PHOTOSYNTHETIC ADAPTATION TO LIGHT INTENSITY IN LEAVES OF *ACER PSEUDOPLATANUS*

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INTRODUCTION

During 1952 dry matter production in *Acer pseudoplatanus* L. (sycamore) growing under different light intensities was investigated. Two series of experiments were carried out, one under laboratory conditions at relatively low light intensities from daylight fluorescent tubes, and one under field conditions in the garden of the laboratory.

To investigate the capacity of sycamore to adapt itself to the intensity of the light field in which it is growing, determinations of the light intensity dependence of photosynthesis of the leaves, the relative chlorophyll content and the protein content of the leaves were made. Some of the findings which emerged will be discussed here.

METHODS

In each experimental series four light intensity classes were used. In the laboratory these different light intensities were obtained by varying the distance of the lamp sets from the plants, oustide by using gauze screens of different mesh width so that the sunlight was differentially intercepted.

In the indoor experiment the light intensities amounted to 24500-27000 ergs/cm^2 sec. (5000-5500 lux), 20000-22000 ergs/cm^2 sec. (4000-4500 lux), about 9800 ergs/cm^2 sec. (about 2000 lux), and 5880 ergs/cm^2 sec. (1200 lux), for 16 hours/day; in the outdoor experiment light intensities were roughly defined as 100 %, 75 %, 50 % and 25 % of the natural daylight. Owing to the irregular growth of the plants both indoors and outdoors it was impossible to ensure that every individual plant received the nominal amount of light energy, but in the indoor experiment the *average* amount of light energy in a light intensity class could be kept fairly constant. Thus, although the largest plants got somewhat too much light and the shorter ones too little, such differences were minimal. From the indoor experiment, leaves for the study of light-dependent properties were selected with the aid of a light meter. From the outdoor experiment the youngest fully expanded leaves from the various light intensity classes, were chosen.

TABLE 1

Rate of photosynthesis (expressed in relative units) at different light intensities in leaves from plants raised under various light intensities

Part A: Indoor experiment

Light intensity in ergs/cm²/sec. (watercooled high pressure mercurylamp)

Mean exposition light intensity in ergs/cm²/sec.	Nr. of leaf	2200	4400	6600	8800	11000	13200	15400	17600	19800	22000	24200	26400	28600	30800	33000	35200	37400
6100	1	1.3	2.5	3.4	3.8	3.9	3.9	3.9	3.9									
	2	1.2	2.1	2.8	3.0	3.0	3.0	3.0	3.0									
	3	1.3	2.2	2.8	2.9	2.9	2.9	2.9	2.9									
	4	1.3	2.4	3.0	3.3	3.5	3.6	3.7	3.7									
	5	1.2	2.3	2.7	2.7	2.7	2.7	2.7	2.7									
	6	1.0	1.9	2.5	2.6	2.6	2.6	2.6	2.6									
	7	1.2	2.1	2.7	3.1	3.1	3.1	3.1	3.1									
	8	1.4	2.2	2.7	2.8	2.8	2.8	2.8	2.8									
	9	1.1	1.7	1.8	1.8	1.8	1.8	1.8	1.8									
	10	0.8	1.3	1.5	1.5	1.5	1.5	1.5	1.5									
	av.	1.2	2.2	2.8	3.0	3.0	3.0	3.0	3.0									
15700	1	1.2	2.2	3.1	3.9	4.3	4.8	5.1	5.3	5.5	5.7	5.9	6.0					
	2	1.4	2.4	3.2	3.9	4.2	4.8	5.4	5.7	5.9	6.1	6.1	6.1					
	3	1.5	2.7	3.9	4.4	4.9	5.2	5.3	5.4	5.4	5.4	5.4	5.4					
	4	1.0	2.0	2.7	3.1	3.3	3.3	3.3	3.3	3.3	3.3	3.3	3.3					
	av.	1.3	2.3	3.2	3.8	4.2	4.5	4.8	4.9	5.0	5.1	5.2	5.2					
27000	1	0.9	1.8	2.7	3.5	4.4	5.2	6.0	6.7	7.6	8.1	8.6	8.9	9.3	9.5	9.6	9.7	9.7
	2	0.9	1.7	2.2	2.7	3.2	3.7	4.2	4.5	4.7	4.8	4.9	5.0	5.0	5.0	5.0	5.0	5.0
	3	0.7	1.7	2.5	3.1	3.5	4.0	4.3	4.7	5.0	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4
	4	0.7	1.2	1.6	1.9	2.2	2.4	2.7	3.0	3.1	3.3	3.4	3.4	3.4	3.4	3.4	3.4	3.4
	av.	0.8	1.6	2.2	2.8	3.3	3.8	4.3	4.7	5.1	5.4	5.6	5.7	5.8	5.8	5.9	5.9	5.9

