investigated by a new and precise method. The optimal temperature for the process is 32°C, and above this ethylene production falls off rapidly. The heat inactivation slowly disappears when the tissue is exposed to lower temperatures. Ethylene production and oxygen consumption show almost identical dependence upon oxygen tension, the half maximum value for both being reached at 1.5–2.0 per cent O_2. Although the synthesis of ethylene ceases almost immediately under anaerobic conditions, a precursor accumulates which can be rapidly oxidized in air with the production of ethylene. Tritiated water transfers its label to ethylene in such a manner as to indicate that one of the terminal steps in the process is a reversible dehydration. The final reaction leading to ethylene does not require the participation of oxygen. A scheme for ethylene production is proposed in which one or more reductions are followed by a rapid oxidation, a reversible dehydration, and a nonoxidative terminal step.

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[*] This investigation was carried out while Stanley P. Burg was a holder of a research fellowship from the National Cancer Institute, Public Health Service. It was supported by a grant to Prof. K. V. Thimann from the Maria Moors Cabot Foundation.

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PHOTOCONTROL OF PLANT DEVELOPMENT BY THE SIMULTANEOUS EXCITATIONS OF TWO INTERCONVERTIBLE PIGMENTS

By S. B. HENDRICKS AND H. A. BORTHWICK

U.S. DEPARTMENT OF AGRICULTURE, AGRICULTURAL RESEARCH SERVICE, PLANT INDUSTRY STATION, BELTSVILLE, MARYLAND

Communicated January 26, 1959

Flowering, seed germination, stem elongation, and many other aspects of growth and development of seed plants are influenced by a reversible photoreaction.[1, 2] This reaction can be written:

$$PH_2 + A \underset{7{,}350\ \text{A max}}{\overset{6{,}600\ \text{A max}}{\rightleftharpoons}} P + AH_2$$

in which PH_2 and P are the reduced and oxidized forms of a pigment with absorption maxima near 6,600 and 7,350 A, respectively, and A and AH_2 are a hydrogen acceptor and donor. The oxidized pigment, P, is an enzyme controlling an essential reaction.

Interconversion of the oxidized and reduced forms of the pigment adequate to produce striking biological responses can be achieved with low irradiances. In other words, because of the high absorption coefficients, these being greater than 10^7 cm^2/mol as measured by the reversibility of the photoreaction,[3] change in the form of the pigment can readily be affected. An example is the response of imbibed lettuce seeds to an alternation of low irradiances in the region of 6,600 and 7,350 A, respectively. Germination of the seeds is suppressed or potentiated depending upon the final exposure.[1] In a more quantitative way, an incident energy of 10^{-7} einsteins/cm^2 (1.54×10^4 ergs/cm^2) in the region of 7,350 A can diminish P to $1/e$ of its initial value when the quantum efficiency is forced toward 1.0 by a high ratio of $[AH_2]$ to $[A] + [AH_2]$, and an incident energy of 10^5 ergs/cm^2 under these conditions can diminish P to 0.15 per cent of its initial value.

TABLE 1

Effects of Exposure to Sunlight on Germination of *L. virginicum* Seeds

	Germination with Prior Treatment	
Exposure to Full Sunlight, sec	Red Radiation, %	Darkness, %
0	64	0
1	42	21
2	51	27
4	53	29
8	85	30
16	87	36
32	93	48
64	93	62

Plants under high irradiances in the region of 6,000 to 8,000 A show responses arising other than from the reversibility of the preceding photoreaction. Thus cocklebur (*Xanthium pensylvanicum*) growing on short days and long nights fails to flower if the night is interrupted near the middle with a low irradiation of 5×10^4 ergs/cm^2 in the region of 6,600 A in the order of 1 min. They are readily reinduced to flower if this irradiance is followed by an equivalent one in the region of 7,350 A. If the irradiance in the region of 7,350 A is greater than the order of 10^6 ergs/cm^2, however, the plants fail to flower. The high incident energy in the region of 7,350 A produces a biological response similar to that in the region of 6,600 A. The effects with high irradiances are now found to arise from the continued photoexcitation of the pigment in those spectral regions where both the oxidized and reduced forms have appreciable absorptions. In the further excitation, reactions other than the reversible one occur which, at least, change the ration of [A] to $[AH_2] + [A]$ by inducing reactions of A and AH_2 with reactants other than the pigments. The phenomenon warrants further explanation before experimental results are presented.

