EMERSON ENHANCEMENT EFFECT AND THE REACTIVATION OF PHOTOSYNTHESIS IN PHOSPHATE DEFICIENT LEMNA MINOR*

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SUMMARY

Photosynthetic enhancement, studied in the wavelength pair 650/717 nm, is expressed as
$$E_{650(717)} = \frac{PS_{650\ +\ 717} - PS_{717}}{PS_{650}} \text{ and as } E_{717(650)} = \frac{PS_{650\ +\ 717} - PS_{650}}{PS_{717}}.$$ The maximum
values of enhancement are considered to represent the ratio between the "potential coopera-
tive activities" (PCA) of the two photosystems:
$$E_{717(650)}^{max} = \frac{PCA_I^{717}}{PCA_{II}^{717}} \text{ and } E_{650(717)}^{max} = \frac{PCA_{II}^{650}}{PCA_I^{650}}$$
Under conditions of P-deficiency $E_{650(717)}^{max}$ tends to increase. However, when deficient plants
have reactivated their photosynthesis (PS) by P-uptake, it decreases. This result demonstrates
that far red light to a certain degree overcomes the inhibiting effect of P-deficiency.
   A tentative explanation is based on the hypothesis that in P-deficient plants PS operates with
the less efficient pseudocyclic photophosphorylation at 650 nm as a 12-quanta process, whereas
with background light of 717 nm a switch takes place to a more efficient PS, operating with
cyclic photophosphorylation. PS, making use of the cyclic pathway, is thought to operate in
plants with normal P-content, thus showing the normal high efficiency.

1. INTRODUCTION

1.1. General

When the combination of two light beams of different wavelength brings about
a rate of PS[1], which exceeds the sum of the rates obtained at each wavelength
alone, the phenomenon of photosynthetic enhancement, also known as the
(second) Emerson effect, has been achieved (EMERSON & RABINOWITCH 1960).
Recently, the phenomenon has been reviewed by MYERS (1971).

   The external conditions for observations of enhancement are low, rate limiting
light intensity and properly chosen wavelengths. Generally, in green plants far
red light of $\lambda = 700$ to 720 nm and red light of 650 nm make an effective com-
bination (MYERS & FRENCH 1960; MYERS 1963).

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synthesis.
[1] The following abbreviations are used: PS: photosynthesis. S I, S II: photosystem I, II. PCA I,
PCA II: potential cooperative activity in photosystem I and II, respectively. ATP: adenosine
triphosphate. P_i = orthophosphate.

The Emerson enhancement effect has contributed in an important way to the current views on the mechanism of PS (cf. BOARDMAN 1968), according to which light reaction 1, located in photosystem I, operates in series with light reaction 2, located in photosystem II, by means of an electron transport chain.

Due to high content of in vivo forms of chlorophyll a with absorption maxima between 680 and 700 nm, far red is absorbed in relative excess by S I, whereas due to high content in chlorophyll a with an absorption maximum around 675 nm and to high content of chlorophyll b, red light of 650 nm is absorbed in excess by S II.

The Emerson effect is interpreted as the result of mutual utilization of excess activation in one photosystem at one wavelength, and in the other photosystem at the other wavelength.

Photophosphorylation is linked to photosynthetic electron transport (ARNON 1961). In this process ATP is formed, indispensable for CO_2 reduction. Under conditions of P-deficiency, the phosphate level of the plant may drop so far that photosynthetic electron transport is impaired (LINDEMAN 1972). The present study deals with the question, to which extent this effect on electron transport becomes manifest in the Emerson enhancement effect. MCLEOD (1961) described the disappearance of enhancement in P-deficient *Chlorella*. The data obtained with P-deficient *Lemna* point in quite another direction.

1.2. Theoretical: Maximum enhancement characterized as ratio of "potential cooperative activities"

Starting from the concept of two photosystems packed separately and connected for collaboration by an e^--transfer chain, the diagrams in *fig. 1* illustrate mutual enhancement of photosynthesis when short-wave and far-red light are combined.

Enhancement has been characterized as function of the rates of PS in short-wave and far-red light (MYERS 1963). The action spectra of enhancement suggest a close relationship to light absorption in the two photosystems (EMERSON & RABINOWITCH 1960). However, since not only absorbance but rather the efficiency of the light absorbed determines the effect of collaboration resulting in PS, the term "potential cooperative activity" is proposed.

The diagrams in *fig. 1* illustrate enhancement in terms of "potential cooperative activity" (PCA) of the two photosystems in dependence on incident radiation in a short-wave region (λ_2) and in far-red (λ_1). Connecting to the experimental part, as λ_2 was chosen 650 nm and as λ_1 717 nm. It is clear that any wavelength with the character of "light 2" or of "light 1" (cf. MYERS 1971) will do. PCA is defined as the rate of transfer of e^--equivalents brought about by photochemical activity resulting in photosynthetic CO_2-reduction under the condition of relative excess in e^--acceptors and e^--donors in the e^--transfer chain, as is characteristic for light limited PS.