av = average

TABLE 1, continued.   Part B: Outdoor experiment

Exposition light intensity in % of daylight	Nr of leaf	Light intensity in ergs/cm² sec. (watercooled high pressure mercury lamp)													
		4400	8800	13200	17600	22000	26400	30800	35200	44000	48400	52800	57200	61600	66000
25 %	1	1.3	2.1	2.6	2.6	2.6	2.6								
	2	1.6	2.8	3.3	3.6	3.7	3.7								
	3	1.6	2.8	3.6	4.0	4.2	4.2								
	4	1.5	2.6	3.4	3.8	3.9	3.9								
	5	1.4	2.8	4.0	4.8	5.1	5.2								
	av.	1.5	2.6	3.4	3.7	3.9	3.9								
50 %	1	1.4	2.4	3.4	4.3	5.0	5.7	6.1	6.3	6.3	6.3				
	2	1.4	2.6	4.0	4.9	5.3	5.6	5.7	5.8	5.9	5.9				
	3	1.9	3.6	4.7	5.8	6.7	7.3	7.6	7.8	7.8	7.8				
	4	1.4	2.6	3.5	4.2	4.6	4.8	4.9	4.9	4.9	4.9				
	av.	1.4	2.8	3.9	4.8	5.4	5.8	5.9	6.2	6.2	6.2				
75 %	1	1.4	2.5	3.2	3.9	4.4	4.8	5.3	5.6	5.9	6.1	6.4	6.6	6.6	6.6
	2	1.4	2.5	3.2	3.8	4.5	5.0	5.3	5.5	5.6	5.6	5.6	5.6	5.6	5.6
	3	1.4	2.5	3.4	4.1	4.7	5.2	5.6	5.9	6.1	6.2	6.4	6.5	6.5	6.5
	4	1.2	2.6	3.5	4.2	4.8	5.4	5.9	6.3	6.6	6.9	7.1	7.2	7.3	7.3
	5	1.4	2.4	3.1	3.6	4.2	4.5	4.7	4.9	5.1	5.3	5.4	5.4	5.4	5.4
	6	1.4	2.6	3.8	5.0	5.9	6.7	7.5	8.2	8.7	9.0	9.4	9.7	9.7	9.7
	7	1.2	2.5	3.7	4.7	5.7	6.7	7.6	8.4	9.2	9.7	10.4	11.0	11.5	11.5
	av.	1.3	2.5	3.4	4.2	4.9	5.5	6.0	6.4	6.6	7.0	7.2	7.4	7.5	7.5

av = average

Measurements of the light intensity dependence of photosynthesis in detached leaves were made using a Kipp diaferometer. For this purpose, a single leaf at a time was enclosed in an assimilation chamber and illuminated from one side with a watercooled high pressure mercury-lamp. With the aid of a water bath the temperature of the assimilation chamber was held at the constant level of 20° C. Water vapour saturated air with a CO_2-content of 5 % passed through this chamber. For the first determination a relatively high illumination-intensity was chosen in order to secure light saturation, a period of about $3/4$ of an hour being required to reach the maximum assimilation level (induction phenomena). By gradually lowering the light intensity, it was then possible to determine quickly the remaining points on the intensity curve. Respiration was measured as CO_2-exchange in the dark.
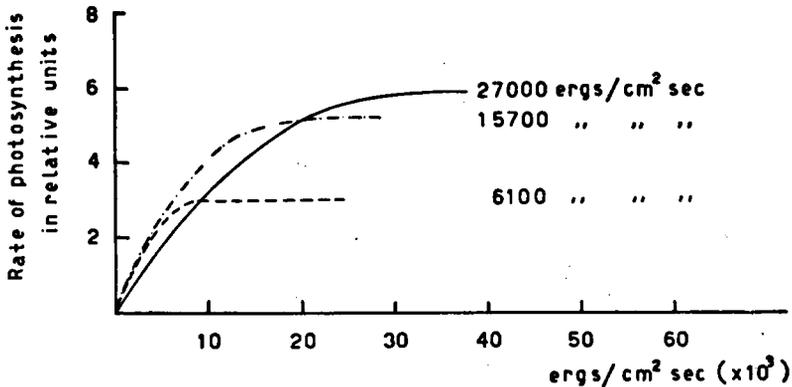
Fig. 1.   Indoor experiment
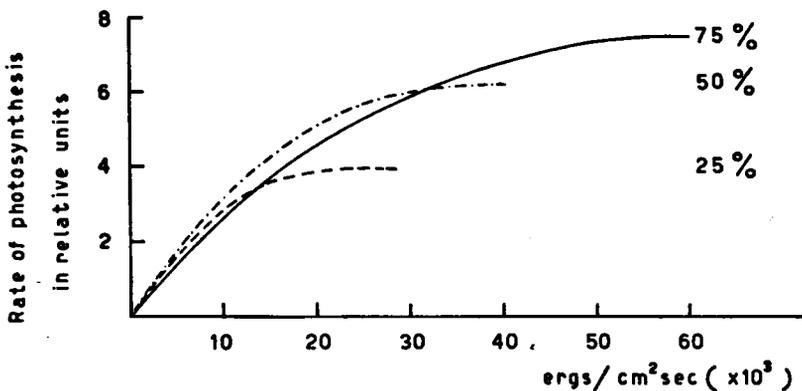
Fig. 2.   Outdoor experiment

