

# Quantum Requirement for Photosynthesis in Chlorophyll-Deficient Plants with Unusual Lamellar Structures

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**ABSTRACT** Neither an over-all deficiency of chlorophyll, nor an increased enzymatic capacity for maximal rates, nor an unusual lamellar structure was found to change the number of quanta required for the evolution of one molecule of oxygen in healthy aurea mutants of tobacco. The average minimal quantum number remains 10 (efficiency 0.1) as in many algae and typical higher plants. Most of the time the optimal efficiency depends on the availability of some far-red radiation, particularly in the blue region of the spectrum where blue light alone is rather inefficient. These results fit an explanation offered earlier in connection with the hydrogen or acetate photometabolism of algae in far-red light.

## INTRODUCTION

During the last two years we have investigated the light metabolism of higher plants having different chlorophyll contents, mainly chlorophyll-deficient aurea mutants (33). The present paper is a continuation of work published in this *Journal* (32) and expanded elsewhere (31). We were able to show that some aurea mutants of tobacco have a very high capacity for photosynthesis on the basis of chlorophyll and sometimes also on the basis of illuminated area. No normal green plant has ever been shown to have rates of photosynthesis as high per chlorophyll as the aurea mutants of Willstätter and Stoll and our tobacco mutants (36). We have found healthy aurea plants not only in different tobacco strains but also in *Lespedeza procumbens* (30). What prompted the continuation of this work was the discovery that high rates of photosynthesis per chlorophyll molecule are correlated with an unusual chloroplast structure.

An extremely high photosynthetic capacity may be due either to a greater enzyme content or to a more effective ratio of enzyme to chlorophyll or both, with or without a change in the size of the photosynthetic unit. Saturation

rates and structural differences, however, tell us nothing about the efficiency of the photosynthetic mechanism at low light intensities where the number of absorbed quanta determines the over-all rate. At low light intensities a chlorophyll-deficient leaf always fixed less carbon dioxide per leaf area than the green control. The question we are answering in this paper is to what degree, if any, can enzymatic rates and structure of chloroplast lamellae influence the efficiency of the energy conversion process. Until 1960, about 90% of the determinations of quantum requirements were made with *Chlorella* and other algae (see the tabulated data in Steward's Plant Physiology [18]). There are few determinations of quantum numbers for photosynthesis in leaves of higher plants. Nothing is known about the number of quanta required to evolve one molecule of oxygen in aurea mutants (compare reference 29).

The outcome of our experiments again raises the question of how the light energy is most effectively distributed among the various light-absorbing chloroplast pigments. The basis for further discussion is the confirmation that the optimal quantum number for complete photosynthesis remains about 10—irrespective of lamellar structure or enzymatic capacity.

#### MATERIALS AND METHODS

##### *Description of the Tobacco Plants*

The tobacco with the designation Su/su is a dominant aurea mutant discovered by Burk and Menser (reference in 33). Its green control is the cigar variety John Williams Broadleaf (JWB).

There are several lines of Virescent tobacco. The tobacco we used was Virescent 402, a mutant which was induced by X-irradiation by J. L. Apple. The mutant was increased by Dr. D. U. Gerstel, cytogeneticist in Raleigh, North Carolina, in 1958. The inheritance is not known.

##### *Energy Measurements*

Light energies were measured with a large surface bolometer (H. Röhrig, Berlin, Germany) and a homemade integration sphere which contained three silicon photocells facing the sphere wall. The photocells were connected in parallel. Calibration was done with a standard carbon filament lamp (E 6410, The Eppley Laboratory, Inc., Newport, R.I.)

Light energies outside the sphere, in such places as along optical benches or inside thermostats etc., were measured with movable photocells and an ISCO Spectroradiometer (Instruments Specialties Co., Lincoln, Neb.).

##### *Light Sources and Filters*

We used either 150 w floodlights or 150 w cool beam spotlights (General Electric). To divide the spectrum of visible light into red and blue halves, we used plastic filters whose transmittances measured for an ordinary incandescent lamp are shown in Fig. 1. A combination of these lamps and filters gave the results contained in

Tables I to IV. From the transmittances of these filters, the emission spectra of the light sources, and the absorption characteristics of the leaf samples (measured with a Perkin-Elmer model 350 spectrophotometer) we calculated the average absorbed light to be  $3 \times 10^{-12}$  ergs/quantum for red light and  $4.5 \times 10^{-12}$  ergs/quantum for blue light. As a source of far-red light we used a Sun gun lamp from Sylvania (movie lamp type DWY). In the text and tables we shall abbreviate blue light as B and far-red light  $\lambda > 700 \text{ m}\mu$  as FR.