At 650 nm S I activity limits PS. Then, PCA_I^{650} is equivalent to PS_{650} (*fig.1c*). At 717 nm S II activity limits PS, consequently PCA_{II}^{717} is equivalent to PS_{717} (*fig. 1b*). Combining the figures 1b and 1a further illustrates enhancement at 650 nm on a constant background PS at 717 nm ($= p_{717}$). The combination of
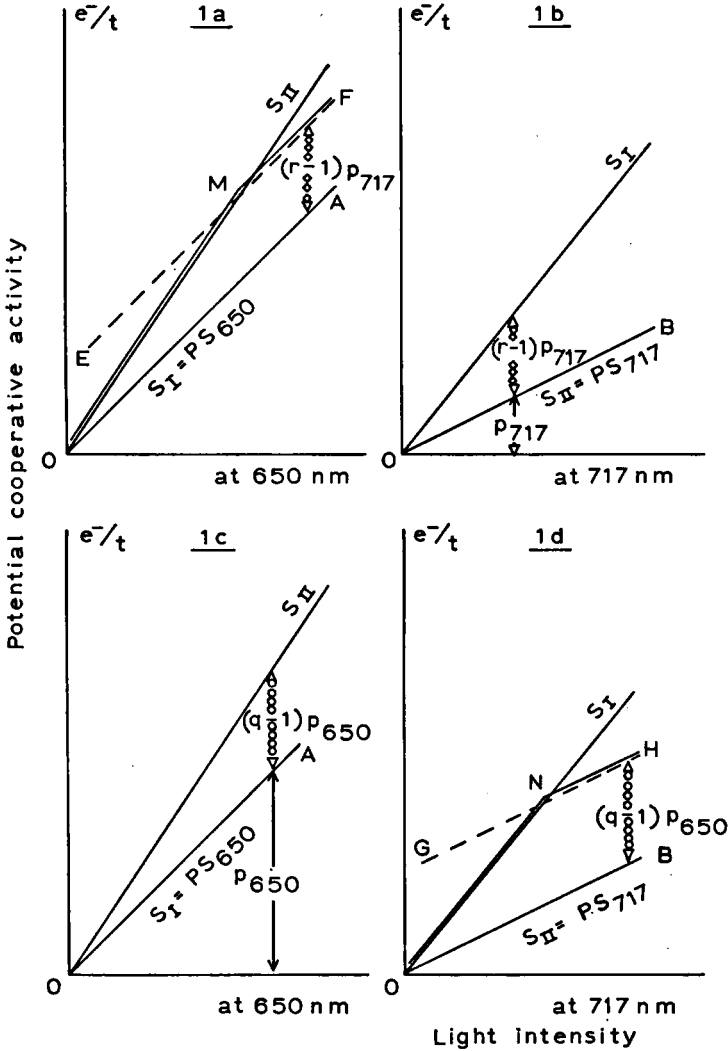
Fig. 1. Diagrams illustrating enhancement on the basis of mutual potential cooperative activity of the photosystems I and II (S I and S II). r, q: ratios of potential cooperative activities of S I and S II at 717 and 650 nm, respectively, according to:
$r = PCA_I^{717}/PCA_{II}^{717}$. $q = PCA_{II}^{650}/PCA_I^{650}$
1a: double line: enhanced photosynthesis at 650 nm on constant background rate at 717 nm ($= p_{717}$).
1b: PCA at 717 nm, with excess activation in photosystem I.
1c: PCA at 650 nm, with excess activation in photosystem II.
1d: double line: enhanced photosynthesis at 717 nm on constant background rate at 650 nm ($= p_{650}$).
Further explanation: see text.

the figures 1c and 1d does so for enhancement at 717 nm on a constant background PS at 650 nm ($=$ p_{650}).

The ratio between the potential cooperative activities of the two photosystems at 650 nm and at 717 nm is given by:

$$\frac{PCA_{II}^{650}}{PCA_{I}^{650}} = q \quad \text{and}: \frac{PCA_{I}^{717}}{PCA_{II}^{717}} = r.$$ With certain restrictions, q and r can be considered to have constant values.

The excess activation of S I at 717 nm is given by (r-1). PS 717; for the constant background rate p_{717} this is written as (r-1). p_{717} (see *fig. 1b*). At 650 nm the excess activation of S II is (q-1). PS_{650}; at the constant background rate p_{650} it is (q-1). p_{650} (see *fig. 1c*). In the combination of PS_{650} with the constant background rate p_{717} (see *fig. 1b & 1a*), the excess activation in S I at 717 nm is met by the excess activation in S II at 650 nm, bringing about enhancement. In *fig. 1a* this is shown by the line EF drawn parallel to OA, at a distance given by (r–1). p_{717}. The double broken curve OMF can be realized as enhancement in a range of varying intensities at 650 nm on the constant background rate p_{717}. Enhancement at 650 nm on 717 nm background is expressed, in principle according to

MYERS (1963), as $E_{650(717)} = \dfrac{PS_{650+717} - PS_{717}}{PS_{650}}$. In the range OM the rate at combined wavelengths, $PS_{650+717}$, is: $PS_{650} + p_{717} + (q-1)PS_{650}$ (see *fig. 1 a, b & c*). It follows:

$$E_{650(717)} = \frac{\{PS_{650} + p_{717} + (q\text{-}1)PS_{650}\} - p_{717}}{PS_{650}}; E_{650(717)} = q.$$

This q is the maximum value of $E_{650(717)}$, which occurs with excess background 717 nm.

This means: $E_{650(717)}^{max} = q = \dfrac{PCA_{II}^{650}}{PCA_{I}^{650}}$

In the range MF (fig. 1a) the rate of PS in the combination of wavelengths $PS_{650+717} = PS_{650} + p_{717} + (r\text{-}1) p_{717}$. It follows

$$E_{650(717)} = \frac{PS_{650} + p_{717} + (r\text{-}1)p_{717} - p_{717}}{PS_{650}}$$

$$= 1 + \frac{p_{717}}{PS_{650}} (r\text{-}1)$$

Here, $E_{650(717)}$ is a linear function of the ratio between the rates of PS at 717 nm and at 650 nm.