Absorbances of the oxidized and reduced pigment in the region of 5,800 to 8,000 A are shown in Figure 1, *C*. The solid lines are derived from measurements of reversibility of specific responses and the courses of the dotted extensions are obtained from the present work. A crossover or isobastic point exists near 6,950 A. Under continuous irradiation in this region both pigment forms are excited. Since

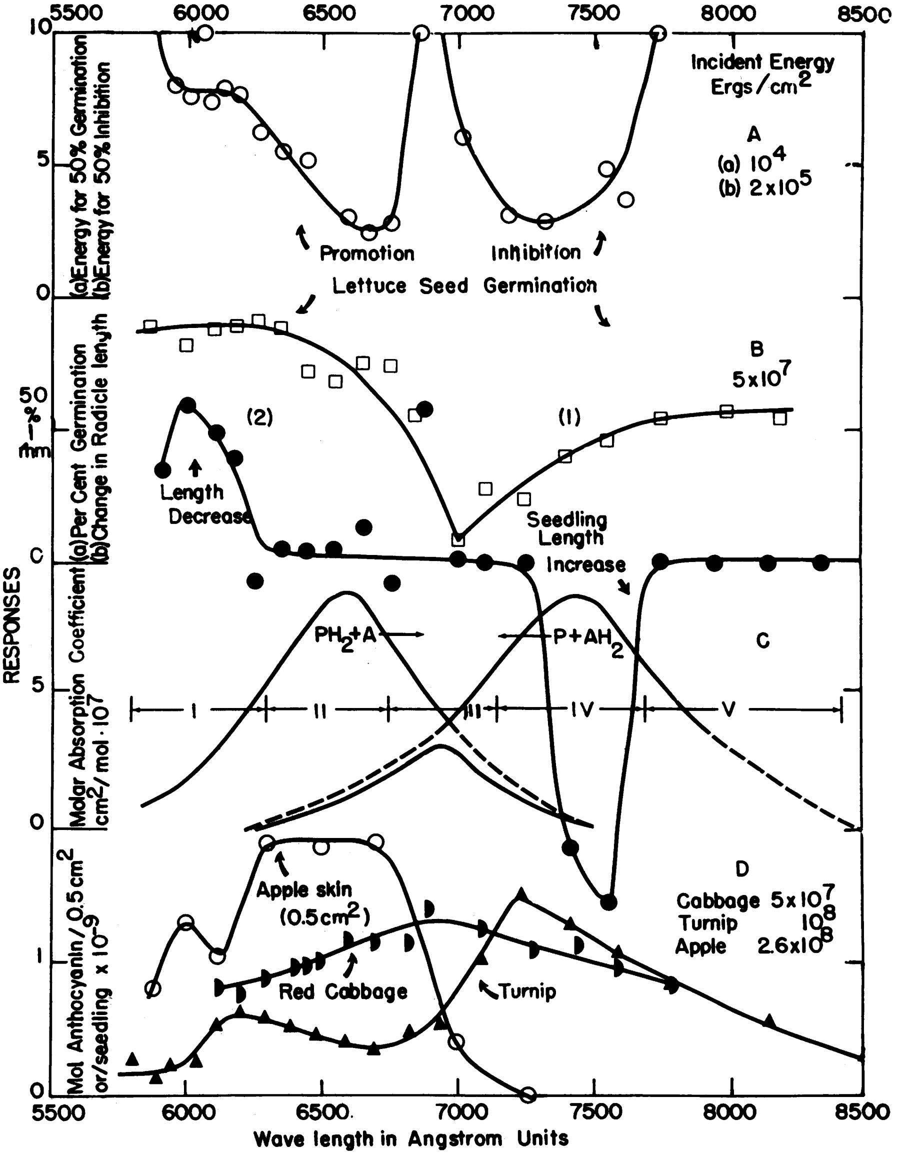

FIG. 1, *A–D*.—Action spectra in the region of 5,800 to 8,500 A for the control of some aspects of plant development. Note text for explanation.

these are photochemically effective pigments, they can take part in reactions other than the reversal. The probability of repeated excitation, because of the possibility of reversal, depends upon the absorbancies of both forms of the pigment in any given region as well as upon the ratio of the oxidant to the reductant in the photoreaction. Thus, if the concentrations of A and AH_2 are about equal, the maximum of an action can be near the isobastic point, as shown by the lowest curve in Figure 1, *C*, instead of near the absorption maxima.

