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SIMPLE OSCILLATIONS IN PHOTOSYNTHESIS OF HIGHER PLANTS

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Illumination of leaves of *Vicia faba* L. provoked oscillations in the rates of CO_2 uptake and O_2 evolution. The oscillations were marked under anaerobic conditions, but were absent at 20% O_2. The minimum CO_2 concentration required for the appearance of oscillations was 600 $\mu l \cdot l^{-1}$. The higher the CO_2 concentration, the stronger the oscillations. The effect of CO_2 concentration was saturated at 1000 μl $CO_2 \cdot l^{-1}$. The period of the oscillations was 5–6 min at a light intensity of 80 $nE \cdot cm^{-2} \cdot s^{-1}$ and became longer on lowering of the intensity. No oscillations appeared at intensities below 12 $nE \cdot cm^{-2} \cdot s^{-1}$. Oscillations could also be generated by increasing the CO_2 concentration in the atmosphere during strong illumination under anaerobic conditions. The chlorophyl *a* fluorescence yield showed oscillations, similar in shape and frequency to those of photosynthesis, after such an environmental change. Oscillations were also observed in photosynthesis of other C_3 plants, *Lycopersicon esulentum* Mill and *Glycine max* Merrill, under the same conditions as those required for *V. faba*, but were absent for the C_4 plants, *Zea mays* and *Amaranthus retroflexus* L.

Introduction

Many studies have been reported on the biochemical reactions which give rise to simple oscillations, i.e., oscillations of constant period and simple exponential damping [1–12]. Most of these studies deal with the oscillations in glycolysis. Except for oscillations related to the water-splitting system [11,12], only few examples of oscillatory phenomena in photosynthesis have been reported. One is the oscillation, with a period of about 2 min, in photosynthetic CO_2 uptake in *Holeus lanatus* leaves, reported by Van der Veen [1]. The oscillation occurs after illumination of the leaves in air containing 21% O_2 and 3% CO_2 and lasts about 5 min. The second example is the oscillation in photosynthetic O_2 evolution in *Chlorella* cells with much shorter periods of 4–60 s [2]. Partial inhibition of the photosynthetic carbon cycle is required to observe the oscillation in *Chlorella* cells. Oscillations have also been reported on the ATP level in *Chlorella* cells [3] and on the membrane potential of *Hydrodictyon* cells [4].

Recently, we have found with *Vicia faba* leaves simple oscillations in the rates of CO_2 uptake and O_2 evolution, which were inducible by strong illumination under conditions of low O_2 and high CO_2 concentrations. An attempt was made to see such oscillations as a common phenomenon for higher plants, using three species of C_3 plants and two species of C_4 plants. The results demonstrated marked differences between these two groups of higher plants in their oscillatory behavior which are reported in this paper.

Materials and Methods

Plants of *V. faba* L., *Zea mays* and *Amaranthus retroflexus* L. were grown in a greenhouse and those of *Lycopersicon esulentum* Mill and *Glycine*

Abbreviation: Chl, chlorophyll.

max Merrill in fields for a period of 1–2 months. Plants were harvested in the morning and placed in the dark for 2 h prior to gas-exchange measurements.

The gas exchange of leaves was measured with an open gas-analysis system equipped with a standard gas generator unit (SGGU-712; Standard Technology, Kyoto) as described previously [13]. When measuring O_2 evolution, a trace oxygen analyzer (model 11000; Delta Corp., U.S.A.) was added to this system. A leaf on a plant was placed in an acrylic sample chamber (volume 72 ml) with the roots dipped in water through a hole at the bottom of the chamber. To minimize stomatal control of photosynthesis, the sample leaf in the chamber was preilluminated with strong light in an atmosphere containing 1% O_2 and 340 μl $CO_2 \cdot l^{-1}$ until the transpiration rate reached a high stationary level. Measurements of CO_2 uptake and O_2 evolution were made at 25°C with such preilluminated leaves with open stomata.