Dealing with the *figs. 1c & 1d* in an analogous way, $E_{717(650)}$ has its maximum value in the range ON:

$$E_{717(650)}^{max} = r = \frac{PCA_{I}^{717}}{PCA_{II}^{717}}.$$

In the range NH: $E_{717(650)} = 1 + \dfrac{PS_{650}}{PS_{717}} (q\text{-}1)$, which means that $E_{717(650)}$ is

a linear function of the ratio between the rates of PS at 650 nm and at 717 nm.

The relationships as described above are illustrated in MYERS' fig. 1 (1963) and in *fig. 3* of this paper. In the present concept of enhancement in any combination of PS_{650} and PS_{717} (provided PS remains light limited) either $E_{650(717)}$ or $E_{717(650)}$ reaches the maximum value, which means that either

$$q = \frac{PCA_{II}^{650}}{PCA_{I}^{650}} \text{ or } r = \frac{PCA_{I}^{717}}{PCA_{II}^{717}} \text{ can be estimated. The points of intersection M}$$

(*fig. 1a*) and N (*fig. 1d*) represent the interesting case in which $E_{650(717)}$ and $E_{717(650)}$ both have the maximum value. Then, the quantum efficiency has reached the maximum value possible in the combination of wavelengths given.

The double, broken lines OMF (*fig. 1a*) and ONH (*fig. 1d*) are thought to be realized experimentally by MYERS (1963, fig. 7, curves F & G) and in the present study (*fig. 2 & 4*).

No enhancement should occur, when at some wavelength combination or under some internal physiological condition one and the same photosystem is rate limiting for PS. Then, the slopes of the potential cooperative activities will have the same relative positions: either is S I more active than S II at both wavelengths, or the reverse happens. Depending on the physiological or structural condition, enhancement also might be variable at the same wavelength pair (cf. MYERS 1971; PUNNETT 1971; this paper). Then, the values of q and r (considered to be generally constant) may have altered.

2. METHODS

Most of the details on growing *Lemna minor* in axenic culture (+P and −P) and on measurements of PS are given in a previous paper (LINDEMAN 1972). Some basic as well as some additional information follows here. PS was measured by means of a diaferometer (katharometer). Air enriched with 5% CO_2 was used. Connected to the Kipp Micrograph BD_5 recorder, a full scale deflection corresponding to a voltage change of 0.1 mV was obtained with a change in CO_2 content of 204 ppm.

The katharometer is also sensitive to O_2 changes. As can be computed from data of PIETERS (1971, table 3.7), in air + 5% CO_2, the sensitivity for O_2 is 11.8% of the CO_2 sensitivity, with the opposite sign. In PS measurements the deflection of the recorder thus is mainly caused by decrease in CO_2, but it is enlarged by increase in O_2. The data on CO_2 uptake as given in this article have been obtained by correcting the readings for O_2 sensitivity in multiplying the difference "deflection in light" minus "deflection in dark" with the factor $100/111.8 = 0.895$. They are based on the assumption of a constant assimilation quotient of 1.

The gas flow in the PS measurements was 4 liters/hour.

In the first series of experiments the two light beams of different wavelength were combined by directing one beam from a slide projector at an angle of 90° on the fronds, the other beam from a second slide projector at an angle of 45°. In the second series beam splitting filters (Balzer no. 93 or B_1/K_1 1256/283) were

used, which allowed both beams to fall on the fronds at an angle of 90°.

Balzer interference filters B40 mounted in a water cooled frame attached to the slide projectors provided the 650 and 717 nm regions.

In the experiments the $-P$ sample of *Lemna* plants takes up phosphate in the dark, generally for 16 hrs, and thus becomes the $-P+$ sample. The PS measurement in the $-P+$ condition takes place 20 to 24 hrs after the measurement in the $-P$ condition. Some expansion in frond area, amounting to 5 to 10%, may occur in this period.

However, after prolonged P-deficiency conditions for growth may be considered less favourable than after a short period of P-depletion. Since in the latter case frequently no effect is observed of P-supply on PS, extension of the photosynthetic apparatus caused by P-uptake probably is negligible.
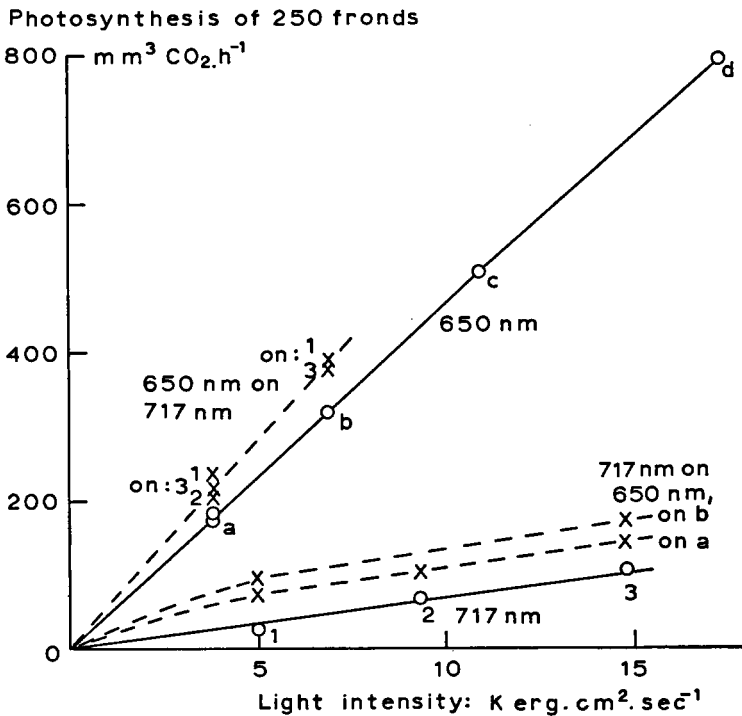

