On the Seasonal Change of Photosynthetic Activity of Some Deciduous and Evergreen Broadleaf Trees

by Toshiro SAEKI* and Nobuo NOMOTO**

佐伯敏郎*・野本宣夫**：二三の樹種における光合成能力の季節変化。

Received April 21, 1958

For the causal understanding of the geographical distribution of plant species, the variation of photosynthetic activity in each species must be followed throughout its whole growing period. We have some informations concerned in herbs and grasses, while in the case of trees only a few reports have been presented. For example Willstätter and Stoll worked with *Acer* and *Tilia*, but with the view of clarifying the mechanism of photosynthesis they always measured it under abnormally high CO₂ concentration. Reports by other investigators were almost concerned in restricted period as in summer or winter. Among them Kusumoto's (1957, 1958) are worthy to be noticed.

In the present paper we describe the changing features of photosynthetic activity in deciduous as well as evergreen broadleaf trees under normal air conditions against Willstätter and Stoll's experiments, and discuss the meaning of difference in activity-curves between deciduous and evergreen trees on their lives and geographical distributions, comparing with the Kusumoto's results obtained in a southern part of Japan.

Method

Trees used for measurements were *Zelkova serrata* (deciduous), and *Shiia Sieboldi*, *Pittosporum Tobira* and *Cinnamomum Camphora* (evergreen), growing in the campus of the University of Tokyo, ages of which were all more than 30 years. After cutting off a twig from the southern sunny side of a crown, a test leaf was again cut in water at the base of its petiole for assurance of water absorption, and it was laid in an assimilation chamber moistened with wet filter paper, in a laboratory. The leaf was preilluminated with 15-20 kilolux light for about 30 minutes, being exposed to air-flow from the open air. These treatments were useful to make the stomata widely open in the most species so far tested. For the light source 300 W flood or 500 W spot reflector lamps, sometimes for weak illumination ordinary tungsten bulbs, were employed, combined with sky light. Air temperature in the assimilation chamber

* Botanical Institute, Faculty of Science, University of Tokyo. 東京大学理学部植物学教室

** Biological Institute, Faculty of Arts & Science, Ibaraki University, Mito, Ibaraki. 茨城大学文理学部生物学教室

was adjusted to 25°, but lowered in winter to 20°, or winter optimum temperature for photosynthesis (c. f. Kusumoto 1957). The assimilation chamber was sustained at 10 cm. depth in a water bath, to intercept the excess heat radiation, although sometimes even under such a condition overheating of leaf was observed at strong light intensity, e.g. in 30 kilolux illumination leaf temperature of *Zelkova* detected with a thermocouple was 5° higher than air in the chamber. The net assimilation obtained at high light intensity, therefore, might be estimated somewhat lower on account of respiration activated with the high leaf temperature. In this paper, however, only the air temperature in the assimilation chamber was noticed because it was too complicated to measure every time the temperature at each test leaf.

Photosynthesis and respiration were measured with Boysen Jensen's method (1932) with some modifications. The obtained values were corrected to 0.03 volume percent CO₂. The photosynthetic ability at light saturation, compensation point, etc., of each leaf were determined after defining the light-photosynthesis curve with a series of measurements. Chlorophyll content of leaves was measured after the procedure of Kasanaga and Monsi (1954).

Seasonal change of photosynthetic activity

A. Deciduous tree. In Fig. 1 we summarized the results obtained in the leaves of *Zelkova serrata*, concerning the maximum net photosynthetic ability at 25°, respiration, compensation point and chlorophyll content. The experiments were carried out in 1953, 1954 and partly in 1955. After sprouting of new shoots in late spring, rapid development of photosynthetic activity of all young leaves follows. Early in June it reaches already the maximum of about 6 mg. CO₂/50 cm²/hr. (Fig. 1). In 1953 and

Fig. 1. Seasonal changes of photosynthetic activity, respiration, compensation point and chlorophyll content (broken line) in *Zelkova serrata*. The values were derived from the measurements in 1953, except for the photosynthetic course in 1954 (thin line).

1955, this high value persisted for about two and a half months. Then the activity declined gradually from the middle of August, until all leaves turned yellow losing perfectly their activities and fell in November. In 1954, however, it was somewhat different; so soon did the curve begin to fall as in the middle of July. This might have been caused by the unusually continuous cloudy and rainy days from May to June in that year—in Japan we have ordinarily a rainy season in this time of year. Actually in June 1954 severe leaf fall took place which meant a getting worse of the dry matter economy in the shaded leaves inside the crown, because the daily maximal light intensities measured even in the open were sometimes only 3 kilolux or less.

The trend of the activity curves is principally the same as that obtained by Willstätter and Stoll (1918) in *Acer* and *Tilia*, except for long duration of high activity for more than 4 $\frac{1}{2}$ months, which seems to be caused by extremely high CO_2 concentration in their experiments (5%). In *Zelkova* the activity above the value of a half of the maximum could extend over 4 $\frac{1}{2}$ months, from the middle of May to the end of September, and it corresponds to the period of mean monthly temperature above 17°.

