells. Unlike visible light, ultraviolet activates a number of eggs (e.g., starfish, Lillie and Baskerville, 1922 a; sea urchin, Lillie and Baskerville, 1922 b), but only if calcium is present (sea urchin, Heilbrunn and Young, 1930). Harvey and Hollaender (1938) have shown that short ultraviolet (λ2260–2480 Å) activates non-nucleated fragments of sea urchin eggs, obviously by action on the cytoplasm. Hollaender (personal communication) has also observed that ultraviolet activates Fucus eggs. Ultraviolet induces mutations in Drosophila (Altenburg, 1934) and in corn pollen (Stadler and Sprague, 1936). λ3130 Å and longer wave-lengths are relatively ineffective in the case of the corn pollen. Wave-lengths shorter than 3000 Å are absorbed by proteins, which they denature (Clark, 1936), and they also inhibit plant growth (Popp and Brown, 1936).

Since the place of rhizoid origin in the Fucus egg may be determined by applying gradients of a considerable number of chemical substances and physical conditions (see Introduction), the fact alone that unilateral irradiation by ultraviolet light is effective gives no clue as to which of the
general or more nearly specific effects of ultraviolet light is involved, or
whether it is a combination of effects. Fig. 1 shows that each successive
increment of dosage is less effective than its predecessor in evoking further
response of a population of eggs. The response is proportional to the
logarithm of the total dosage applied. The rhizoid formation itself is of
course not a simple process, but this simple relation of dosage to response
suggests that the radiation acts on the population in a relatively simple
way rather than through a complicated combination of general effects.
No conclusion can be drawn at present as to the mode of action of the
ultraviolet in the egg, but two reactions in particular are suggestive and
perhaps may be profitably considered: The denaturation of protein, and
the inactivation of growth substance (auxin).

The action of ultraviolet light on proteins is reviewed by Clark (1936)
and is considered in a review of protein coagulation by Anson (1938).
Anson states that protein denaturation is a monomolecular reaction, and
that denaturation by ultraviolet probably breaks bonds not broken in
ordinary heat denaturation. Denaturation is commonly followed by
coagulation, but even when it is not the viscosity of a protein solution is
increased by denaturation. Clark (1936) cites work which indicates that
denaturation causes a certain amount of pH change, acid solutions becoming
more basic, and vice versa. Localized denaturation on one side of a cell
might therefore result in an internal pH gradient. Since Fucus eggs do
not transmit $\lambda$2804Å readily, such localization is to be expected. It is
already known (Whitaker, 1938) that pH gradients can determine the
developmental axis. Denaturation would result in physiological and
metabolic changes which would obviously be extensive and complicated.
Localized denaturation would give rise to gradients across the cell, and in
the Fucus egg the axis of differentiation may be determined by externally
causd gradients of a number of substances and conditions, as postulated
by Child (1940) in his generalized concept of the origin of axial differentia-
tion. Full understanding of the nature of the differentiation processes
must ultimately depend on discovering their specific chemical basis.

If the response of Fucus eggs to shorter ultraviolet results from localized
protein denaturation, the effectiveness of different wave-lengths shorter
than 2900Å should correlate with the typical absorption curve of proteins.
As indicated earlier, the exploratory measurements made at wave-lengths
shorter than 2804Å are not adequate to show whether this is the case, and
this question remains to be answered.

Plant growth is inhibited by short ultraviolet, and one of the ways in
which it exerts its effect appears to be to inactivate or destroy growth
hormone (auxin). Went and Thimann (1937) in their monograph on phytohormones cite work showing that unfiltered ultraviolet inactivates auxin solutions almost completely. Wave-lengths between 2300 and 3300 Å inactivate auxin-a lactone with great rapidity, and ultraviolet light can inactivate auxin-a by shifting the place of attachment of an OH group. Skoog (1935) has shown that hard x-rays inactivate auxin in vitro and in vivo.