Fig. 2. Enhancement in normal (+P) *Lemna minor* plants.
O——O : photosynthesis at either wavelength alone.
×– – –× : enhanced photosynthesis at 650 nm on background rates at 717 nm indicated by 1,2,3.
×– – –× : enhanced photosynthesis at 717 nm on background rates at 650 nm indicated by a,b. Photosynthesis measured at 30°C in air enriched with 5% CO_2.

3. EXPERIMENTS

3.1. Enhancement in normal (+P) plants

In the experiment of *fig. 2* two light intensities of 650 nm are combined with three of 717 nm, all of which probably are high enough to saturate enhancement at 650 nm. Consequently, $E_{650(717)}$ has reached the maximum value, and, expressed as

$$E_{650(717)} = \frac{PS_{650+717} - PS_{717}}{PS_{650}}, \text{ amounts to 1.23.}$$

Only the lowest rate of PS at 717 nm, combined with high PS at 650 nm, approaches the maximum enhancement at 717 nm on background 650 nm (*fig. 2*, "1 on b"). There, $E_{717(650)}^{max} = \dfrac{PS_{650+717} - PS_{650}}{PS_{717}}$ amounts to 2.7.

In *fig. 3* the data of five experiments with +P plants have been plotted according to MYERS (1963). From this graph, as mean values of maximum enhancement in +P plants were estimated:
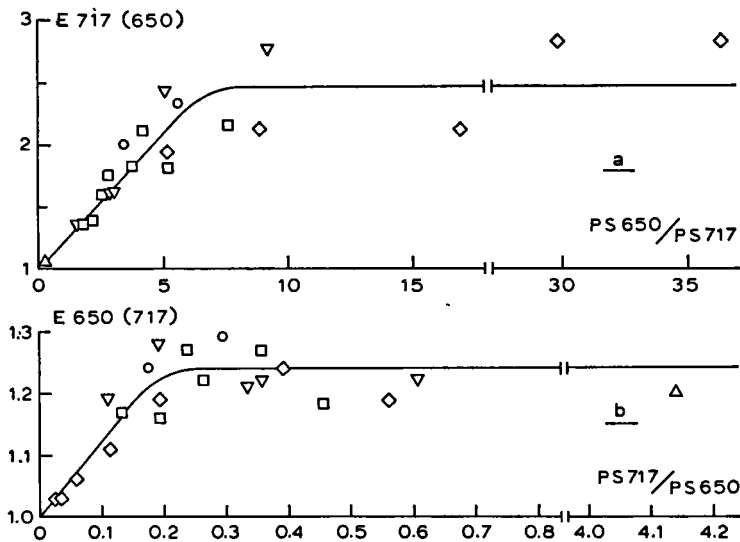$E_{650(717)}^{max} = 1.22$ and $E_{717(650)}^{max} = 2.5$.

Fig. 3. Average enhancement in normal (+P) *Lemna minor* plants in relationship to the ratio between rates of photosynthesis at either wavelength alone.
a. Enhancement at 717 nm on background 650 nm, expressed as $E_{717(650)} = \dfrac{PS_{650+717} - PS_{650}}{PS_{717}}$, versus the ration between the rates of photosynthesis at 650 nm alone and at 717 nm alone.
b. Enhancement at 650 nm on background 717 nm, expressed as $E_{650(717)} = \dfrac{PS_{650+717} - PS_{717}}{PS_{650}}$, versus the ratio between the rates of photosynthesis at 717 nm alone and at 650 nm alone.
Different symbols refer to different experiments.

These enhancement values are fairly close to those measured in higher plants by other authors. LITVIN & HO I-T'AN (1967) reported in *Elodea* an enhancement at 650 nm on background 717 nm of 1.5, and for enhancement at 715–720 nm on background 650 nm 4.5; in rice it was 2 in the latter combination. PUNNETT (1971) reports a maximum value of 18 % in *Egeria densa* in the combination 647/700 nm, which corresponds well with the maximum of 19 % found in point 1,b (*fig. 2*), representing $E^{max}_{650(717)} = 1.23$ in the formula of Myers.

3.2. Enhancement in phosphate deficient (−P) plants

Table 1 gives the data concerning the influence of P-deficiency. In the 2nd and 3rd column, they demonstrate that the effect of P-supply on PS of deficient plants in the light-limited range is generally larger at 650 nm than at 717 nm. This difference, described in a previous study, has been interpreted as the inhibiting effect of P-deficiency on PS, which is larger at 650 nm than at 717 nm (LINDEMAN 1972).

