

Apollo 11 rocks, additional measurements of K and U on subsamples of individual Apollo 11 rocks by members of the Preliminary Examination Team (15) and other investigators (16) have been reported. The final results of O'Kelley *et al.* (the Preliminary Examination Team) (16), based on longer counting times and more refined analytical techniques, would plot close to the Apollo 11 and Apollo 12 trend lines (Fig. 1) and show even less scatter than the preliminary results.

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17. This report presents the results of one phase of research carried out at the Jet Propulsion Laboratory, California Institute of Technology, under contract No. NAS7-100, sponsored by the National Aeronautics and Space Administration.

25 May 1970; revised 15 October 1970

Environmental Control of Photosynthetic Enhancement

Abstract. *The transition from granular to homogeneous chloroplasts in vivo in Egeria densa caused by environmental conditions was paralleled by a decrease in photosynthetic enhancement from 30 percent to nearly zero. The drop in enhancement can be explained either by a change in the partitioning of light energy between the two photosystems or a change to a single photosystem.*

Chloroplasts of higher plants are known to have grana at some times and at others to be homogeneous when observed in the light microscope in vivo (1). The transformation from the granular to the homogeneous state can be effected by illumination in red light and is reversed by illumination in blue light or incubation in darkness (2). This reversible change in appearance is probably due to a change in fine structure which in turn ought to have an effect on the photosynthetic reactions occurring in the chloroplasts. In order to test this presumed relation between structure and function, photosynthetic enhancement was measured with leaves from plants that had been illuminated with red light long enough to cause the chloroplasts in most of them to become homogeneous. Enhancement decreased from its maximum value of 20 to 30 percent to nearly zero in response to these environmental conditions.

Egeria densa (*Elodea densa* or *Anacharis densa*) was grown under day-

light supplemented with fluorescent light. The growth jars contained soil with added nitrate, phosphate, and iron and medium consisting of 200 μM KCl, 100 μM MgSO_4 , and 200 μM CaCl_2 . In these experiments 4 to 6 cm of the apical ends of the intact plants in growth jars supplied with 5 percent CO_2 in air and kept at 17°C were first illuminated for 6 to 12 hours with high-intensity red light (2.4×10^4 erg/cm²-sec). For measurements of enhancement of photosynthesis a leaf was then excised, examined in a light microscope under oil immersion, placed adaxial surface up on a platinum oxygen electrode covered with a Teflon membrane similar to that described by Fork (3), and fastened in place with dialysis membrane. The electrode was polarized at -0.55 volt with a circuit powered with an alkaline manganese battery (4). The electrode current was measured with an F-1-7 differential amplifier (Computer Techniques Ltd.) used as a d-c microammeter and recorded on a 10-mv po-

tentiometric recorder. The response of the microammeter recorder combination was linear over at least four orders of magnitude. Monochromatic light was produced with Balzer B-40 interference filters and Calflex C heat filters. The wavelengths used were the pairs 482 and 700 nm or 647 and 700 nm which have been reported to give maximum enhancement (5). The light intensity was controlled with neutral density filters. The rates of oxygen evolution as a function of illumination (Fig. 1) could be extrapolated linearly to the origin. Thus, there were no detectable systematic errors caused by nonlinear light curves (6). Periods of 2 to 4 minutes of illumination in monochromatic light, followed by 2- to 4-minute dark intervals, were randomly interspersed between the periods of illumination in light of two wavelengths. Corrected rates of oxygen evolution were calculated from the differences between the oxygen electrode currents in light and in dark measured after the end of the 40- to 70-second electrode-transient periods. Percent enhancement was calculated according to the formula

$$\%E = \left(\frac{PS_{1,2}}{PS_1 + PS_2} - 1 \right) \times 100 \quad (1)$$

where $PS_{1,2}$, PS_1 , and so forth are defined as the rates of oxygen evolution corrected for the rates of respiration in light of wavelength 1 and 2 together, wavelength 1 alone, and so forth, respectively. This formula gives lower values for enhancement than the formula