The sample leaf in the chamber was illuminated from one side with white light filtered through 0.5% $CuSO_4$ solution (7 cm in thickness). The source of this light was a 650 W halogen lamp with a fan-cooled heat-absorbing filter. When measuring Chl *a* fluorescence yield, the sample leaf in the chamber was illuminated with strong blue light (40 $nE \cdot cm^{-2} \cdot s^{-1}$; Corning glass filter No. 4–76 placed in front of a 500 W xenon lamp) filtered through the $CuSO_4$ solution. Changes in Chl *a* fluorescence yield were measured with a photomultiplier (R-666; Hamamatsu TV Co., Hamamatsu) with a glass filter (VR-67; Toshiba Co., Tokyo) placed in front of the sample leaf at an angle of about 45°. Light intensity was measured with a Lamda quantum sensor (L1-190S; Lamda Co., U.S.A.).

Pigments were extracted from leaves with methanol and chlorophyll in the extracts was determined as described previously [14].

Results

After illumination of *Vicia* leaves, the rates of CO_2 uptake and O_2 evolution showed oscillations. In order to find out the conditions under which oscillations are regularly observed, photosynthesis was measured under various O_2 and CO_2 concentrations and light intensities. Fig. 1 shows changes in the rates of CO_2 uptake (solid curves) and O_2 evolution (broken curve) measured with a *Vicia* leaf under three different O_2 concentrations of 0, 1 and 20%. These curves shows the results obtained by (a) illuminating with strong white light (80 $nE \cdot cm^{-2} \cdot s^{-1}$) until steady-state photosynthesis was obtained, (b) extinguishing the light for 60 s and (c) illuminating once again. Under anaerobic conditions, the rates of CO_2 uptake and O_2 evolution showed marked oscillations, as shown by the curves on the left-hand side of Fig. 1. Each of these curves consists of a spike in the first 90 s of illumination followed by a number of waves superimposed on a declining (or rising) curve. The intervals between each maximum were constant at 5–6 min, which indicates a simple oscillation. The transpiration rate stayed at a high level during the measurements without any oscillations (data not shown). Obviously, the observed oscillations are not due to stomatal control of photosynthesis.

Oscillations were less marked at 1% O_2 (Fig. 1,

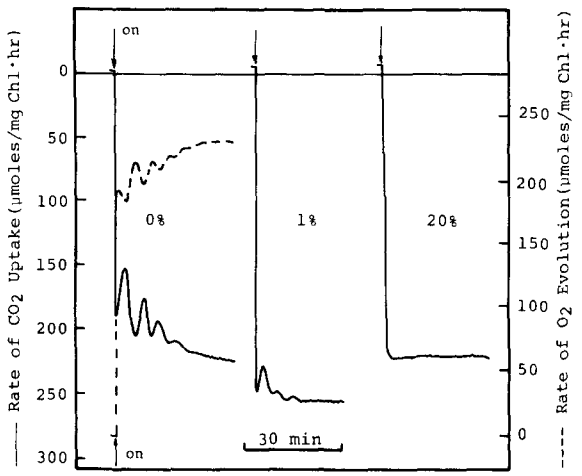

Fig. 1. Effect of different concentrations of O_2 on the rates of CO_2 uptake (———) and O_2 evolution (— — —) of a *Vicia* leaf. Conditions: 1000 μl $CO_2 \cdot l^{-1}$ and varied concentrations of O_2 in N_2; light intensity 80 $nE \cdot cm^{-2} \cdot s^{-1}$. The value on each curve indicates the O_2 concentration (%). The leaf in the chamber was preilluminated in an atmosphere containing 1% O_2 and 340 μl $CO_2 \cdot l^{-1}$ until the transpiration rate attained a high stationary level, then the O_2 and CO_2 concentrations were changed. After a steady-state photosynthetic rate was attained, the light was extinguished for 60 s, then turned on again.