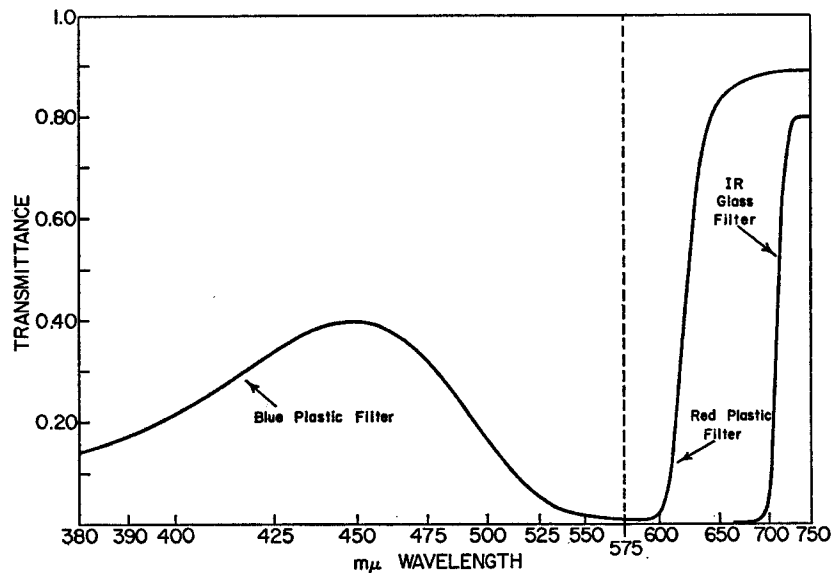


FIGURE 1. Characteristics of filters for red, blue, and dark red light. Transmittance vs. wavelength.

#### *Light Absorption in Leaves*

As Willstätter and Stoll found (36, 37), light absorption in pale and dark green leaves is not proportional to chlorophyll content. The light passes through the epidermis and after entering the palisade cells strikes the chloroplasts. Light is reflected at each partition. The light which is not absorbed passes into the sponge cells and most of this light is scattered in all directions. In this way, the chloroplasts are illuminated from all sides, and part of the incident light may pass through the chlorophyll-containing layers several times. Light will be reflected more often in a pale leaf than in a strongly absorbing dark green leaf. Chlorophyll content and relative light absorption are given in Table I. At three considerably different intensities in the linear region of the light curve, and for all the plants listed in Tables II and III, we always obtained the same results.

The light energy in the spectral region  $\lambda$  600–700  $\text{m}\mu$  was determined separately with the ISCO Spectroradiometer mentioned above. Knowing that leaves absorb very little light beyond  $\lambda$  700  $\text{m}\mu$ , we measured the far-red absorption with a bolom-

eter and integration sphere. Of the energy beyond  $\lambda$  700  $m\mu$  transmitted through our IR glass filter of Fig. 1, the leaf sections absorbed only 0.3 to 0.6% of the incident energy. Obviously our energy measurements in this spectral region were not as accurate as those in the visible part of the spectrum. Even these low absorption values are likely to be too high because cell water and mineral salts probably absorbed a considerable portion of the light. To get a clearer picture of the light scattering in the far-red, we sometimes used several leaf sections piled on top of each other and measured the absorption increment per additional leaf section in the same manometer vessels in which the rate of photosynthesis had just been determined. Empty vessels were used as controls.

TABLE I  
RELATIVE LIGHT ABSORPTION OF LEAVES WITH DIFFERENT  
CHLOROPHYLL CONTENTS IN RED LIGHT AT 25°C  
Valid for energy range of 2700–6900 ergs/sec/cm<sup>2</sup>.