Figs. 1 and 2.   The relations between photosynthesis and light intensity. These curves are drawn from averages of data in Table 1. With increasing exposition light intensity the saturation intensity and maximum rate of photosynthesis increase.
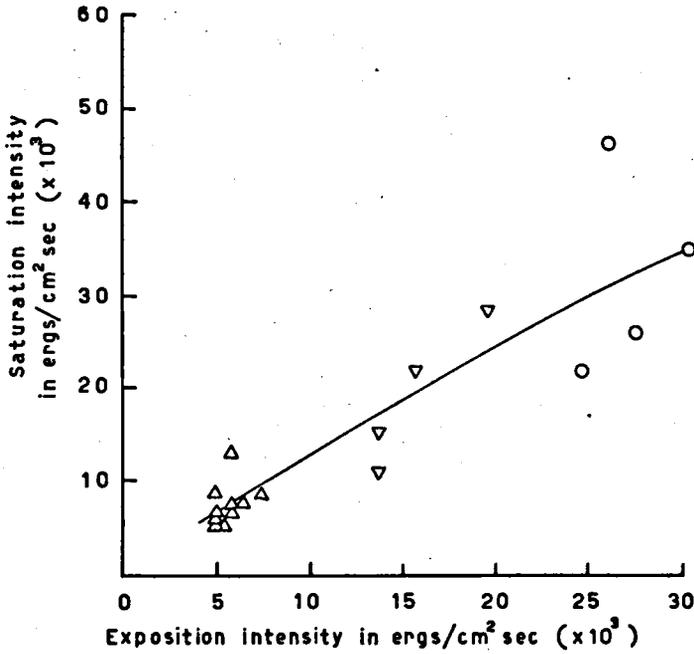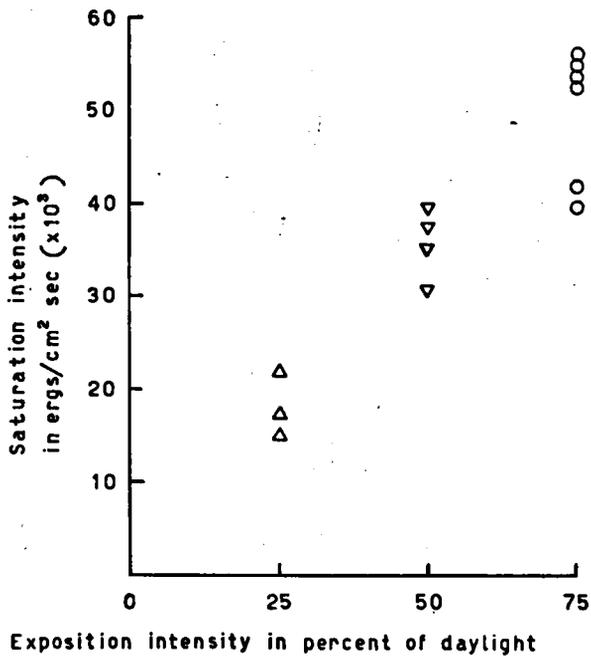
Fig. 3. Indoor experiment

Fig. 4. Outdoor experiment

Figs. 3 and 4. The relation between saturation light intensity and exposition light intensity.