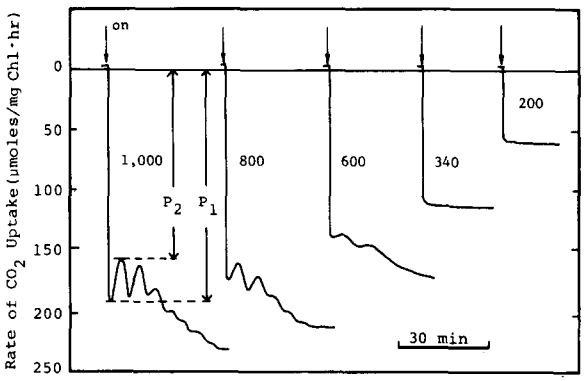

Fig. 2. Effect of different concentrations of CO_2 on the rate of CO_2 uptake of a *Vicia* leaf. Conditions: varied concentrations of CO_2 in N_2; light intensity 80 nE·cm^{-2}·s^{-1}. The value on each curve indicates the CO_2 concentration (μl·l^{-1}). Experimental procedure as in Fig. 1.

middle curve) than at 0% O_2. No oscillations appeared at all at 20% O_2 (the curve on the right-hand side). In some experiments, oscillations were hardly noticeable even at 1% O_2, although simple oscillations were regularly observed under anaerobic conditions. It is evident from these results that low O_2 concentration is a prerequisite for the appearance of oscillations.

Another requirement for the observation of oscillations is high CO_2 concentration in the atmosphere. Fig. 2, showing the effect of various CO_2 concentrations on the rate of CO_2 uptake of a *Vicia* leaf, indicates that the oscillations appear at a CO_2 concentration of 600 μl·l^{-1} and become marked on increasing of the CO_2 concentration. Fig. 3 shows the effects of CO_2 and O_2 concentrations on the magnitude of the oscillations. To describe the magnitude quantitatively, the rates of CO_2 uptake at the first peak of the oscillations (P_1 in Fig. 2) and at the subsequent dip (P_2) were measured and are expressed as the ratio, P_1/P_2. Under anaerobic conditions or at 1% O_2, the ratio increased as the CO_2 concentration increased. The effect of CO_2 concentration was saturated at 1000 μl CO_2·l^{-1}. No oscillations were observed at 20% O_2 even at 4000 μl CO_2·l^{-1}. Evidently, increased oxygen levels are not tolerated by the oscillatory system even under high CO_2 concentrations.

When the conditions of low O_2 and high CO_2 concentrations were satisfied, and strong light was applied, photosynthesis showed marked oscillations. Fig. 4 shows the effect of light intensity on the rate of CO_2 uptake of a *Vicia* leaf and indicates that both the period and magnitude of the oscillations are dependent on light intensity. The higher the intensity, the stronger the oscillations. The period of the oscillations was 5–6 min at 80 nE·cm^{-2}·s^{-1} and became longer on lowering of the intensity: 7–8 and 9–10 min at 40 and 24

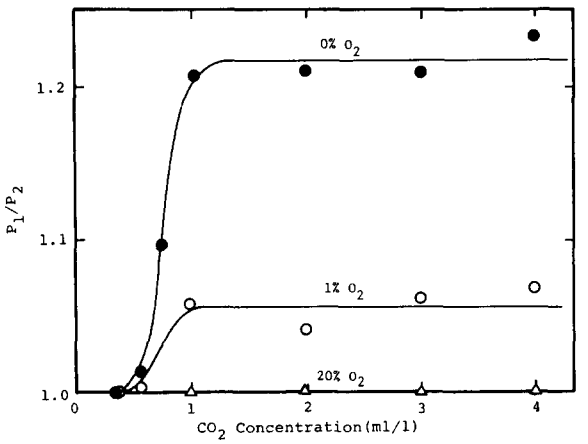

Fig. 3. Effect of different concentrations of CO_2 on the magnitude of oscillations (P_1/P_2) of the CO_2-uptake rate of a *Vicia* leaf observed at three different O_2 concentrations of 0, 1 and 20%. Conditions: varied concentrations of CO_2 and O_2 in N_2, 80 nE·cm^{-2}·s^{-1}. P_1 and P_2 are the rates of CO_2 uptake at the first peak and at the subsequent dip, respectively, of the oscillations, as shown in Fig. 2.