Tobacco	No. of experiments	Total chlorophyll	Absorbed energy % of incident light of the region 600 < $\lambda$ < 700 $m\mu$ *
		$\gamma/cm^2$	
N. t. Burley var.	4	35±9	80 (72–93)
N. t. Rg. Y. Gr.	7	8±3	57 (52–65)
N. t. Su/su	9	7.6±3.4	62 (59–64)
N. t. Burley 21	4	4.6±1	44 (41–47)
N. t. aurea from Japanese Bright Yellow	2	2.1±0.5	27 (24–30)

N. t. = *Nicotiana tabacum* in Tables I to III.

\* Red plastic filter (Fig. 1).

#### Measuring Photosynthesis

Photosynthesis was measured as <sup>14</sup>CO<sub>2</sub> fixation or as O<sub>2</sub> exchange. Because respiration may change in the course of the experiment, it was determined before and after illumination. With 0.5% CO<sub>2</sub> in air, carbon dioxide was neither limiting nor inhibitory, and 20% oxygen, as compared with 1% O<sub>2</sub> in nitrogen, did not inhibit photosynthesis significantly. We mention this because, in some plants, oxygen seems to inhibit photosynthesis strongly, especially when carbon dioxide is as low as in normal air (0.03% CO<sub>2</sub>) (9). Leaves were cut into carefully measured sections of 4 cm<sup>2</sup> each with a sharp razor blade. Depending on the light intensity, the rates of photosynthesis in these sections varied between 30 and 100  $\mu$ l O<sub>2</sub> evolved per hour. We found it advantageous to work at a light intensity where the rate of photosynthesis was about four times the rate of respiration (compare figs. 2 and 3). The quantum yields obtained in this way matched precisely the yields calculated from <sup>14</sup>CO<sub>2</sub> fixation.

#### Emerson Enhancement

Emerson enhancements are given simply as per cent increase of the rate of oxygen evolved during simultaneous exposure above the sum of the separate rates found in

the visible and far-red light (corrected for respiration). These numbers are comparable to the "excess rate" in the terms of Bannister (3). We see no advantage in defining enhancement as a ratio out of ratios unless one has a special hypothesis in mind.

## RESULTS

### *Quantum Number in Red plus Far-Red Light*

Table II summarizes the results obtained with red + far-red light (red plastic filter of Fig. 1). There is no correlation whatever between chlorophyll content and molecular photosynthetic efficiency. The latter remained constant. Nearly all the leaves tested gave quantum numbers per O<sub>2</sub> evolved (measured by

TABLE II  
CHLOROPHYLL CONTENT AND QUANTUM NUMBER FOR OXYGEN  
EVOLUTION IN RED + FAR-RED LIGHT AT 25°C

Plant species	No. of experiments	Chlorophyll averages $\gamma/cm^2$	Quanta/O <sub>2</sub> evolved
<i>Cassia obtusifolia</i>	2	57	11
<i>Lespedeza spec.</i>	7	45	8
N.t. Burley var.	5	35	10
N.t. JWB green	3	20	9
N.t. X-ray 402	2	18.6	10
N.t. Rg. Y. Gr.	9	8	12
N.t. Su/su Y. Gr.	16	7.6	13
N.t. Burley 21	10	4.6	10
N.t. Jap. br. yellow	3	2.1	11
<i>Scenedesmus D<sub>2</sub></i> *	16	—	11

\* For *Scenedesmus* we measured the light absorption in 15, 30, and 45  $\mu$ l of cells.

manometry) which oscillated around the number 11. These values were found without searching for special physiological conditions (compare Bishop (7), for instance). But numbers as low as 8 were found occasionally. The values in Table II do not show more variation than can be seen in most of the earlier determinations of quantum numbers by other authors. It is noteworthy that neither a 25-fold change in chlorophyll content nor the fact that the path of light was different in pale and dark green leaves (see Methods and Table I) had a conspicuous influence on the quantum yield.

### *Quantum Numbers in Blue Light*

It is well known that in the blue region of the spectrum, light energy is lost due to absorption by inactive pigments. But the loss is mostly smaller than would be expected from the pigment content. This discrepancy was noted by various authors (compare Gabrielsen, 1960 [17]), and was later explained by the discovery of energy transfer between unlike pigments. It is certain that some light energy can be transferred from part of the yellow pigments to chlorophyll

(Dutton [10], French [15], Duysens [11]). As long as the quanta are absorbed by, or transferred to, the same pigment, it should be of no importance whether the quanta are those of red or blue light. With the same leaf material, we determined the number of quanta required per oxygen evolved or  $^{14}\text{C}$  fixed in the blue part of the spectrum and found only half the efficiency of red light (Table II). For many of the leaves, the quantum numbers for blue light shown in Table III ranged between 18 and 20.