Indoor experiment:	△	exposition intensity 6100 ergs/cm²/sec.
	▽	exposition intensity 15700 ergs/cm²/sec.
	○	exposition intensity 27000 ergs/cm²/sec.
Outdoor experiment:	△	exposition intensity 25 % of daylight.
	▽	exposition intensity 50 % of daylight.
	○	exposition intensity 75 % of daylight.

Determinations of chlorophyll concentration were made using the same leaves. A number of discs (3 to 9) were cut out of a leaf with a punch and quickly killed by dipping them into boiling water for some seconds. They were then extracted repeatedly with 60 % ethanol at 70° C to remove the chlorophyll as completely as possible, the extract made up to 25 ml with 60 % ethanol and the extinction value of this
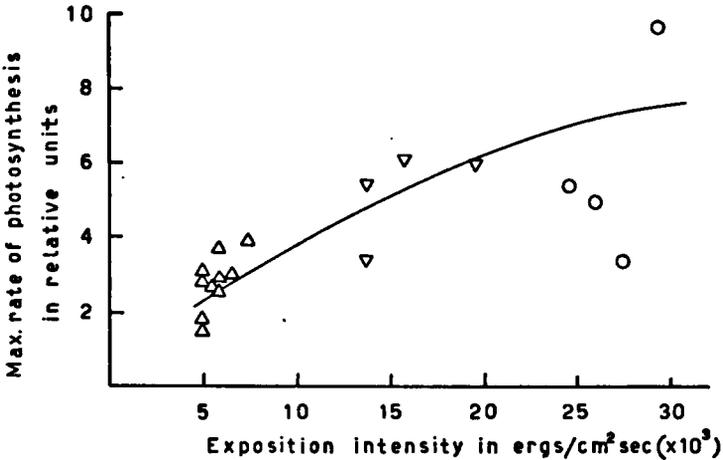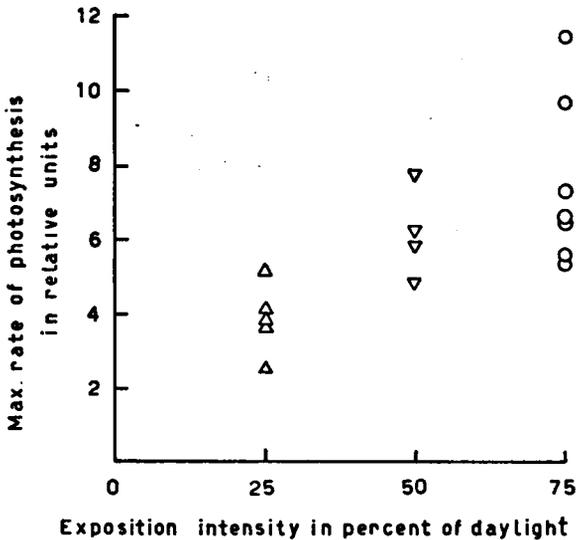

Fig. 5.   Indoor experiment

Exposition intensity in percent of daylight

Fig. 6.   Outdoor experiment

Figs. 5 and 6.   The relation between maximum rate of photosynthesis and exposition light intensity.

The spreading of the different points is partly due to the different chlorophyll concentrations (cf. fig. 7). For explanation of symbols, see figs. 3 and 4.

extract determined with a Bleeker extinction meter at a wavelength of 665 mμ. The resultant value was taken as a measure of the chlorophyll content of the leaves. Finally, micro-protein determinations were made, again on the same leaves.

RESULTS

Sycamore appears to be capable of adaptation to the intensity of the light field in which it is growing, in several respects. Certain properties of the assimilation apparatus, its chlorophyll content and its protein content were found to depend on this light intensity.

In figs. 1-6 the light intensity dependence of CO_2-assimilation is illustrated. Figs. 1, 3 and 5 represent leaves of plants belonging to the indoor experiment, while figs. 2, 4 and 6 illustrate the behaviour of leaves from plants of the outdoor experiment (cf. also Table 1). It can be seen that the intensity curves of leaves adapted to low light intensities show the characteristics of "Blackman curves" (fig. 1) while those of leaves adapted to high light intensities show the characteristics of "Bose curves", (fig. 2) with a gradual transition from one type to the other (cf. RABINOWITCH, 1951).

At least two specific values can be derived from these intensity curves, viz.:

1°   The saturation intensity, i.e. the light intensity, at which photosynthesis has reached complete light saturation.

2°   The maximum rate of photosynthesis, i.e. the rate of photosynthesis obtaining at the saturation intensity.