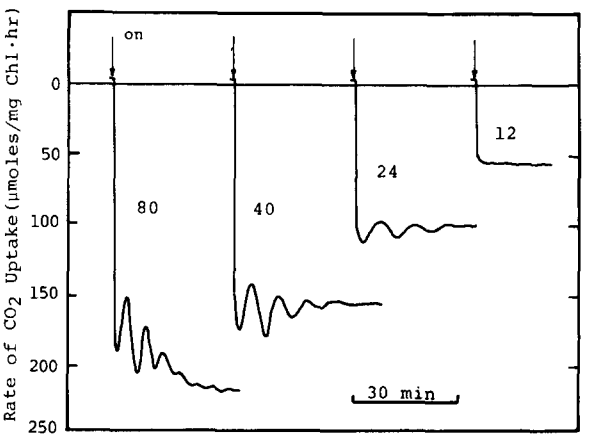

Fig. 4. Effect of different light intensities on the rate of CO_2 uptake of a *Vicia* leaf. Conditions: 1000 μl CO_2·l^{-1} in N_2. The value on each curve indicates the light intensity (nE·cm^{-2}·s^{-1}). Experimental procedure as in Fig. 1.

$nE \cdot cm^{-2} \cdot s^{-1}$, respectively. No oscillations appeared at light intensities below 12 $nE \cdot cm^{-2} \cdot s^{-1}$.

Oscillations could also be induced by increasing the CO_2 concentration in the atmosphere during illumination. The results of such an experiment are shown in Fig. 5. A leaf was first illuminated with strong light (80 $nE \cdot cm^{-2} \cdot s^{-1}$) under an atmosphere containing $N_2 + 340$ μl $CO_2 \cdot l^{-1}$ until steady-state photosynthesis was obtained and then the CO_2 concentration was increased to 1000 $\mu l \cdot l^{-1}$ during illumination with the same light. The rates of O_2 evolution and CO_2 uptake (Fig. 5, curves A and B, respectively) showed marked oscillations after increasing of the CO_2 concentration. The period of the oscillations was 5–6 min, being identical with that of the oscillations induced by light (curves on the left-hand sides of Figs. 1, 2 and 4). No oscillations appeared when the CO_2 concentration was lowered (Fig 5, right-hand side of curve A). Low O_2 concentration and strong illumination were required for the observation of oscillations, and oscillations could be induced only when the CO_2 concentration was increased to a level above 600 $\mu l \cdot l^{-1}$. These conditions are apparently the same as those required for the appearance of oscillations induced by light. Thus, the same mechanism seems to be involved in oscillations induced by CO_2 and by light.

Oscillations of photosynthesis were always accompanied by oscillations of the Chl *a* fluorescence yield. Curves B and A in Fig. 6 show changes in the fluorescence yield of Chl *a* and in the rate of O_2 evolution, respectively, simultaneously measured on a *Vicia* leaf under anaerobic conditions. When the CO_2 concentration in the atmosphere was increased from 340 to 1000 $\mu l \cdot l^{-1}$ during illumination with strong blue light (40 $nE \cdot cm^{-2} \cdot s^{-1}$), both the fluorescence yield of Chl *a* and O_2 evolution rate exhibited marked oscillations. The fluorescence yield and rate of O_2 evolution oscillated in phase. The absence of a complementary relationship between the rate of O_2 evolution and fluorescence yield indicates that the observed fluorescence cannot be regarded as an inefficiency index of photosynthesis; although competition between photosynthesis and fluorescence is seen under certain conditions, it is not a general occurence [15]. Evidence has been reported which shows that photoinduced quenching of Chl *a* fluorescence reflects predominantly reoxidation of the primary