$$\%E = \frac{PS_{1,2} - PS_2}{PS_1} \times 100 \quad (2)$$

and it also avoids the artificial bias toward greater enhancement at high ratios of auxiliary light to 700-nm light. For example, the low enhancements of 1 to 10 percent calculated according to Eq. 1 becomes 3 to 13 percent at low ratios of auxiliary light to 700-nm light and 21 to 35 percent at high ratios when calculated according to Eq. 2. Similarly, the high enhancements of 20 to 35 percent calculated according to Eq. 1 become 35 to 65 percent at low ratios and 65 to 135 percent at high ratios of auxiliary light. The two methods give roughly the same proportionate change in enhancement, however.

The duration of the illumination of the intact plants with red light needed to effect the transformation from granular to homogeneous chloroplasts is variable because it depends on many

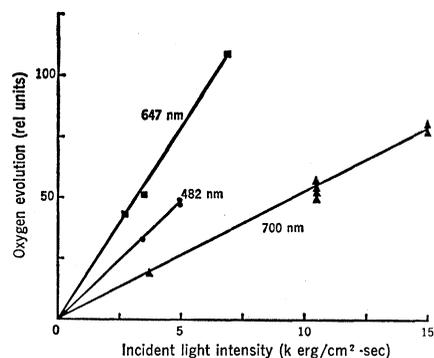


Fig. 1. The dependence of photosynthetic oxygen evolution on intensity of incident light. The intensities at the three wavelengths were measured with a radiometer (Yellow Springs Instrument Co.). Data are taken from experiment 3 (Table 1). The shapes of the light curves did not depend on the duration of the prior illumination or the magnitude of the enhancement. One hundred "relative units" of oxygen production corresponds to an electrode current of $7.5 \mu\text{a}$.

physical and physiological factors. For this reason most, but not all, of the leaves had homogeneous chloroplasts after the illumination used in these experiments. Despite this variability, photosynthetic enhancement decreased after prior illumination in all experiments (Table 1). In two of the experiments (Table 1; experiments 2 and 3), leaves were removed from a single plant at different intervals thus providing a rough measure of the time course of the decrease. The correlation between homogeneous morphology and low enhancement was good but not perfect. One reason for the imperfect correlation may be the occasional difficulty in scoring the morphology of the chloroplasts. For example, in experiments 1 and 7 (Table 1) the chloroplasts had small granules that were recorded as starch but which could have been grana in a transitional state. The imperfect correlation may also arise because neither of these effects is the direct cause of the other; both may be the consequence of some other change occurring in the cells. Light-induced ion transport is implicated as the possible cause of the structural change and the decrease of enhancement for two reasons. First, we have observed large increases in the calcium concentration in the medium during the illumination of some of the plants. Second, the plant in experiment 7 was grown with potassium added to the soil rather than a 2:1 potassium-to-sodium mixture. Both the structural change and a 50 per-

cent decrease in enhancement were found after 8 hours illumination with low-intensity white light. Plants grown with the usual 2:1 potassium-to-sodium nutrient solution did not exhibit the structural or photosynthetic changes unless illuminated with high-intensity red light.

Enhancement in these experiments was often a function of the ratio of auxiliary light to 700-nm light with the greatest enhancement found at high proportions of auxiliary light (6) (Fig. 2). When this occurred, the values recorded in Table 1 were the maximum enhancement values obtained. When enhancement was low, it was almost always low at all ratios of auxiliary light to 700-nm light from 0.25 to 0.75 with both wavelength pairs used and it was independent of the total light intensity which was varied by a factor of 2 to 3. These decreases in enhancement were not accompanied by any appreciable changes (greater than 15 percent) in the rate of photosynthesis in either wavelength alone or in respiration and were observed in experiments lasting from 30 minutes to several hours. Thus, they were based on long-term changes in photosynthesis. In 5 of 13 experiments the first period of illumination in two wavelengths combined gave a significantly different degree of enhancement from that given by subsequent periods of illumination in the same two wavelengths (Table 1). In these experiments, this first period of illumination with two wavelengths was omitted so that the remaining enhancement values from these experiments showed greater internal consistency. There was no correlation between the wavelength of light in the preceding illumination period and the existence of the aberrant first determinations of enhancement and this phenomenon remains unexplained.