From figs. 1 and 2, and 3 to 6 it appears that both the saturation intensity and the maximum rate of photosynthesis increase with increasing intensity of the "light field"—the intensity at which the leaves have grown.

The chlorophyll content of the leaves also varies in relation to the light intensity at which the plants have grown. The higher this intensity, the lower is the chlorophyll content of the leaves. This could readily be seen by eye from the colour of the leaves; "shadow leaves" were a fresh dark green and "sun leaves" a pale-yellowish green. Fig. 7 shows the dependence of the chlorophyll content on the exposition light intensity, and clearly illustrates this adaptive effect.

Finally, fig. 8 gives some idea of the increase in leaf thickness under the influence of an increasing light intensity, and the rise in dry weight/cm² must be ascribed almost entirely to an increase in the non-protein compounds.

The points in this graph were computed from a smoothed curve of mg protein per g dry weight of the leaf plotted against the exposition light intensity and a curve of mg dry weight of the leaf per cm² against the exposition light intensity. While the percentage of protein in the dry weight of the leaf decreases with increasing exposition light intensity, the dry weight per cm² of the leaf increases correspondingly. It

follows that the absolute amount of protein per cm² in the leaf is
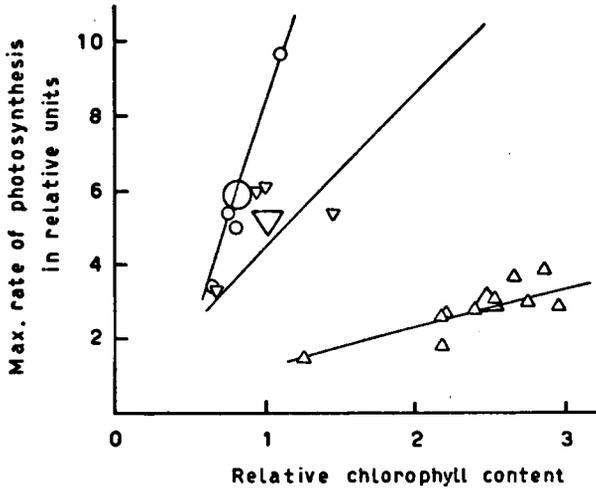hardly influenced by the intensity of the light field.

Fig. 7.   Indoor experiment. The relation between maximum rate of photosynthesis
and relative chlorophyll content.
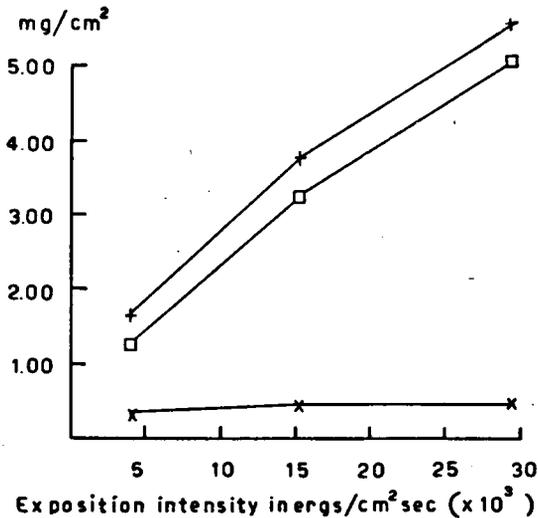For explanation of symbols, see figs. 3 and 4.

Fig. 8.   Indoor experiment. The relation between leaf dry weight and exposition
light intensity

      X   —   Amount of protein in mg/cm².
      □   —   Amount of non-protein-compounds in mg/cm².
      +   —   Total dry weight of the leaf in mg/cm².

DISCUSSION

It appears from literature that adaptation phenomena of plants in relation to light are well known. Those of the chlorophyll system in particular have been frequently investigated. Before 1918 it was generally held that during photosynthesis there is a continuous destruction and resynthesis of chlorophyll. In 1918, however, WILL-STÄTTER and STOLL claimed that in adult leaves chlorophyll was present in a fixed form and in a definite amount. On the authority of these investigators this was generally accepted for a long time, although results of later experiments have repeatedly raised doubts about the generally accepted stability of chlorophyll. For instance, BUKATSCH (1940), WENDEL (1940) and HENRICI (1919) found regular variations in the chlorophyll content of leaves during the day. Since, however, they relate chlorophyll content to the fresh weight of the leaves, the data are of limited relevence. MONTFORT (1941) distinguishes two types of plants: the photostable type, reacting upon increasing intensity of the light field by increasing its chlorophyll content and *vice versa*, and the photolabile type, reacting upon increasing intensity of the light field by decreasing its chlorophyll content. According to these views sycamore as demonstrated by the present experiments should belong to the photolabile type. Montfort ascribes the diminution in chlorophyll content with increasing light intensity to its destruction by ultra-violet radiation. However, the mechanism of the production of chlorophyll under these circumstances is not clear, and Montfort does not discuss the question of a physiological equilibrium.