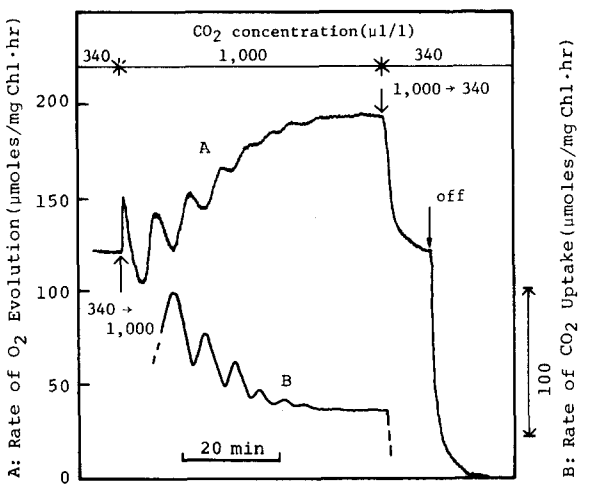

Fig. 5. Changes in the rates of O_2 evolution (A) and CO_2 uptake (B) of a *Vicia* leaf upon changing of the CO_2 concentration in the atmosphere during continuous illumination with strong white light (80 $nE \cdot cm^{-2} \cdot s^{-1}$). After a steady-state photosynthetic rate was attained in an atmosphere containing $N_2 + 340$ μl $CO_2 \cdot l^{-1}$, the CO_2 concentration was increased to 1000 $\mu l \cdot l^{-1}$. The CO_2 concentration was lowered to 340 $\mu l \cdot l^{-1}$ after the oscillations subsided.

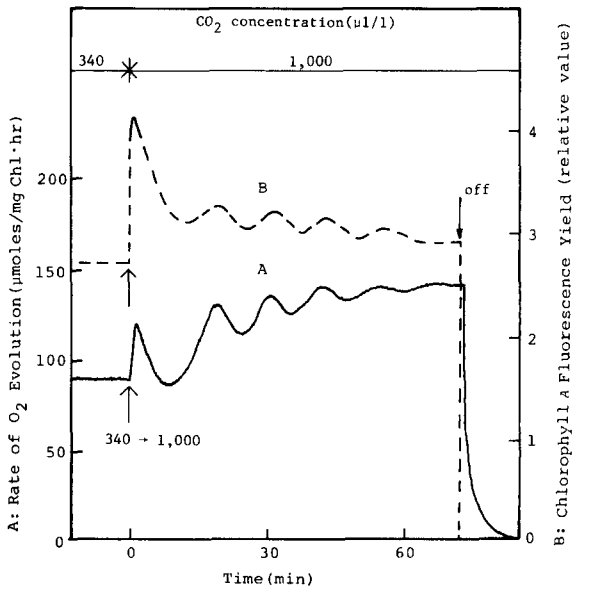

Fig. 6. Changes in the fluorescence yield of Chl *a* (B) and rate of O_2 evolution (A) of a *Vicia* leaf upon increasing of the CO_2 concentration in the atmosphere during illumination with strong blue light (360–600 nm, 40 $nE \cdot cm^{-2} \cdot s^{-1}$) under anaerobic conditions. Experimental procedure as in Fig. 5.

electron acceptor, Q, of Photosystem II and photo-induced acidification of the intrathylakoid space [16–19]. Thus, the observed similarity in shape and frequency between oscillations of the O_2 evolution rate and fluorescence yield strongly suggests that oscillations in the photosynthetic rate are closely associated with those of the redox state of Q and/or the high-energy state of the intrathylakoid system.

Experiments with two other species of C_3 plants showed the same trend as did *Vicia* leaves. Fig. 7, showing the effects of various concentrations of O_2 and CO_2 on the rate of CO_2 uptake of soybean (*G. max*; curves A–D) and tomato (*L. esulentum*; curves E–H) leaves, clearly demonstrates that the presence of oscillations in these plants requires the same conditions as those required for *Vicia* leaves.

In contrast to C_3 plants, C_4 plants did not exhibit any oscillations even under conditions in