The 4th column of *table 1* shows that with proceeding P-deficiency, as indicated by the increase in reactivation of PS upon P-supply to −P plants ("−P+ effect"), the general trend is an increase of enhancement at 650 nm on excess background light of 717 nm: $E^{max}_{650(717)}$ increases from the average value of 1.23 in +P plants up to 1,49 in −P plants. *Fig. 4* shows the effect of P-deficiency and of subsequent P-uptake in detail. In *fig. 5* $E^{max}_{650(717)}$ of −P plants is plotted versus the −P+ effect, obtained with the same plants after P-uptake. The graph suggests a value of $E^{max}_{650(717)}$ in −P plants of about 1.4 at a −P+ effect of 60 %. In the few cases of very high −P+ effects $E^{max}_{650(717)}$ is lower again. A high −P+ effect may be due in part to the rather non-specific effect of reactivation of that part of the photosynthetic apparatus, which has been inactivated completely by P-deficiency. Tentatively, the −P+ effect at 717 nm may be considered to represent the extent to which total, but reversible inactivation took place. PS_{650} both in −P and −P+ plants decreases with increasing −P+ effect (*table 1*, col. 9 & 10), which points to a structural influence of P-deficiency on PS.

The cases with high $E^{max}_{650(717)}$ values at moderate −P+ effects probably demonstrate a specific P-dependent efficiency of the photosynthetic apparatus, in which complete inactivation of part of it plays only a minor role. There (expts. no. 24, 28 … 30) the −P + effect has an average value of 52 % at 650 nm, and of 16 % at 717 nm. The difference between these two values, 36 %, might be the specific −P+ effect at 650 nm. The improvement in light yield, which it represents, is very close to the improvement brought about at 650 nm by background light of 717 nm in −P plants, which amounts to 40 % (as follows from the mean value of $E^{max}_{650(717)} = 1.40$). Far red thus "replaces" phosphate when light yield at 650 nm is concerned.

Rather in contrast to $E^{max}_{650(717)}$, $E^{max}_{717(650)}$ does not show any clear trend during P-deficiency. It is variable, with a mean value of 2.3.

Table 1. Photosynthetic enhancement in *Lemna minor* in relationship to P-deficiency and subsequent P-uptake.

−P: phosphate deficient plants.

−P+: the same plants after uptake of phosphate for 16 hours in the dark from 1 mM KH_2PO_2 solution.

−P+ effect as per cent increase of light-limited photosynthesis after P-uptake.

$E_{650(717)}^{max}$: maximum enhancement at 650 nm on background 717 nm.

$E_{717(650)}^{max}$: maximum enhancement at 717 nm on background 650 nm.

Measurements are made at 30°C, in air enriched with 5% CO_2.

Expts. numbered 1–18: 650 nm beam falls on the fronds at an angle of 90°, 717 nm beam at 45°; expts. numbered 19–30: both beams at 90°.

The experiments are arranged according to increasing −P+ effect at 650 nm.

1	2	3	4	5	6	7	8	9	10
No expt.	−P+ effect at 650 nm %	at 717 nm %	$E_{650(717)}^{max}$ −P	−P+	S.F. $\frac{E_{650(717)}^{max}-P}{E_{650(717)}^{max}-P+}$	$E_{717(650)}^{max}$ −P	−P+	PS at 650 nm, 1 k erg.sec^{-1}.cm^{-2} mm^3 CO_2.h^{-1}.cm^{-2} −P	−P+
14	0	0	1.18	1.18	1.00	−	−	3.4	3.4
22	0	0	1.25	1.18	1.06	−	−	3.4	3.4
16	7	0	1.19	1.21	0.98	−	−	3.0	3.2
5	7	8	1.22	1.21	1.01	−	−	3.0	3.2
13	7	12	1.26	1.23	1.02	2.15	2.15	3.4	3.6
15	12	0	1.24	−	−	1.8	1.95	3.5	3.8
29	13	0	1.25	1.20	1.04	−	−	2.5	2.8
2	14	0	−	−	−	3.3	3.2	4.4	5.0
23	14	0	1.30	1.16	1.12	−	−	3.3	3.8
11	14	14	1.27	1.25	1.02	2.5	1.75	5.7	6.4
6	16	0	1.22	−	−	3.1	2.7	4.3	5.0
9	16	0	−	1.19	−	1.96	2.6	4.1	4.8
10	18	0	−	1.13	−	1.95	2.25	3.8	4.5
31	19	0	1.34	1.21	1.10	1.9	1.9	2.4	2.9
27	22	10	1.40	1.22	1.15	−	−	2.4	2.9
12	23	0	1.10	1.10	1.00	−	−	2.9	3.6
21	23	2	1.31	1.24	1.06	1.65	1.7	2.9	3.6
19	33	0	1.30	1.31	0.99	1.9	1.65	2.2	2.9
24	42	26	1.35	1.24	1.09	−	−	2.7	3.8
28	44	12	1.44	1.19	1.21	−	−	2.0	4.0
17	47	0	1.31	1.15	1.14	2.15	2.75	2.5	3.7
7	47	21	−	−	−	2.9	3.1	3.4	5.0
1	47	27	1.40	1.23	1.14	−	−	3.1	4.6
8	48	0	−	−	−	2.4	2.55	3.4	5.0
25	55	41	1.51	1.13	1.34	−	−	2.2	3.4
4	57	0	−	−	−	3.4	3.0	3.2	5.0
3	57	23	1.33	1.14	1.17	−	−	2.7	4.2
26	63	0	1.49	1.24	1.20	−	−	2.0	3.3
30	66	24	1.37	−	−	2.05	1.55	1.6	2.7
20	92	10	1.29	1.16	1.11	−	−	1.4	2.7
18	175	87	1.25	1.09	1.15	−	−	0.8	2.2