Several investigators have already reported failure to find enhancement, in some cases, because of the use of particular algal species or organisms grown in deficient media (7, 8). In this study, by contrast, the decrease in enhancement was reproducible and controlled by environmental conditions imposed on healthy plants growing in a sufficient medium. There are several hypotheses which could account for this controlled variation in enhancement. For example, if the shift in the partitioning of light energy absorbed by the chloroplast pigments which has been proposed many times (9) occurs so that nearly equal amounts of energy are delivered to

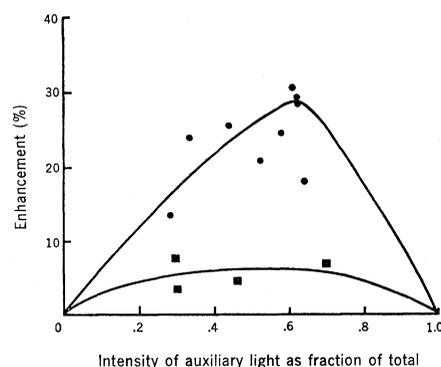


Fig. 2. Dependence of enhancement on the proportion of total photosynthesis caused by the auxiliary light alone. Circles, 482-nm auxiliary light (experiment 2); squares, 647-nm auxiliary light (experiment 3). In both experiments, the first determinations of enhancement gave aberrant values and were omitted. Their values were 8 percent enhancement at 0.46 auxiliary light (experiment 2) and 13.5 percent at 0.42 auxiliary light (experiment 3).

photosystems I and II, enhancement will approach zero. Analysis of a simple kinetic model shows that two conditions must be satisfied in order to account for the higher enhancement at higher ratios of auxiliary light and the relatively small changes in the photosynthetic rates in either wavelength alone during the decrease in enhancement. Using the nomenclature

Table 1. Variability of photosynthetic enhancement. The temperature of the electrode chamber during the enhancement experiments was 17° to 18°C . Results below are selected from 20 experiments. The numbers in parentheses beside the values for percent enhancement indicate the number of determinations that were averaged. There was no effect of age of plant which varied from 13 to 53 days. A single plant was used for each experiment; H, homogeneous chloroplasts; G, granular chloroplasts.

Experiment	Prior illumination (hr)	Chloroplast morphology	Enhancement	
			At 482 nm (av. %)	At 647 nm (av. %)
1	9	H*	30 (5)	18 (6)
2	10	G	28 (9)	
2	12	H	11 (5)	
3	6	G	35 (4)	18 (6)
3	11	H		6 (4)
4	8	H	17 (6)	1 (4)
5	12	H	7 (5)	
6	8.5	G	8 (4)	
7	†	H*	19 (10)	10 (6)

* The chloroplasts contained small starch grains (see text). † The plant was grown in soil to which only potassium ions were added rather than the usual solution with a 2:1 ratio of potassium-to-sodium ions. The prior illumination consisted of 8 hours of low-intensity white light rather than the usual illumination with high-intensity red light (see text).