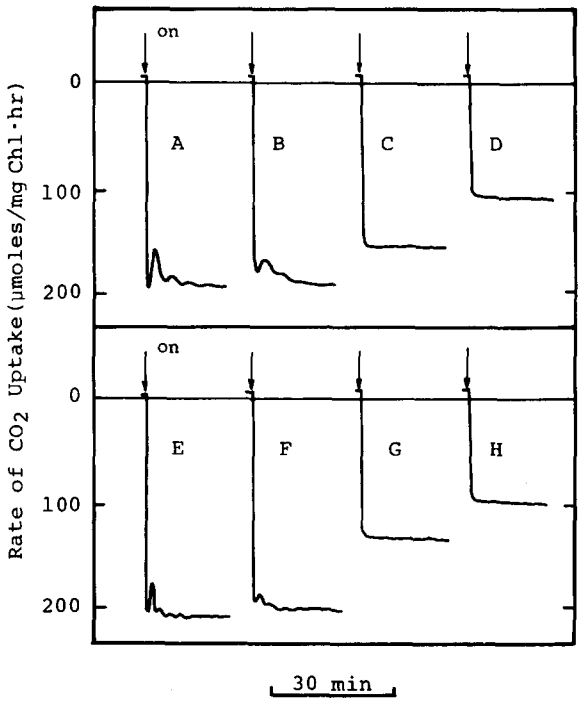

Fig. 7. Effect of different concentrations of O_2 and CO_2 on the rate of CO_2 uptake of soybean (*G. max*; A–D) and tomato (*L. esulentum*; E–H) leaves. Conditions: 1000 μl $CO_2 \cdot l^{-1}$ in N_2 (A and E), 1% O_2 and 1000 μl $CO_2 \cdot l^{-1}$ in N_2(B and F), 20% O_2 and 1000 μl $CO_2 \cdot l^{-1}$ in N_2 (C and G) and 340 μl $CO_2 \cdot l^{-1}$ in N_2 (D and H); light intensity 80 nE·cm^{-2}·s^{-1} (A–H). Experimental procedure as in Fig. 1.

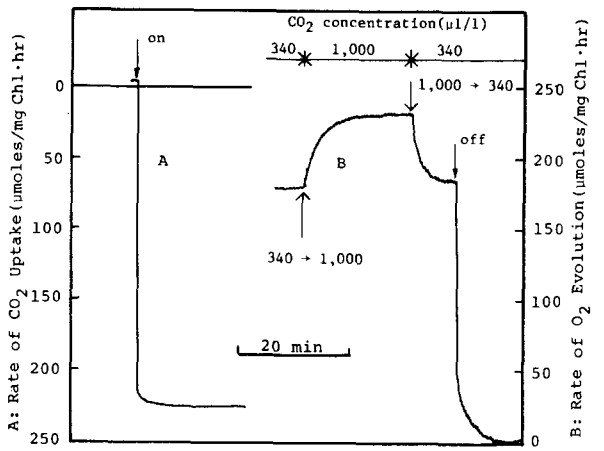

Fig. 8. Changes in the rate of CO_2 uptake of an *Amaranthus* leaf upon illumination with strong white light (80 nE·cm^{-2}·s^{-1}) in an atmosphere containing N_2 + 1000 μl $CO_2 \cdot l^{-1}$ (A), and those in the rate of O_2 evolution of the same leaf upon changing of the atmospheric CO_2 concentration during illumination with the same light under anaerobic conditions. Experimental procedures as in Figs. 1 and 5.

which marked oscillations were observed for C_3 plants. Curve A in Fig. 8 shows changes in the rate of CO_2 uptake of an *Amaranthus* leaf observed upon switching strong light on and off under an atmosphere containing N_2 + 1000 μl $CO_2 \cdot l^{-1}$, and curve B shows changes in the rate of O_2 evolution of the same leaf on changing the atmospheric CO_2 concentration during illumination under anaerobic conditions. These curves clearly demonstrate the absence of oscillations in *Amaranthus* leaves; the above-mentioned environmental changes provoked marked oscillations in C_3 photosynthesis (cf. Figs. 1–7). Experiments with corn (*Z. mays*) leaves showed the same trend as did *Amaranthus* leaves. It appears, therefore, that the absence of oscillations is a common characteristic of C_4 photosynthesis.

Discussion

The present study demonstrates a marked difference between C_3 and C_4 plants with respect to the oscillatory behavior of photosynthesis. C_3 plants exhibited marked oscillations in photosynthesis, while none were observed for C_4 plants. Oscillations occurred only under the limited environmental conditions of low O_2 and high CO_2

concentrations and strong light. These conditions are apparently different from those required for observation of oscillations in *Holeus* leaves and *Chlorella* cells [1,2]. Oscillations in these leaves and cells occur in air containing 21% O_2, whereas low O_2 concentration was a prerequisite for the observation of oscillations found in this study. Furthermore, the presence of oscillation in *Chlorella* cells requires low CO_2 concentration or the presence of poisons which inhibit the photosynthetic carbon cycle [2]. Therefore, a different mechanism seems to be involved in the oscillations described in this paper.