### *Emerson Effect*

Emerson et al. (12) discovered a few years ago that a combination of visible and far-red light may often produce a higher photosynthetic rate (quantum efficiency) than the sum of the rates determined separately for each light. As

TABLE III  
CHLOROPHYLL CONTENT AND QUANTUM NUMBER FOR  
OXYGEN EVOLUTION IN BLUE LIGHT AT 25°C

Plant species	No. of experiments	Chlorophyll averages	Quanta/O <sub>2</sub> evolved
		$\gamma/\text{cm}^2$	
<i>Lespedeza spec.</i>	5	45	11
N.t. X-ray 402	2	18.6	23
N.t. Rg. green	2	—	13
N.t. Su/su Y. Gr.	5	7.6	18
N.t. Burley 21	7	4.6	15
N.t. Jap. br. yellow	3	2.1	21
<i>Scenedesmus D<sub>3</sub></i> *	3	—	19

\* For *Scenedesmus* we measured the light absorption in 15, 30, and 45  $\mu\text{l}$  of cells.

said before, the quantum numbers of Table II were determined in red light which included the far-red region. Our blue light did not contain measurable amounts of far-red light. We, therefore, had to test for Emerson effects. With very sensitive methods, such as  $^{14}\text{C}$  fixation or the platinum electrodes of Myers and Graham (27), it is always possible to discover some complete photosynthesis (the normal gas exchange) in "pure" far-red light ( $\lambda > 710 \text{ m}\mu$ ), particularly if the amount of incident energy is high. When measuring quantum yields by means of oxygen evolution, the gas exchange due to FR alone was either not measurable at all, or was an insignificant percentage of the total. For instance, in yellow light isolated from a G. E. Lucalox lamp by an interference filter ( $\lambda 580 \text{ m}\mu$ ), the quantum number in mutant Virescent 402 was 16. The FR light isolated through a band filter of  $\lambda 721 \text{ m}\mu$  gave no measurable response (photosynthesis in both FR and Y was measured by the fixation of  $^{14}\text{CO}_2$ ). The quantum number for FR was therefore  $\infty$ . The combination of both lights gave a quantum number of 13, or an improvement of 24%. For technical reasons, most of our Emerson effect studies were not done

with a band filter but with a cool light mirror and the IR filter shown in Fig. 1. Again we found that FR alone did not give a measurable evolution of oxygen.

Fig. 2 shows a very clear-cut Emerson effect in the tobacco X-ray mutant "Virescent 402". For this mutant the quantum number in blue light was approximately 25. In far-red light alone, the respiratory gas exchange continued as if in complete darkness. The combination of ineffective FR with B about doubled the rate of photosynthesis in B. This means that a few quanta of FR light suffice to increase the efficiency of the blue light process so much that the over-all efficiency approaches the normal range, particularly if we

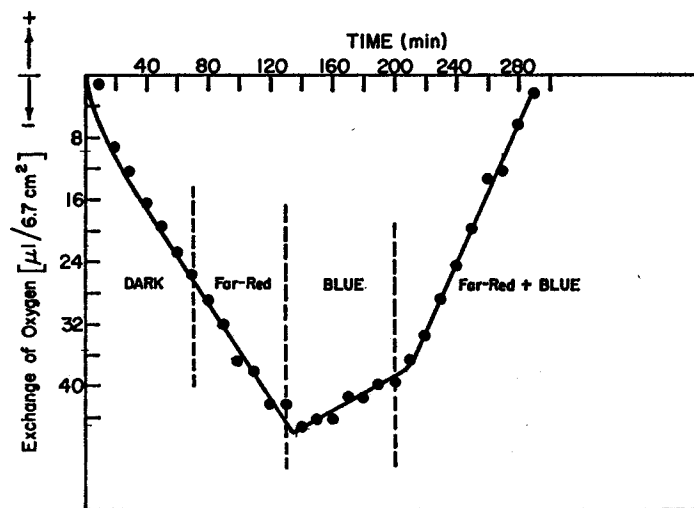


FIGURE 2. Time course of Emerson enhancement in *Nicotiana tabacum* Virescent 402. Far-red 25,300 ergs/sec/cm<sup>2</sup>; blue 3080 ergs/sec/cm<sup>2</sup>. Leaf area 6.7 cm<sup>2</sup>; 7.2  $\gamma$  total chlorophyll/cm<sup>2</sup>. Age of tobacco: 4 months after germination.

consider that there ought to be some ineffective absorption among the yellow pigments.