average expts. with −P+ effect

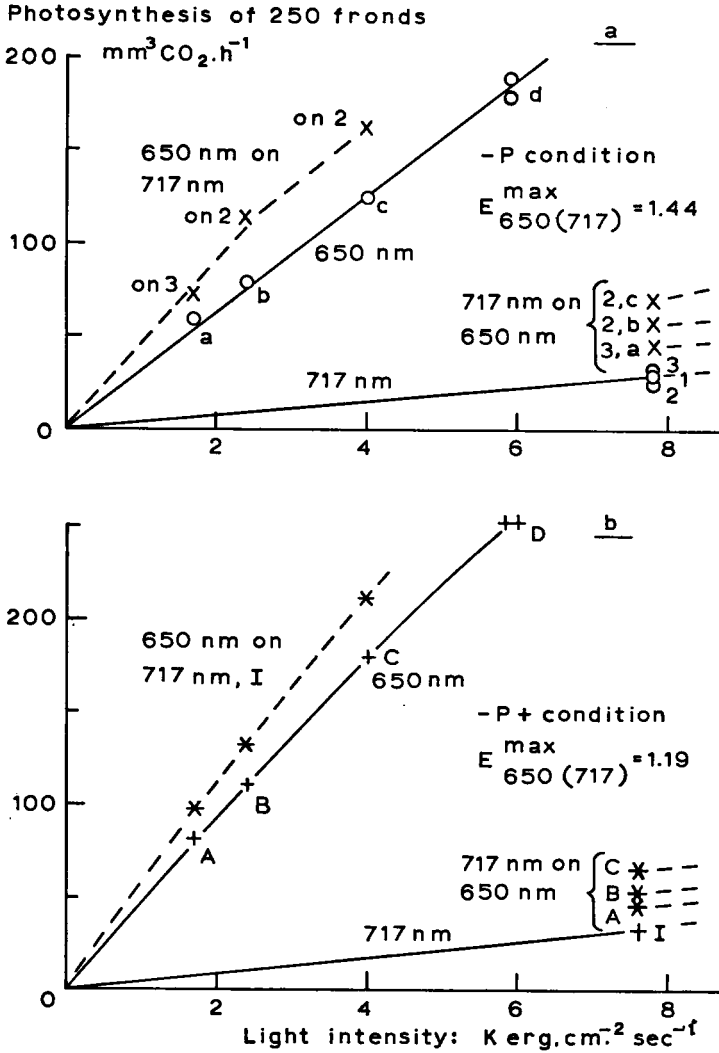|									
< 40%	14 ±2.0	2.6 ±1.1	1.26 ±0.02	1.20 ±0.01	1.04 ±0.01	2.2 ±0.2	2.2 ±0.15	3.4 ±0.4	3.8 ±0.5
40–70%	52 ±2.5	16 ±4.5	1.40 ±0.03	1.19 ±0.02	1.18 ±0.03	2.6 ±0.25	2.6 ±0.3	2.6 ±0.4	4.1 ±0.5

Fig. 4. a. Enhancement in phosphate deficient $(-P)$ *Lemna minor* plants.
b. Enhancement in the same plants after uptake of phosphate (from 1 mM KH_2PO_4 for 16 hrs. in the dark).
Solid lines: photosynthesis at either wavelength alone.
Dashed lines: enhanced photosynthesis at 650 nm on background rates at 717 nm in a) indicated by 2, 3; in b) by I.
Asterisks: enhanced photosynthesis at 717 nm on background rates at 650 nm indicated in a) by the combinations 2,c 2,b 3,a; in b) by A, B, C. Photosynthesis measured at 30 °C in air enriched with 5 % CO_2.
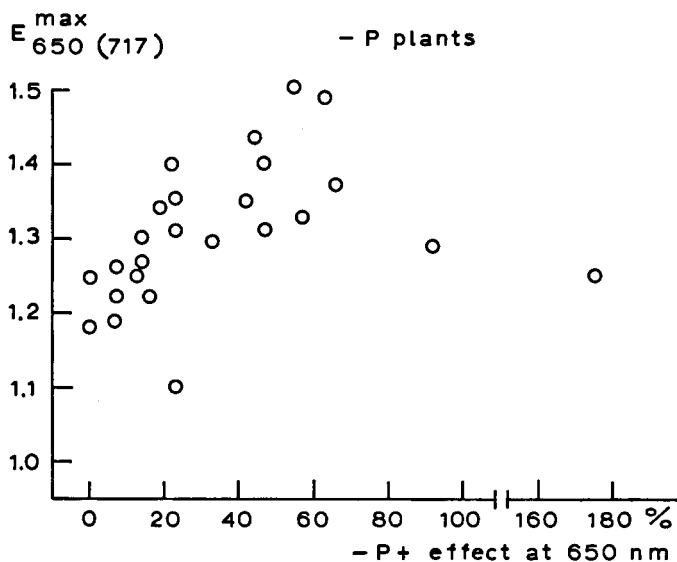
Fig. 5. Maximum value of enhancement at 650 nm on background 717 nm in connection with the $-P+$ effect of light limited photosynthesis of *Lemna minor* at 650 nm. $-P+$ effect: percent increase in photosynthesis after phosphate uptake.