In order to explain the oscillations, an 'oscillatory center', i.e., a group of reactions which together generate the oscillations, must exist somewhere in the overall photosynthethetic process. From the conditions required for the appearance of oscillations, one can infer some specific characteristics of this center. The requirement of low O_2 concentration indicates that some of the reactions in the center are suppressed by low O_2 concentration and that the suppression is a prerequisite for generating the oscillations. Another requirement, high CO_2 concentration, indicates that oscillations occur only when a high rate of regeneration of the CO_2 acceptor, ribulose 1,5-biphosphate, is used. In view of the fact that photophosphorylation supplies ATP for ribulose 1,5-bisphosphate regeneration and is suppressed by low O_2 concentration [20–23], we inferred that some mechanism regulating phosphorylation may be involved in the observed oscillations, as discussed below.

CO_2 reduction in the Calvin-Benson cycle requires ATP and NADPH at a ratio of 1.5 [24]. It is considered that the ATP produced during linear electron transport to NADP is insufficient to satisfy the ATP requirement of photosynthesis and that additional ATP is provided by cyclic or pseudocyclic photophosphorylation [25–27]. Arnon and Chain [20] and Heber and co-workers [21,22] reported that cyclic photophosphorylation is inhibited by anaerobiosis, and ascribed this inhibition to over-reduction of the electron-transport carriers of the cyclic pathway. Precise poising of the electron-transport carriers is required for cyclic photophosphorylation and electron flow to O_2 appears to be important in poising the carriers [21,22]. The rates of photophosphorylation and electron transport are controlled by the intrathylakoid H^+ gradient, ΔpH [28,29]. Slovacek and Hind [28] showed that maximal rates of CO_2-dependent O_2 evolution in intact chloroplasts are associated with a critical ΔpH of 3.9 and that CO_2-dependent O_2 evolution is inhibited by changes of 0.1–0.2 in ΔpH.

From the results obtained in this study together with the information referred to above, we may speculate on the mechanism of the oscillations. At the beginning of illumination at low O_2 and high CO_2 concentrations, photosynthesis was accelerated and at a certain point was inhibited (e.g., the curves on the left-hand side of Fig. 1). This inhibition may reflect suppression of photophosphorylation due to over-reduction of the electron-transport chain and/or a decrease in ΔpH. The decrease in the rates of electron transport and ATP consumption would release the over-reduction and increase the ΔpH, thereby relieving the suppression. This explains the increase in photosynthetic rate in the second wave of oscillations. The rates of electron transport and ATP consumption will increase again, resulting in over-reduction of the electron-transport chain and/or a decrease in ΔpH. Thus, oscillations could occur and continue with damping until the conditions needed for maximal photosynthetic rate are attained. Such changes in the redox state of the electron-transport carriers and ΔpH as hypothesized above are suggested by the results shown in Fig. 6; the fluorescence yield of Chl *a* and the O_2 evolution rate oscillated in phase.

No oscillations were observed at high O_2 or low CO_2 concentrations or low light intensities. The following explanations are possible. (i) Over-reduction of the electron-transport carriers does not occur at high O_2 concentrations. Cyclic photophosphorylation proceeds normally and the intrathylakoid H^+ gradient is maintained at an optimal level under these conditions. (ii) The rate of CO_2 uptake is limited by the rate of ribulose 1,5-bisphosphate regeneration only at high CO_2 concentrations, as suggested by Von Caemmerer and Farquhar [30]. Oscillations could occur when the rate of ribulose 1,5-bisphophate regeneration and, therefore, the rate of ATP production limit photosynthesis. (iii) The absence of oscillations

under low light intensities can be explained by the fact that the contribution of cyclic photophosphorylation, which is inhibited by anaerobiosis, is much less at low than at high light intensities [21].