of Eley and Myers (10), α , the proportion of energy absorbed by photosystem II at 482 or 647 nm must be only slightly greater than 0.5 and at 700 nm must be much less than 0.5, as Eley and Myers concluded. Furthermore, the shift in α at auxiliary wavelengths must be small and negative, whereas the shift at 700 nm can be either negative or positive but must be small, preferably zero. A second explanation of the variation in enhancement is that the mechanism of photosynthesis changes from a reaction that involves two photosystems in series to a simpler single photosystem perhaps similar to that proposed by Govindjee *et al.* (8) or by Hoch and Owens (11). This latter mechanism is operationally equivalent to the two-light mechanism for the special case in which $\alpha = 0.5$ and thus the two are not distinguishable on the basis of enhancement determinations alone. One factor in favor of the hypothesis of a controllable α is that it can be used to explain some of the observations of Knaff and Arnon (12). If α for the auxiliary wavelengths has changed enough so that it is less than 0.5, the wavelength that activates photosystem II will behave like the one that activates photosystem I and oxidize the cytochromes between the two photo-reactions. Furthermore, there should be no enhancement, as Knaff and Arnon have reported. This kind of extreme change in α could have been caused by the isolation of the chloroplasts in a medium that contains a high concentration of sodium chloride which stimulates galactolipases (13) and promotes the generation of free fatty acids that are known to damage chloroplasts (14).

Regardless of the interpretation of the phenomenon, the finding of controlled photosynthetic enhancement means that most of the kinetic studies of individual components of oxidation-reduction reactions in chloroplasts should be redone to see whether the kinetic properties change as predicted. Finally, control of enhancement found in a vascular plant is most likely characteristic of many photosynthetic organisms because it has also been found in synchronized green algae grown in sufficient media (15). It may also be analogous to the environmental control of fluorescence (9), although the amount of prior illumination needed to decrease enhancement in these experiments is much greater than that

used in studies of fluorescence by Bonaventura and Myers (9). The difference may be partly due to the influence of nutritional factors on the transformation occurring in higher plants.

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 16. Supported by a study leave granted by Temple University. I thank Dr. F. R. Whatley and his colleagues of the Botany Department, King's College, London, where the research was carried out, and M. A. Kolitsky and M. J. Vrooman for their helpful criticism of the manuscript.
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26 August 1970; revised 9 November 1970

Stereoscopic Depth Aftereffect Produced without Monocular Cues

Abstract. *Random-dot stereograms when used as adaptation stimuli can influence the perceived depth of similar test stimuli. Adaptation for 1 minute is sufficient to evoke this three-dimensional aftereffect for several seconds. This aftereffect must occur after stereopsis because prior to stereopsis no relevant monocular cues exist in these adaptation and test stimuli.*

Ever since Gibson (1) discovered the tilt aftereffect the question of whether such phenomena may occur in the third dimension of perceptual space has aroused much interest. Köhler and Emery (2) found that prolonged observation of an object at one depth can change the apparent distance of objects seen afterward. These phenomena occur after one adapts to stereoscopic pictures, which suggests that they depend only on disparity cues. However, there remains the obvious possibility that the effects could be explained solely by the induction of monocular aftereffects of the type described by Gibson (1) and Köhler and Wallach (3). Different monocular changes in position, curvature, or orientation in the two eyes after adaptation could produce changes in stereoscopic depth. Köhler and Emery (2) tried to control for the problem of monocular aftereffects by adapting to stereograms with quick alternation between right and left eyes. They chose a high rate of alternation in order to produce adaptation but not so rapid a rate that stereopsis should ensue;

and indeed no three-dimensional aftereffects occurred under these conditions. However, it is most likely that this procedure also abolished any independent monocular adaptation for the left and right pathways, respectively. So the question of genuine three-dimensional aftereffects is still open.

We wondered whether adapting to a random-dot stereogram (4) might afterward produce apparent changes in depth. This would indicate that there can be genuine adaptation of disparity-analyzing mechanisms and that monocular contour is not necessary for this adaptation (for such stereograms contain no monocular shape prior to stereoscopic combination). Random-dot stereograms do produce such a stereoscopic aftereffect (Fig. 1).

The upper stereo pair (Fig. 1A) is for adaptation. In the center is a horizontal, white fixation bar raised in depth from the background. Above it is a square that stands out even closer to the observer and below is a square that is the same distance behind the fixation mark. All three objects are floating well in front of the background. The