3.3. Enhancement in reactivated $(-P+)$ plants

From *table 1* (5th column) it follows, that in deficient plants phosphate uptake brings about an enhancement of PS at 650 nm on excess 717 nm background, which at moderate low $-P+$ effect does not differ much from the mean value found in normal $(+P)$ plants. In *fig. 6* the value of $E_{650(717)}^{max,-P}$ is plotted versus $E_{650(717)}^{max,-P+}$ obtained from the same sample of plants. This plot shows clearly the shift from higher to lower values in the plants with a $-P+$ effect $> 40\%$. The analogous plot of $E_{717(650)}^{max}$ values shows a random distribution, which seems in agreement with the experience that at 717 nm the effect of the P-content of the plant on light-limited PS is lacking, or much smaller than at 650 nm. The mean value of $E_{717(650)}^{max}$ in $-P+$ plants is 2.3, the same as in $-P$ plants.

4. DISCUSSION

In the present study PS at 650 nm on excess background 717 nm shows an enhancement, which is considerably higher in P-deficient plants than in normal plants and in deficient plants, which have taken up phosphate.

At 650 nm alone P-uptake by $-P$ plants, too, leads to an improvement in light yield: far red light and phosphate can "replace" each other in $-P$ plants.

The phenomenon of high enhancement in $-P$ plants may bear relationship to the different effects of P-supply in short-wave and long-wave light that were
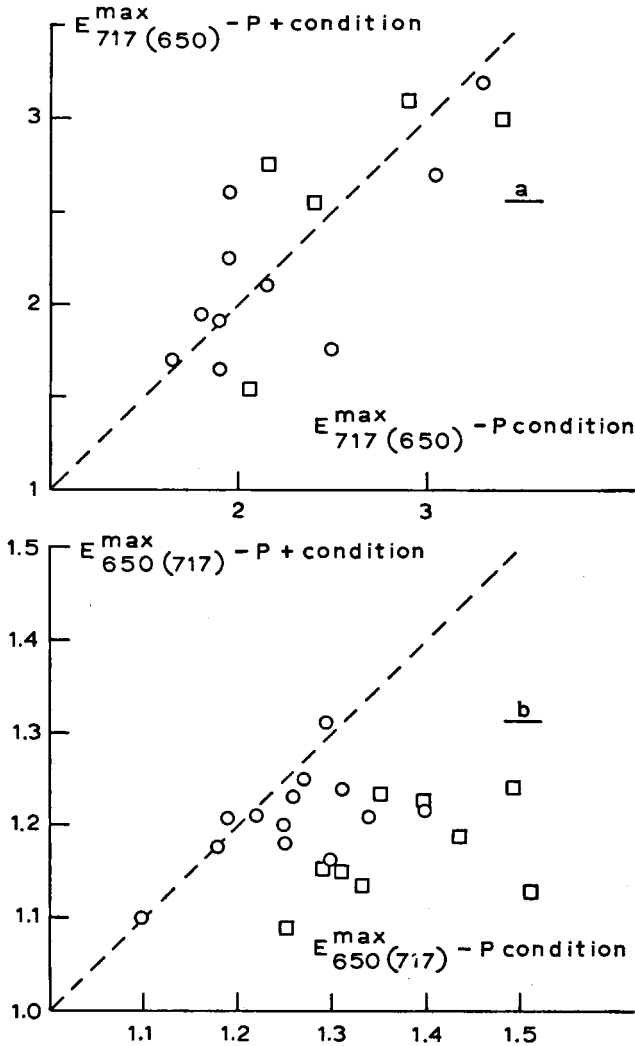
Fig. 6. Maximum values of enhancement in *Lemna minor* plants, in which after phosphate deficiency photosynthesis has been reactivated by phosphate uptake ($-P+$ condition), versus maximum values in enhancement before phosphate uptake ($-P$ condition).

○: $-P+$ effect $< 40\%$
□: $-P+$ effect $> 40\%$

described previously (LINDEMAN 1972). Light-limited PS in white light and in red light of 650 nm appeared much more sensitive to P-deficiency and subsequent P-supply than PS in far red light. Two causes for this dependency have been mentioned:

1. a change in efficiency in P_i controlled non-cyclic e^--transfer, due to a wave-

length dependant change in $[C_{red}]$, the reduced form of an e^--carrier linked to photophosphorylation.

2. the support given in far red light by highly activated cyclic photophosphorylation in providing the "3rd ATP".

Possibility 1) only may explain why in far red the inhibiting effect of P-deficiency is felt less than in short-wave light, without relationship to the high enhancement observed in $-P$ plants.

A connection with possibility 2), especially with the efficiency in the various mechanisms of photophosphorylation, seems more likely.

The expression $E_{650(717)}^{max} = \dfrac{PCA_{II}^{650}}{PCA_I^{650}}$ ($= q$, see *fig. 1 c, d*) generally can be considered to have a constant value, dependent on the ratio of absorbances in the two photosystems at constant efficiencies. If, however, the efficiencies alter in a way that differs in one photosystem from the other, $E_{650(717)}^{max}$ will follow this change. Due to a change in efficiency of photophosphorylation, this may happen with $-P$ plants, which after P-uptake become $-P+$ plants.

Cyclic photophosphorylation as a S I activity may well be a more efficient process than pseudocyclic photophosphorylation in providing the "3rd ATP", as required in the Calvin scheme of CO_2-reduction. From the work of TANNER et al. (1968) can be concluded to a quantum requirement of 2 or less for 1 ATP formed by *Chlorella* in the cyclic process. On the other hand, AVRON & BEN-HAYYIM (1969) estimated 3 as lowest requirement in chloroplasts. However, the plot in which this value has been obtained by extrapolating quantum requirement to zero absorption does not seem to exclude a much lower requirement. Pseudocyclic photophosphorylation, as a variant of the non-cyclic process, will need 2 quanta absorbed in S II and 2 absorbed in S I (cf. Loos 1967). This makes, theoretically, a 12-quanta process of PS in which the "3rd ATP" is formed in the pseudocyclic pathway.