Table IV gives quantum yields found in blue (B) and blue plus far-red light (B + FR) for the X-ray mutant and two other tobacco varieties. The data show that by the addition of FR the number of quanta required for photosynthesis was lowered. With all three types of leaves, FR alone produced only negligible amounts of oxygen. The absorption of B by the leaf tissues ranged from 81% to nearly 100%, while that of FR was at best 0.65%; i.e., over 99% of FR was photochemically ineffective. By changing the light filter so as to include more light around  $\lambda$  700 m $\mu$ , the fraction of the incident energy absorbed within the region  $\lambda$  700–750 m $\mu$  rose to 5%. Under these conditions, an oxygen evolution could be detected in FR alone which, however, remained about one-tenth of the rate in blue light. By comparing experiments IIIa and IIIb in Table IV, done on the same plant, we can see the difference between

absolute gain in terms of photosynthetic products (due to the simultaneous exposure to B and FR) and the improvement in quantum efficiency. With increasing FR intensity, the Emerson enhancement reaches an optimum. Any excess absorbed light is wasted but nevertheless enters into calculations and therefore the latter will not show an improvement in terms of quantum efficiency.

For the determination of quantum numbers, we preferred intensities decidedly above the compensation point (above  $3 \times 10^3$  ergs/sec<sup>-1</sup>/cm<sup>-2</sup>) in order to stay away from the complications connected with the respiratory metabolism and particularly the Kok effect. The course of the light curves in

TABLE IV  
EMERSON EFFECT IN BLUE LIGHT

Tobacco	Quanta absorbed/sec [ $\times 10^{14}$ ]		Molecules O <sub>2</sub> /sec [ $\times 10^{14}$ ]		Quantum number		Emerson enhancement
	B	B + FR	B	B + FR	B	B + FR	
I	49	54	3.1	3.8	16	14	20
II	56	61	3.1	4.6	18	13	50
IIIa	60	65	2.34	3.84	26	17	65
IIIb	60	100	2.34	3.84*	26	26	45

Leaf area 8.2 cm<sup>2</sup>. I. Su/su yellow-green absorbed 81.5% of the incident blue light 380  $<\lambda < 580$  m $\mu$ ; 0.65% of incident far-red  $\lambda > 700$  m $\mu$ . II. Green part of green variegated leaf NC 95 absorbed 93% of incident blue light 380  $<\lambda < 580$  m $\mu$ ; 0.65% of incident far-red  $\lambda > 700$  m $\mu$ . IIIa. Virescent 402 absorbed 100% of incident blue light 380  $<\lambda < 580$  m $\mu$ ; 0.65% of incident far-red  $\lambda > 700$  m $\mu$ . For I, II, and IIIa quantum number for oxygen evolution in the far-red was  $\infty$ . IIIb. Virescent 402 absorbed 100% of incident blue light 380  $<\lambda < 580$  m $\mu$ ; 5% of the far-red energy 700  $<\lambda < 750$  m $\mu$ . Different filter from IIIa.

\* This far-red evolved 6.4  $\mu$ l O<sub>2</sub>/hr/8.2 cm<sup>2</sup>. The quantum number for oxygen evolution in this case was 95 for far-red.

Fig. 3 demonstrates what we mean. Kok discovered that the very first part of the light intensity curve, starting from darkness, may sometimes be steeper than the rest of the linear section of the curve up to and around that intensity which compensates respiration (24).

In Fig. 3, there are two examples of tobacco metabolism, one of which shows a pronounced Kok effect. In the latter, the steep slope corresponds to a quantum number of 9 for oxygen evolution (perhaps more correctly described as compensation). Further up the number is higher, and in this region the efficiency can be improved by the addition of FR. We agree with Myers, who could not find an Emerson enhancement in the steeper part of the Kok curve.

#### DISCUSSION

We shall begin with a set of statements expressed in the most self-evident manner we know of, because of late discussions on the role of coupled pigment



systems have assumed an air of complexity which seems to discourage all but a few specialists from acquainting themselves with the basic issues.

