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ON THE RELATION BETWEEN THE MAXIMUM RATE OF PHOTOSYNTHESIS AND THE THICKNESS OF THE MESOPHYLL IN SUN- AND SHADE LEAVES OF *ACER PSEUDOPLATANUS* L.

by

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INTRODUCTION

There are two sources of knowledge about sun and shade leaves, anatomical and physiological ones. Anatomically, it is generally accepted that the sun leaf is thicker than the shade leaf. The increasing thickness is mainly due to elongation of the palissade cells and/or to the development of a second layer of palissade cells and to a smaller degree to additional cell layers in the spongy parenchyma (1).

In the physiological literature it is agreed that photosynthesis pro unit area of a sun leaf is higher than that of a shade leaf (2a–c). About these facts practically no doubt exists. Little work has been done about the causes of these differences. Doubtlessly, the light intensity under which the leaves have grown is an important factor in determining the properties of the leaf, but temperature (3) and humidity (4) of the environment which usually are interrelated with the light field (5) are also involved. Genetical factors (4) and the root environment play a rôle in the development of the leaf primordium to the full grown leaf, while, moreover, the age of the leaf is of importance (6).

It seems unrealistic to hope to solve the complicated problems involved without cultivation of plants under highly conditioned circumstances inside the laboratory and work along such lines is now in progress. Nevertheless, some interesting results may be obtained from plant material grown in an entirely or nearly natural way in the open air, as will be shown in this paper, relating maximum photosynthesis and anatomical structure in leaves of *Acer Pseudoplatanus.*

METHODS

Plant material

Two experiments will be discussed. One makes use of three large sycamore trees, the other of one-year old seedlings.

In the first experiment, mature leaves were gathered, one by one, from the crown of three big trees. Various measurements, as explained below, were made with these leaves. In this way, a good sample from the whole crown was gradually obtained.

In the second experiment, one year old seedlings were planted in three rectangular plots in the garden. Two of these plots were shaded with gauze screens, resulting in three light-treatments, *viz.* 100%, 80%, and 50% of natural daylight. Also from this material, mature leaves were collected one by one as to gradually form representative samples for the three light-treatments.

Measurements

Two determinations were made on each leaf, *viz.*, maximum photosynthesis, and thickness of the leaf. Maximum photosynthesis is that recorded under saturation for light and CO_2. To this purpose, a single, detached leaf or leaf part was enclosed in an assimilation chamber, and illuminated from one side via a water bath (in order to absorb infra-red radiation as much as possible) with a PHILIPS Attralux incandescent lamp (24 V, 150 W). With the aid of another water bath, the temperature of the walls of the assimilation chamber was maintained at a constant level of 20°C. Water vapour saturated air with 5% CO_2 was passed through the chamber. For the first determination, a relatively high illumination intensity was chosen, in order to secure light saturation; a period of 25 to 40 minutes was required to reach the maximum rate of photosynthesis. By stepwise lowering of the light intensity, it was then possible to quickly determine several points on the light intensity curve. Respiration was measured as CO_2-exchange in the dark.

The petiole of each leaf was shortened under water, a few seconds only after detaching it from the plant, lest air should invade the vascular system and impede the water supply of the leaf. Thereafter each leaf was trimmed in such a way that it suitably filled the area of the assimilation chamber, while its petiole was in a potometer connected to the assimilation chamber. Special care was taken that the petiole was submerged at any time, because only then the maximum rate of photosynthesis remained constant during a long time.

Leaf thickness was measured microscopically on transversal sections of the leaf. The mean of six determinations was used as leaf thickness.

Some further details of technique may be mentioned briefly. The dimensions of the assimilation chamber were: Ø 6 cm, depth 6 mm. The speed of the gas stream was 2 l per hour. The saturation intensity varied from 8.10^4 to 20.10^4 ergs/cm^2.sec^2 of visible light. Lower light intensities were obtained by intercalating photographic plates of different density between the light source and the assimilation chamber. The measurements were made with the aid of a home-made, registrating diaferometer or catharometer; the full-scale deflection of 12 cm represents a difference in CO_2-content of 0.12%, the drift was less than 2 mm per hour. The instrument will be more fully described in a subsequent, more extensive paper.

Results

The result of the first experiment is shown in fig. 1. The abscissa represents the thickness of the mesophyll in μ, the ordinate the maximum photosynthesis in mm^3/hour/cm^2 leaf area.