The existence of a dynamic equilibrium has, however, been accepted by various investigators including STÅLFELT (1927), ZACHEROWA (1929), SCHERTZ (1929), SJÖBERG (1931), ROUX and HUSSON (1952). SCHENK (1952-1953) found a yearly periodicity in the amount of chlorophyll in the cortex of *Tilia*, *Fagus* and *Populus*, which fact he ascribes to an endogenous rhythm in the plant. An interesting contribution to this subject was made by RANDALL (1953) in his study on water relations and chlorophyll content of forest herbs in Southern Wisconsin. He found that the different herbs of the forest border show a gradual drop in chlorophyll content of their leaves from high forest to savanna, i.e. from low to high light intensity conditions.

It seems, therefore, that, although some minor indications point to the existence of a reversible equilibrium between chlorophyll content and light intensity during growth, the existence of such an equilibrium is far from being sure and further investigations on this subject are now in progress.

Equally little appears to be known about other adaptation phenomena in the photosynthetic apparatus. There are many references in the literature to sun leaves and shade leaves, sun leaves having the capacity of using more of the sunlight for photosynthesis than shade leaves, and this view is fully in agreement with our findings. As to the reason for variation in photosynthetic capacity, however, it is not possible at this stage to be definite, although RABINOWITCH (1945)

ascribes such differences to an enzymatic factor. The present experiments demonstrate that the difference in capacity cannot at any rate be correlated with the thickness of the leaf, since it has been established that the increment in thickness is almost entirely accomplished by the formation of non-protein compounds.

The relation between chlorophyll content and maximum rate of photosynthesis is complex. Thus, while the correlation between the maximum rate of photosynthesis and the chlorophyll content of the different light classes is negative, within each light class this correlation seems to be positive. It is possible that hereditary factors are involved here and this suggestion is also being further investigated.

SUMMARY

Some preliminary experiments on light adaptation phenomena in *Acer pseudoplatanus* L. (sycamore) are described. First year seedlings were grown under four different light intensities. The light intensity dependence of photosynthesis, and the relation between exposition light intensity and both chlorophyll content and protein content were measured on single leaves.
1. It appeared from the photosynthesis curves that, with increasing exposition light intensity, the saturation light intensity as well as the maximum rate of photosynthesis, increases.
2. The chlorophyll content/cm^2 decreases with increasing exposition light intensity.
3. Within each light intensity class, the maximum rate of photosynthesis seems to be directly correlated with the chlorophyll content.
4. In strong light, the leaves are thicker, however, without conspicuous increase in protein content.

REFERENCES

BUKATSCH, F. 1940. Zeitschr. Ges. Naturwiss. 6: 197–198.
HENRICI, M. 1919. Verh. Naturf. Ges. Basel 30: 43–136.
MONTFORT, C. 1941. Naturwiss. 29: 238.
MONTFORT, C. and G. ZÖLLNER. 1942. Bot. Archiv. 43: 393–460.
RABINOWITCH, E. I. 1945. Photosynthesis I. Interscience Publish., New York.
RABINOWITCH, E. I. 1951. Id. II, 1: p. 861 ff.
RANDALL, W. E. 1953. Ecology 34: 544–553.
ROUX, E. and C. HUSSON. 1952. Comptes rendus hebd. des séances de l'Acad. des sciences 234: 1154; 235: 1573.
SCHENK, W. 1952–'53. Planta 41: 290–311.
SCHERTZ, F. M. 1929. Plant Physiology 4: 135–141.
SJÖBERG, K. 1931. Med. Centralanst. Försök. Jordbr., Stockholm 404: 1–19.
STÅLFELT, M. G. 1927. Planta 4: 201–213.
WENDEL, K. 1940. Zeitschr. Ges. Naturwiss. 6: 327–329.
WILLSTÄTTER, R. and A. STOLL. 1918. Untersuchungen über die Assimilation der Kohlensäure, Berlin.
ZACHAROWA, T. M. 1929. Planta 8: 68–83.