1. The complete unaided and uninhibited mechanism of photosynthesis, defined as the production of sugar and oxygen, requires a minimum amount of energy equivalent to 10 light quanta from the spectral region between  $\lambda$  360 and 700 m $\mu$ . 10 is a nice round number that happens to be the average of a thousand or so reliable determinations of the smallest photosynthetic quantum numbers which have been made in the course of the last 30 yr. Quibbling about whether the true number is 9 or 11 is beside the point we want to make here.

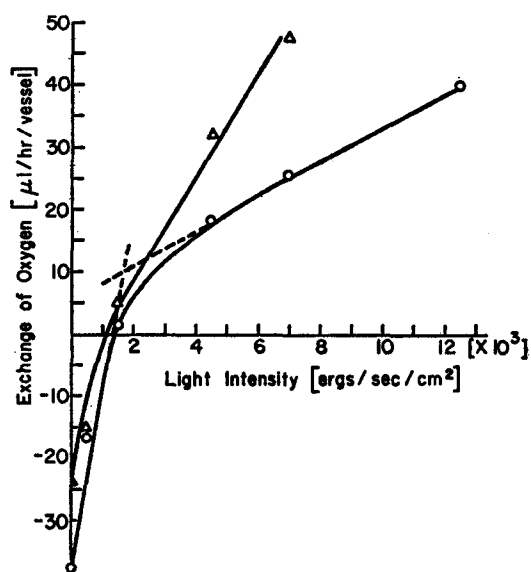


FIGURE 3. Rate of photosynthesis vs. light intensity in blue light on the basis of leaf area. Temperature 25°C. Open triangles, *Nicotiana tabacum* "Rg derivative with Y. Gr. character" 526-1-2y. Leaf section contained 49  $\gamma$  total chlorophyll. Age 8 wk after germination. Open circles, *Nicotiana tabacum* Virescent 402. Age 5 months after germination. Leaf section contained 67  $\gamma$  total chlorophyll.

2. Within the mechanism driven by 10 quanta, we have to accommodate three energy-requiring partial reactions, which on a molecular basis are (a) the reduction of two coenzyme molecules; (b) the production of a minimum of three molecules of ATP; and (c) the oxidation of four molecules of water to yield one molecule of oxygen.

3. Each of the three reactions could be driven by its own specific chlorophyll system provided that the energy of 10 light quanta becomes distributed among the three chlorophyll systems so as to satisfy the energetic as well as the stoichiometric requirements of each. More than three systems are not needed, and two may be sufficient if one of them can play a double role. The double system is the present dogma propounded by a very impressive literature (11, 38).

4. Redistribution of the absorbed quanta among the pigments involved, either by changing and mixing the colors of the incident light, or by changing

the relative distribution of absorbing pigments within the lamellar structure, cannot better the over-all optimal efficiency. This means that an improvement or enhancement of photosynthetic rates or efficiencies by mixing lights or tampering with the growth of plants is possible only when the efficiency has been suboptimal in the first place.

5. Because the spectral region  $\lambda$  700–750  $m\mu$  is able to promote complete photoreduction in hydrogen-adapted algae (4, 5, 6, 19) or the aerobic assimilation of acetate in air (34, 35) and because photophosphorylation in chloroplast preparations also proceeds well in FR light (1), we believe that nothing more may be needed to explain the Emerson effect than a pigment (chlorophyll?) which produces an extra supply of ATP. Its absorption happens to reach farther into the FR region around  $\lambda$  720  $m\mu$  than the absorptions of the other chlorophylls. This has been said often enough before, but was considered too trite an explanation to be unhesitatingly adopted by the experts in our field who are aware of so many other complications. By definition, as derived from direct observation, the Emerson pigment is photochemically unable to take part in the process leading to the oxidation of water. If so, only its energy-rich product ("ATP") is able to influence the over-all process.

The plain data of Table II need no further discussion. This is not as evident for the results on the Emerson enhancement (Table IV).

Quite obviously no amount of FR will be able to lower the quantum number in photosynthesis below the thermodynamic requirement of the combined partial processes. Efficiencies corresponding to the quantum number 9 can hardly be improved upon. And in practice we have not seen such a case, nor have those authors who years earlier devoted their best efforts to the analysis of the enhancement in question.