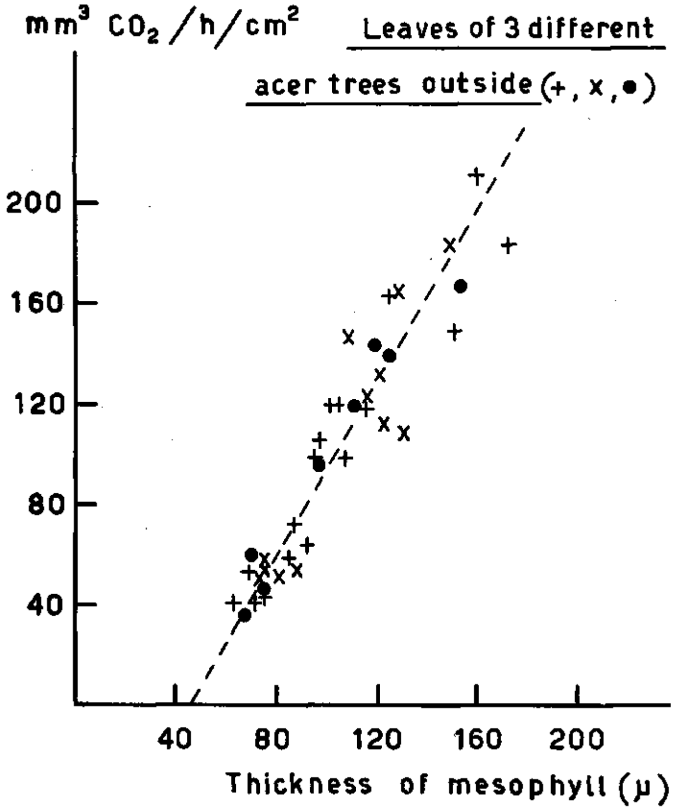

FIG. 1. The relation between maximum rate of photosynthesis (mm^3 CO_2/hour/cm^2 leaf area) and thickness of the mesophyll in leaves of three different full-grown *Acer* trees.

There are three remarkable points, *viz.*:

1. There is a clear correlation between the thickness of the mesophyll of the leaf and its maximum rate of photosynthesis.
2. The curve does not pass through the origin, but cuts the abscissa at about 50 μ. If total leaf-thickness was plotted, the curve would shift about 26 to 45 μ to the right.
3. The relation between the thickness of the mesophyll of the leaf and the maximum rate of photosynthesis is nearly equal for the three different *Acer*-trees used.

It may be added that a leaf from the outside of the crown, without exception had a sun leaf character, while a leaf taken from the inside of the crown had a shade leaf character.

The results of the second experiment is shown in fig. 2. Three observations may be made, *viz.*:

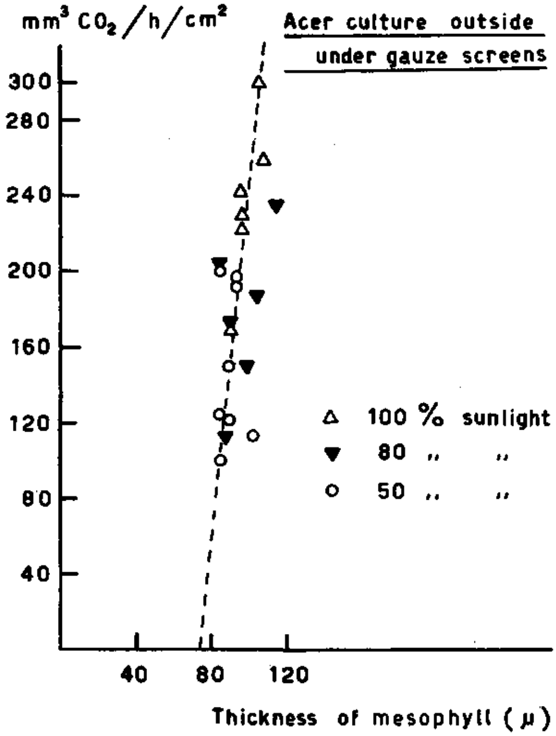

FIG. 2. The relation between maximum rate of photosynthesis (mm³/hour/cm² leaf area) and thickness of mesophyll in leaves of *Acer* seedlings under three different light-treatments.

1. There is a clear difference between the mean maximum rate of photosynthesis of the leaves from the 100%, 80%, and 50% light treatments.
2. There are, however, only minor differences in the thickness of the mesophyll of the leaf under the three light treatments.
3. The curve cuts the abscissa at about 70 μ.

DISCUSSION

The simple and linear relation between the maximum rate of photosynthesis and the leaf thickness suggests a simple and direct connection between the development of the mesophyll and that of the enzyme system limiting photosynthesis. That the linkage of the two processes is not that close is shown by experiment 2, in which the ultimate thickness of the mesophyll does not change much with strongly different maximum rates of photosynthesis. This suggests that factors other than light intensity interfere with the processes in question and in any case partly influence each process in a different way. It will be shown in a subsequent paper that temperature, *e.g.*, is of major importance in leaf development.

It is of interest that the curves cut the abscissa. Obviously, the meaning of the intersection point is that of a theoretical leaf thickness which is to be considered as the minimum, required for photosynthesis. This hypothetical leaf thickness is around 50 μ in experiment 1, around 70 μ in experiment 2. It is not known as yet, how closely this theoretical point can be experimentally approached, and what type of anatomical structure corresponds to it. In experiment 1, in which the most pronounced relation between photosynthesis and leaf thickness was observed, this theoretical leaf thickness is about $\frac{1}{2}$ of that observed for leaves inside the crown of the trees, and about $\frac{1}{4}$ of that observed in leaves exposed to full daylight. One may suggest that it corresponds closely to the thickness of a fully expanded, nearly chlorophyll-free leaf as formed in experiments performed by Batalin (7) and others upon daily exposures to low amounts of light.