Concerning possibility 2), an affinity for P_i, lower in the possibly more efficient cyclic process than in the less efficient pseudocyclic one, has been suggested as the basis for the effect of the P-level on light-limited PS (LINDEMAN 1972). At 650 nm, P-deficient plants might be forced to utilize the pseudocyclic pathway, whereas at 717 nm due to excess activation of S I the cyclic pathway is used. In normal $(+P)$ and reactivated $(-P+)$ plants the cyclic formation of the "3rd ATP" both at 650 and 717 nm should occur, leading to PS with normal efficiency.

In enhancement with $-P$ plants, when PS_{650} showing decreased efficiency is combined with PS_{717}, a switch from the 12-quanta process of "pseudocyclic" PS to the $(8 + x)$-quanta process of "cyclic" PS might occur, x (<4) being the quantum requirement of cyclic photophosphorylation.

In $-P$ plants, $E_{650(717)}^{max} = \dfrac{PCA_{II}^{650}}{PCA_I^{650}}$, then, is not only dependent on the difference in absorbance between S I and S II, but also on a shift in the efficiency of light utilization, which concerns PCA_I^{650}, controlling PS at 650 nm alone,

and PCA_{II}^{650}, controlling enhanced PS at 650 nm on excess 717 nm (cf. *fig. 1a*, where this means that the *slope* of OM increases in the case of enhancement).

In the experiments No. 24–30, *table 1*, the $-P+$ effect is moderately high: 42–66%. There, the average value of $E_{650(717)}^{max,-P}$ amounts to 1.40 ± 0.03, whereas $E_{650(717)}^{max,-P+}$ has the mean value of 1.19 ± 0.02.

The enhancement factor 1.40 found in $-P$ plants can be considered to be the product of two factors:

a. the "true enhancement" factor, not affected by phosphate and based on absorbance differences at constant efficiency; it is the factor measured in $+P$ and $-P+$ plants, in the latter amounting to 1.19 ± 0.02.

b. the "switch factor" (SF) representing an improvement in efficiency of the light absorbed, and hypothetically based on a switch from pseudocyclic to cyclic photophosphorylation, brought about at 650 nm by the background light of 717 nm. The mean value of this factor amounts to $\dfrac{1.40}{1.19} = 1.18 \pm 0.03$.

Applied to the presumed 12-quanta process operating in $-P$ plants at 650 nm, such a switch brings down the quantum requirement to $\dfrac{12}{1.18} = 10.2$.

From the average total enhancement factor in $-P$ plants of 1.40, the basic requirement of PS at 650 nm on excess background 717 nm might be estimated at $\dfrac{12}{1.40} = 8.6$ quanta absorbed per CO_2 reduced.

These values can only be considered as minimum requirements of the basic photosynthetic reactions. They are in agreement with a concept in which enhancement at 650 nm on excess 717 nm light brings about in $-P$ plants a change from a 12-quanta process into a 8 (or 9) quanta process, and in $-P+$ and $+P$ plants a change from a 10-quanta process into an 8 (or 9) quanta process. An 8-quanta process might mean that in PS_{650} on exces 717 nm the "3rd ATP" is provided completely by the background light of 717 nm.

Table 2. Relative and basic quantum requirements in enhanced photosynthesis at 650 nm on excess background 717 nm.
Average values obtained from $-P$ and $-P+$ plants with $-P+$ effect between 42 and 66%

Condition	Quantum requirement		Reference to basic requirement
	Relative %	Basic	
$-P$, 650 nm alone	100	12	hypothesis
$-P$, 650 nm on excess 717 nm	71	8.6	$E_{650(717)}^{max,-P} = 1.40$
$-P$, 650 nm alone, "switched"	85	10.2	hypothesis
$-P+$, 650 nm alone	74	10	"switch factor" $= 1.18$
$-P+$, 650 nm on excess 717 nm	62	8.4	$E_{650(717)}^{max,-P+} = 1.19$

The actual requirements will generally be considerably higher, due to in-effectiveness of part of the absorbed light. The basic requirements are to be multiplied with some inefficiency factor $k \geqq 1$. Next to a higher basic require-ment, in $-P$ plants k^{-P} may be larger than k^{-P+} in $-P$ plants, as result of a less efficient P-controlled non-cyclic e-transfer ("possibility 1"). Upon P-uptake, the decrease in k may contribute to the $-P+$ effect at 650 nm. Consequently, not only the presumed switch from a 12 to a 10 quanta process might occur, but also further decrease in actual quantum requirement.

Table 2 summarizes the relative and basic quantum requirements as derived from the foregoing considerations. With a mean specific $-P+$ effect of 36%, the assumed actual requirement of 12 k^{-P} in $-P$ plants, after P-uptake is de-creased to $\dfrac{12}{1.36} k^{-P} = 8.8 \ k^{-P}$ in $-P+$ plants. On the other hand, on the assumption that in $-P+$ plants the basic quantum requirement is 10, the actual requirement can also be given as 10 k $^{-P+}$. From this it follows: 8.8 k^{-P} = 10 k^{-P+}, and $\dfrac{k^{-P}}{k^{-P+}} = 1.14$. Phosphate uptake by $-P$ plants leading to a mean specific $-P+$ effect of 36% might bring PS $_{650,-P}$ (= 100%) to 114% by the decrease in k, and to 136% by the switch from a 12 to a 10 quanta process.

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