The absorptions in wave-length regions longer than 5,800 A can be grouped into five limiting regions which intergrade as the limits are approached. These regions are:

I. 5,800–6,300 A: Absorption of radiation is due very predominantly to PH_2, thus driving the photoconversion with high irradiance very far toward P.

II. 6,300–6,700 A: Includes the absorption maximum of PH_2 and accordingly requires the least irradiance for conversion of PH_2 to P. The absorption of P is increasing in this region and in the steady state the amounts of both P and PH_2 are appreciable, with P predominant.

III. 6,700–7,200 A: The region of the isobastic point with the maximum of the action near 6,950 A. Amounts of P and PH_2 are of the same order of magnitude provided the concentrations of A and AH_2 are about equal.

IV. 7,200–7,800 A: Includes the absorption maximum of P as well as appreciable absorption of PH_2.

V. >7,800 A: Absorption of radiation due very predominantly to P thus driving the photoreaction very predominantly to PH_2. The absorbancy, however, is small but can still be detected by biological response at wave lengths above 7,800 A.

Action is also evident at wave lengths shorter than 5,800 A with a maximum effectiveness near 4,500 A. Effects in this region have not been fully disentangled.

Action spectra for a number of growth and development responses compel the conclusions and illustrate the Classes I to V as well as the effects of various degrees of oxidation of A. Photocontrol of anthocyanin formation is recognized as a response to be considered, although it previously had not been realized as arising from action of the reversible pigment system. A first example is the action spectrum for anthocyanin production in seedlings of red cabbage (*Brassica oleracea* var. Red Acre)[4] shown in Figure 1, *D*. It has the features of the combined action in region III with a maximum near 6,900 A. The promotion and inhibition with low irradiances of lettuce seed germination (var. Grand Rapids)[1] shown in Figure 1, *A* illustrate Classes II and IV.

An example of all five classes is afforded by the response to high irradiances of seeds of the Great Lakes variety of lettuce, which germinate fully in darkness at 23° and are not inhibited by low irradiances in the region of 7,350 A. Imbibed seeds were held in darkness at 23° for 16 hr after which time some had germinated. They were then irradiated for 12 hr on a two-prism spectrograph with an energy flux of 0.2 milliwatt/cm^2, a dispersion of 70 A/cm, and a slit width of 170 A at 7,000 A. They were returned to darkness for 12 hr after which germination and radicle length of germinated seeds were measured with results as shown in Figure 1, *B*. The action maximum and shape of the action curve for germination are in accord with the action in region III. In particular, supression of germination is detectable near 6,600 where the absorbancy of PH_2 is maximum. The suppression is maximum near 7,000 A and decreases to longer wave-lengths where the absorbancy of P is maximum.

The action spectrum for radicle length of Great Lakes lettuce shown in Figure 1, *B* was most unexpected, and, in fact, was the initial basis for the findings reported here. The elongation is suppressed with a maximum near 6,100 A and is enhanced with a maximum near 7,500 A. There is very little response elsewhere. The suppression of elongation is in region I and is at considerably shorter wave lengths than the maximum absorbancy of PH_2. The enhancement is displaced to longer wave lengths than the absorbancy maximum of P. The apparent lack of effect of radiation in the region of 6,300 to 7,200 A might well result from the balancing of several actions.

The action spectrum for anthocyanin formation in apple skin[5] (Fig. 1, *D*) corresponds to regions I and II. There is no doubt about the experimental presence of the subsidiary maximum in the region of 6,000 A corresponding to the maximum suppression of radicle elongation for lettuce. The most effective region for anthocyanin formation is II, which probably results from a very great predominance of AH_2. Thus, the red absorbing form, PH_2, of the pigment can be repeatedly excited without being converted to the far red absorbing form, P. The synthesis of anthocyanin apparently is limited by the excitation of PH_2. The apple skin also produces ethanol aerobically, which could well be associated with the extreme reduction of A to AH_2.