In a previous paper (2) relations between the maximum rate of photosynthesis and the exposition intensity during growth have been discussed. From the data of figure 2 of the present paper, figure 3 can be constructed, closely resembling figure 6 of (2a).

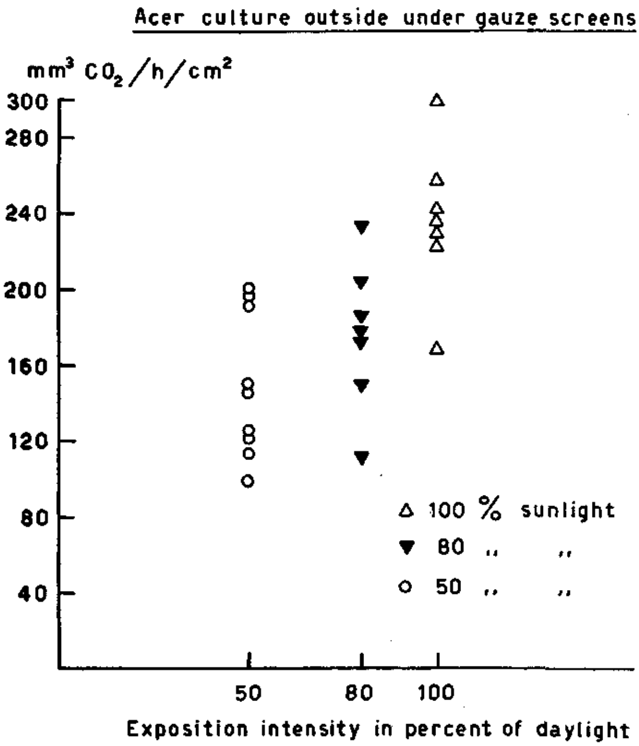

FIG. 3. The relation between maximum rate of photosynthesis and exposition light intensity in the leaves of experiment 2.

With some reserve, a last conclusion might be that ageing of the leaves does not influence the relation between leaf thickness and maximum rate of photosynthesis, since this relation remained similar during the entire summer season. This means that ageing in the mature leaf influences neither photosynthesis nor thickness of the mesophyll, or that it equally influences both.

SUMMARY

The rate of photosynthesis at light and CO_2-saturation and thickness were measured in leaves of some full grown *Acer* trees and in those of *Acer* seedlings, cultivated under different light intensities in the garden. In the crown of full grown *Acer* trees, sun leaves are at the periphery while, towards the inside of the crown, leaves with increasing shade leaf character are found. The maximum rate of photosynthesis of these leaves is correlated linearly with leaf thickness, sun leaves having a high maximum rate and a large thickness, and shade leaves having a low maximum rate and a small thickness.

The leaves of the seedlings clearly showed an adaptation of their maximum rate of photosynthesis to the light intensity under which they were cultivated, their ultimate thickness, however, was nearly the same for the different light treatments.

The curves of maximum rate of photosynthesis versus thickness of the mesophyll of the leaf do not pass through the origin, indicating the minimal thickness that a leaf needs in order to perform photosynthesis.

ACKNOWLEDGEMENT

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REFERENCES

1. DUFOUR, L., Influence de la lumière sur la forme et le structure des feuilles, Paris, 1887.
2a. WASSINK, E. C., S. D. RICHARDSON and G. A. PIETERS, Photosynthetic adaptation to light intensity in leaves of *Acer Pseudoplatanus*, Acta Botanica Neerlandica **5**, 247–256 (1956).
2b. BÖHNING, R. H. and BURNSIDE, C. A., The effect of light intensity on the rate of apparent photosynthesis in leaves of sun and shade plants. Am. J. Bot. **43**, 557–561 (1956).
2c. BURNSIDE, C. A. and BÖHNING, R. H., The effect of prolonged shading on the light saturation curves of apparent photosynthesis in sun plants. Plant Phys. **32**, 61–63 (1957).
3. SIMONIS, W., Handbuch der Pflanzenphysiologie, W. RUHLAND (Ed.) V/2 Berlin 1960, pp. 273–274.
4. WATSON, R. W., The mechanism of elongation in palissade cells, New Phytologist **41**, 206–221 (1942).
5. DAUBENMIRE, R. F., Plants and environment, New York, 1947.
6. ANDERSON, Y. O., Seasonal development in sun and shade leaves, Ecology **36**, 430–439 (1955).
7. BATALIN, A., Ueber die Wirkung des Lichtes auf die Entwicklung der Blätter. Botan. Ztg. **29** (40), 669–686 (1871).