Growth substance, or auxin, has been extracted from *Fucus* eggs by Du Buy and Olson (1937). Van Overbeek (1940) has recently shown that auxin is present in a number of algae in concentrations comparable to those in higher plants such as corn and pea seedlings. He has further shown in the brown alga *Macrocystis* that beta-indole acetic acid (hetero-auxin), or a substance closely related to it, is present rather than auxin-a or auxin-b which are commonly found in higher plants. The presence of beta-indole acetic acid does not prove its activity in the growth of the plant, but activity in the algae is suggested both by the experiments of Olson and Du Buy (1937) who found that gradients of beta-indole acetic acid can determine the developmental axis of the *Fucus* egg, and by van Overbeek's observations on the differential distribution in *Macrocystis* which suggests hormonal function. The beta-indole acetic acid is most concentrated in young blades. The rôle of auxin in the rhizoid formation in *Fucus* has been recently discussed (Whitaker, 1940 a) and for present purposes it need merely be noted that inactivation or destruction, on one side of the egg, of beta-indole acetic acid, or some auxin-like substance active in rhizoid formation, might be an important factor in the present instance. If the destruction extended throughout the entire egg, rhizoid inhibition would be expected and this is observed after strong dosages, without cytolysis or visible breakdown of the protoplasm.

The shorter wave-lengths of the visible spectrum also cause *Fucus* eggs to respond. Whether they act in the same way as ultraviolet of λ2804, or less, Ångstrom units cannot be decided at present. It is not known whether the response of a population to visible light follows the logarithm of the dosage. Shorter visible wave-lengths are known to affect the transport and activity of auxin in higher plants. The fact that λ2804 Å, which has destructive powers not possessed by the long ultraviolet (λ3660 Å), is much more effective than λ3660 Å suggests that destructive effects are involved in the action of λ2804 Å.

The eggs do not become fully responsive to ultraviolet light until about 7 hours after fertilization, as may be seen in Fig. 3. One explanation of this might be that some substance acted upon by the ultraviolet gradually forms
after fertilization and is not present in maximum concentration until after 7 hours have passed. A more probable interpretation is that the eggs recover from the effect of irradiation after a number of hours, and that at 7 or more hours after fertilization there is not time for recovery before the rhizoids form. The rhizoids begin to form in a population at about 12 hours after fertilization, with the mode at 16–17 hours (Whitaker and Lowrance, 1936). The formation of rhizoids in a population follows the form of a somewhat skewed probability curve so that on the basis of the recovery hypothesis Fig. 3 would be expected to be a sigmoid curve. A similar relation was found in the case of white light (Whitaker and Lowrance, 1936), although the eggs did not respond until somewhat longer after fertilization, which suggests that they take somewhat longer to recover from the effects of λ2804 Å, although less energy was applied.

SUMMARY AND CONCLUSIONS
1. When Fucus eggs which have been fertilized for a sufficient length of time are irradiated unilaterally with monochromatic ultraviolet light (λ2804 Å) of adequate dosage, 97–100 per cent form rhizoids on the halves of the eggs away from the source of radiation (see Figs. 1 and 2).
2. The responsiveness of the eggs increases gradually after fertilization and does not reach a maximum until about 7 hours at 15°C. (see Fig. 3). The first rhizoids begin to form in a population at about 12 hours after fertilization. The responsiveness remains maximal until at least 11 hours after fertilization.
3. It is suggested that the low responsiveness of a population of eggs at an earlier period is due to recovery from the effects of irradiation before the rhizoids begin to form.
4. The response of eggs to λ2804 Å is proportional, over a wide range, to the logarithm of the dosage (see Fig. 1). Dosage was regulated by the duration of exposure during the period of maximum response.
5. High dosages of λ2804 Å, of the order of 10,000 ergs per mm.², cause the rhizoids to form fairly precisely away from the source of radiation (see Fig. 2). Twice this dosage inhibits rhizoid formation altogether without causing cytolysis.
6. Other wave-lengths which have also been shown to be effective are: 3660, 3130, 2654, 2537, 2482, and 2345 Å. Only exploratory measurements have been made to test the effectiveness of these wave-lengths, but they show that much greater energy is necessary to obtain a strong response with λ3130 and 3660 Å, especially the latter. The wave-lengths shorter than 2804 Å, on the other hand, show the same order of effectiveness as λ2804 Å. Some may be more effective.
7. A beam of $\lambda 2804$ Å which is incident on a single layer of Fucus eggs is completely extinguished at 2, 3, 6, or $6\frac{1}{2}$ hours after fertilization. About 85 per cent of a beam of $\lambda 3660$ Å is extinguished. The wave-length 3660 Å is thus not so completely absorbed as $\lambda 2804$ Å, but the difference in proportion absorbed by the egg is not nearly so great as the difference in effectiveness.

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