We take the existence of a typical action spectrum for the Emerson effect (Myers [26], French [14], Govindjee [22]), to mean a spectral variation in the distribution and balance of the energies absorbed by two or more pigment systems having separate photochemical assignments (see also Bannister and Vrooman [3]).

The most interesting region of diminished photosynthetic efficiency in green plants is the blue half of the spectrum. Here carotenes absorb a good part of the light energy (see Gabrielsen's review, 1960 [17]) and this may have three consequences. First, the light energy may be wasted, second, it can be transferred to at least one of the chlorophylls (Dutton [10], Duysens [11]), and third, it may cause a new light-induced but nonphotosynthetic metabolism (Kowalik and Gaffron [25]). To what extent this latter independent light reaction, probably first seen as a transient in the quantum yield measurements of Emerson and Lewis 25 yr ago, influences the course of photosynthesis, we do not yet know (13). As the quantum numbers for blue light in Table III show, the efficiency of many leaves in the blue was poor, about half or less of the best

possible. In addition it is worth noting that in the experiments of Fig. 3, a quantum number as low as 9 below compensation in unaided blue light (which was nearly totally absorbed) means that virtually none of the light absorbed by the yellow pigments was wasted.

The good efficiency measured after combining blue with far-red proved that the originally poor efficiency was not so much due to a nonspecific dissipation of energy but rather to a reparable loss in function. Evidently, light absorbed by the leaves in the blue region, in order to be fully effective, had to be supplemented by a certain quantity of Emerson photoproduct (ATP?). This means that the well-known dip around  $\lambda$  480 m $\mu$  in such efficiency spectra may well be an artifact and absent in plants exposed to daylight. Thus, the surprisingly poor photosynthetic rates in blue light, which we reported in the preceding paper (32) for our yellow mutants might become much better with the addition of the proper dose of FR. We did not think of this at that time because we did not expect to find such a large Emerson effect. The situation becomes still more complicated when we consider that the magnitude of Emerson effects varies with the stage of growth in the same plant. The clearest example of a daily variation (in the alga *Scenedesmus*) has just been published by Bishop and Senger (7). We observed that leaves of a single plant (*Nicotiana tabacum* Su/su) either gave up to 44% enhancement or none at all. In our opinion, what varied was the demand for the Emerson photoproduct (ATP?). This demand probably changed with the concentrations of those substances which could compete for the available ATP. Compare, for example, the effect of glucose on photoreduction in algae (Gaffron and Rubin [20], Bishop and Gaffron [6]), or on the phosphorylation of glucose in FR (Kandler [23], Wiessner [34, 35]).

If this is so, any other intracellular source of ATP ought to diminish the enhancement phenomenon and, at the same time, increase the photosynthetic efficiency. It might be more than just a coincidence that leaf sections which had an unusually strong respiration (more than 20  $\mu$ l/hr/4 cm<sup>2</sup> of oxygen uptake) gave consistently lower quantum numbers and the weakest Emerson effects. Such a plant was *Lespedeza procumbens* (see Table II) in which we found quantum numbers of 8. The difference in Emerson enhancement effects between plants grown at high and at low intensities which has been reported from French's laboratory (8), may be a similar case.

The rather obvious explanation offered by Wiessner and Bishop and Gaffron a few years ago for the entire network of FR phenomena (6, 34), namely a separate chlorophyll system designed to deliver energy-rich compounds akin to the system found by Frenkel in purple bacteria (16), and which need not be identical with system I, also fits recent observations by Glenn and Govindjee (21). Heavy water is known to retard enzymatic, not photochemical steps in photosynthesis (28). Glenn and Govindjee found

that throughout the visible spectrum the photosynthesis of deuterated algae was very inefficient (21). By offering a background of  $\lambda$  655  $m\mu$  on FR, they could improve the efficiency. They found that "the quantum yield of photosynthesis at  $\lambda$  730  $m\mu$  in the presence of  $\lambda$  655  $m\mu$  background light was higher than the maximum quantum yield of photosynthesis observed at any wavelength without background light." If we assume an interference of heavy water first of all with the efficiency of Arnon's photosynthetic phosphorylation (2), a few extra quanta absorbed exclusively by the cyclic phosphorylation system would restore the balance (enhance the turnover of ATP).

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