Further features of the combined action of the two pigment forms are evident in the action curve for anthocyanin synthesis in turnip seedlings (*Brassica rapa* var. Purple Top White Globe) inhibited with chloroamphenicol to prevent chlorophyll development. The greater portion of this curve is identical in shape with the germination curve for Great Lakes lettuce seed (Fig. 1 *B*) expressed as effectiveness of irradiance for germination instead of inhibition as shown. The secondary maximum near 6,100 A corresponds to the maximum for suppression of elongation of the lettuce seedling radicles. In the turnip seedlings A must be greatly predominant over AH_2. As a result, the maximum for action is near the absorption maximum for P, the far red absorbing form of the pigment in contrast to results for apple skin. In the region of maximum absorption of PH_2 anthocyanin synthesis is suppressed by excitation of PH_2 with essential quenching of the excitation of P for formation of anthocyanin.

Anthocyanin syntheses in the three objects, apple skins, and red cabbage and turnip seedlings, while having greatly different action spectra are examples of Classes II, III, and IV, respectively. All depend to a marked degree upon simultaneous excitation of PH_2 and P, but the apple skin is driven chiefly by excitation of PH_2, the red cabbage seedlings by PH_2 and P, and the turnip seedlings by P. Two of these three have the subsidiary maximum near 6,100 A corresponding to the predominant conversion of PH_2 to P, with P being effective in the dark synthesis of anthocyanin as is known for red cabbage seedlings.[4]

Further comments about the photoreaction might be illustrative. Pigments P and PH_2 can be associated with either A or AH_2 leading to activation upon photoexcitation. However, when P is associated with A, excitation is ineffective for conversion to PH_2 and similarly for PH_2 associated with AH_2 to be converted to P. The lifetime of excited P and PH_2 would be expected to be enhanced under these conditions. Thus, A and AH_2 could be excited by energy transfer to react with another hydrogen donor or acceptor. The ratio of [A] and $[AH_2]$ to $[AH_2] + [A]$ would be changed by such a reaction in which an alternative hydrogenation could be affected as, for example, one in anthocyanin synthesis. A biological test can be made for the change in ratio of [A] to $[AH_2] + [A]$; namely, the sensitivity of the photoreaction in the two directions can be measured, an increased rate of PH_2 reacting with A under constant irradiance corresponding to an increase in the [A] to $[AH_2] + [A]$ ratio. An example of a change of this type is the response of

Lepidium virginicum seeds to continued irradiation with sunlight as a source of high irradiance after a short irradiance in the region of 6,600 A adequate to potentiate full germination. Results shown in Table 1 indicated that after 1-sec exposure to sunlight the potential germination is at a minimum which is shifted to full germination in 64 sec, supposedly by the conversion of AH_2 to A.

The many evident implications of these findings to the photoperiodic control of flowering and other aspects of plant growth and development will not be discussed. But the fact that anthocyanin synthesis is responsive to photoexcitation of the reversible pigment system merits emphasis. It permits, for instance, estimation of the concentration of the pigment in the cells in which anthocyanin synthesis takes place. This dependence opens the phenomenon to biochemical examination in that the pertinent chemistry is in the utilization of acetyl, both in aromatic synthesis (by still unknown pathways)[6] and in fat metabolism.

Summary.—The pigment in the reversible photoreaction controlling plant growth and development at low irradiances is effective at high irradiances in spectral regions where the absorbancies of the oxidized and reduced pigment form are both appreciable. The action with high irradiance depends in part upon the simultaneous absorptions of the two forms. This action controls anthocyanin formation and many other responses including some aspects of photoperiodic induction of flowering and seed germination.

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*EXTENSIVE DEEP SEA SUB-BOTTOM REFLECTIONS IDENTIFIED AS WHITE ASH**

BY J. LAMAR WORZEL

LAMONT GEOLOGICAL OBSERVATORY, COLUMBIA UNIVERSITY, PALISADES, NEW YORK

Communicated by Maurice Ewing, January 2, 1959

Introduction.—Sub-bottom echoes have been observed since the advent of expanded scale recording sounders. Since the introduction of the Precision Depth Recorder (PDR) with a short ping (about 5 millisec) sub-bottom reflections have been recorded at many locations in the deep sea, e.g., Heezen *et al.*[1] The observed sub-bottom reflections have not been systematically cored. On *Vema* cruise 15 (V-15) such an echo was observed over a very large area of the eastern part of the