C_4 plants did not exhibit any oscillations (Fig. 8). We have shown in a previous paper that photosynthesis in C_4 plants is not, or only weakly, inhibited by anaerobiosis, while that in C_3 plants is strongly inhibited [13]. The results suggest that photophosphorylation proceeds normally in C_4 plants even under anaerobic conditions. Thus, the absence of oscillations in C_4 photosynthesis could be ascribed to the absence of inhibition of photophosphorylation.

Acknowledgement

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References

1 Van der Veen, R. (1949) Physiol. Plant. 2, 285–296
2 Bannister, T.T. (1965) Biochim. Biophys. Acta 109, 97–107
3 Lewenstein, A. and Bachofen, R. (1972) Biochim. Biophys. Acta 267, 80–85
4 Metlicka, R. and Rybova, R. (1967) Biochim. Biophys. Acta 135, 563–565
5 Metzler, H. (1980) Biochim. Biophys. Acta 593, 312–318
6 Hess, B. and Boileux, A. (1971) Annu. Rev. Biochem. 40, 237–258
7 Duysens, L.N.M. and Amesz, J. (1957) Biochim. Biophys. Acta 24, 19–26
8 Higgins, J. (1964) Proc. Natl. Acad. Sci. U.S.A. 51, 989–994
9 Hommes, F.A. (1964) Arch. Biochem. Biophys. 108, 36–46
10 Chance, B., Estabrook, R.W. and Ghosh, A. (1964) Proc. Natl. Acad. Sci. U.S.A. 51, 1244–1251
11 Diner, B.A. and Joliot, P. (1977) in Encyclopedia of Plant Physiology, New Series, vol. 5 (Trebst, A. and Avron, M., eds.), pp. 187–205, Springer-Verlag, Berlin
12 Joliot, P. and Kok, B. (1975) in Bioenergetics of Photosynthesis (Govindjee, ed.), pp. 387–412, Academic Press, New York
13 Ogawa, T. (1980) Photobiochem. Photobiophys. 1, 321–328
14 Ogawa, T. and Shibata, K. (1965) Photochem. Photobiol. 4, 193–200
15 Govindjee and Papageorgiou, G. (1971) in Photophysiology (Giese, A. ed.), vol. 6, pp. 1–46, Academic Press, New York
16 Duysens, L.N.M. and Sweers, H.E. (1963) in Studies on Microalgae and Photosynthetic Bacteria (Japanese Society of Plant Physiologists, ed.), pp. 353–372, The University of Tokyo Press, Tokyo
17 Bradbury, M. and Baker, N.R. (1981) Biochim. Biophys. Acta 635, 542–551
18 Krause, G.H. (1973) Biochim. Biophys. Acta 333, 301–313
19 Krause, G.H., Vernotte, C. and Briantais, J.M. (1982) Biochim. Biophys. Acta 679, 116–124
20 Arnon, D.I. and Chain, R.K. (1977) FEBS Lett. 82, 297–302
21 Heber, U., Egneus, H., Hanck, U., Jensen, M. and Köster, S. (1978) Planta 143, 41–49
22 Ziem-Hanck, U. and Heber, U. (1980) Biochim. Biophys. Acta 591, 266–274
23 Steiger, H.M. and Beck, E. (1981) Plant Cell Physiol. 22, 561–576
24 Bassham, J.A. (1964) Annu. Rev. Plant Physiol. 15, 101–120
25 Arnon, D.I., Tsujimoto, H.Y. and McSwain, B.C. (1964) Proc. Natl. Acad. Sci. U.S.A. 51, 1274–1282
26 Heber, U. (1976) J. Bioenerg. Biomembranes 8, 157–172
27 Gimmler, H. (1977) in Encyclopedia of Plant Physiology, New Series, vol. 5 (Trebst, A. and Avron, M., eds.), pp. 448–472, Springer-Verlag, Berlin
28 Slovacek, R.E. and Hind, G. (1981) Biochim. Biophys. Acta 635, 393–404
29 Kobayashi, Y., Inoue, Y., Shibata, K. and Heber, U. (1979) Planta 146, 481–486
30 Von Caemmerer, S. and Farquhar, G.D. (1981) Planta 153, 376–387