The dry weight per sq. cm. leaf area increased from 4.2 mg. late in April, to about 8-9 mg. early in June. After about two months only a slight increase reappeared, then the weight decreased with yellowing of the leaves. In the younger age of leaves higher respiration and higher compensation point were characteristic in parallel with lower chlorophyll content and lower photosynthetic activity (Fig. 1). This was more conspicuously observed in a Lammas shoot where leaves are successively arranged from younger to older ones. Light-assimilation curves obtained in four leaves of such a Lammas shoot (Fig. 2 and Table 1) show that with maturing of the leaves the photosynthetic activity and chlorophyll content increased, but the respiration and compensation point decreased. The maximum photosynthetic activity of *Zelkova* leaves changed fairly parallel to chlorophyll content (Fig. 1 and Fig. 3-a). Same relationship in the Lammas shoot appeared itself but gave somewhat indifferent curve (Fig. 3-b). This discrepancy in the two kinds of shoots seems to be rather natural, because Gabrielsen (1948) has already pointed out that the quantity of chlorophyll pigment is responsible not for the maximum photosynthesis but for the linear regression

Fig. 2. Light-photosynthesis curves in the leaves of a Lammas shoot. See Table 1. Nodes were numbered from the top to the base. Broken line shows the curve of normal leaves.

Table 1 Leaf size, maximum assimilation, chlorophyll content, respiration and light-compensation point in the leaves of Lammas shoot of *Zelkova serrata*. Nodes were numbered from the top to the base of the shoot.

	Leaf on			
	3rd node	4th node	5th node	7th node
Leaf size (cm ² , unilateral)	8.0	22.8	25.3	27.4
Max. assim. (mg. CO ₂ /50cm ² /hr.)	2.8	6.2	9.0	9.0
Chlorophyll content (γ/cm ²)	7.1	23.0	43.5	60.0
Respiration (mg. CO ₂ /50 cm ² /hr.)	1.3	1.3	0.8	0.7
Compensation point (kilolux)	2.2	1.1	0.6	0.6

Fig. 3. Relation between chlorophyll content and the maximal gross assimilation. a; annual shoots, b; Lammas shoot.

of photosynthesis curve in weaker illumination. This, combined with higher respiration, causes the difference in the light-photosynthesis curve of very young leaves as well as of yellowish old leaves from that of green shade leaves.

B. Evergreen broadleaf tree. The seasonal change curves of photosynthetic activity of *Shiia Sieboldi*, *Pittosporum Tobira* and *Cinnamomum Camphora* are shown in Fig. 4. In the vegetation period these three species gave similar courses as in *Zelkova*, and the maximum rates were also in the same order, i.e. both the types of trees could assimilate CO₂ almost at the same rate in summer. However, autumnal decline of the activity came somewhat later in the evergreen trees and the activity still remained at a low level throughout winter. In spring the older leaves of *Pittosporum* recovered their activity to some extent, before perishing under newly developing leaves in late spring, while *Shiia* (and also

Cinnamomum) had shown scarcely any indication of recovery in the activity. Low winter temperature near the northern limit of natural distribution of such evergreen trees (Tokyo, 35°40' N, mean temp. in Jan. 3.2°) may be responsible for the depression of the photosynthetic activity, because the low temperature is unfavourable for respiration which most possibly supplies the energy for maintaining the photosynthetic apparatus in active condition. The trees used for experiments were grown near such distribution limit. The photosynthetic activity of *Shiia* in winter was scarcely influenced with varying temperature in wide range from 3° to 25°, except for its slight rise at 20°. The values obtained in December fell in the range of 0.5-1.2 mg. CO₂

Fig. 4. Seasonal changes of photosynthetic activity in three species of evergreen trees and *Zelkova serrata* (the same as in Fig. 1).

—●— *Pittsoporum Tobira* —■— *Shiia Sieboldi*
—▲— *Cinnamomum Camphora* —○— *Zelkova serrata*

/50 cm²./hr. and were much lower than those of 2-3 mg. measured by Kusumoto (1957) at Kagoshima (31°30' N., mean temp. in Jan. 6.4°) in southern Kyushu, the distribution centre of the evergreen broadleaf forest.

Ecological meaning of the seasonal change in photosynthetic activity

The amount of organic matter produced by leaves is mainly decided by three factors, that is, photosynthetic activity of leaves, duration of high activity and total area of leaves. Supposing the maximum photosynthetic activity as 6 mg. CO₂/50 cm²./hr. in ordinary leaves of deciduous as well as evergreen trees and 9 mg. in Lammas shoot from the results obtained and photosynthesis for 10 hours and nocturnal respiration for 14 hours per day, so the daily dry matter production with open stomata on sunny day in summer will approximately be calculated as b in Table 2. Dry

Table 2. Comparison between dry matter per unit leaf area and produced dry matter per day per unit leaf area.

	Deciduous tree		Evergreen tree
	Annual shoot	Lammas shoot	Annual shoot
a. g. dry matter/m ² . of leaf	90	90	180
b. g. dry matter produced/m ² ./day	6	10	6
c. Ratio between a and b	15	9	30

matter weights per unit leaf area in the Table were based on the data on *Zelkova* as deciduous type and *Shiia* and *Pittosporum* as evergreen one. Some part of the produced matter must compensate for the invested capital or the dry matter necessary for replacement of fallen leaves. From the Table it may be roughly estimated that the photosynthetic days for the compensation of annual leaves are 15 days in the deciduous type and 30 days in the evergreen, hence, the evergreen leaves must work for maintenance of their leaves at their highest efficiency at least for 15 days more than the deciduous do. Where the winter temperature is enough high to allow effective photosynthesis, it may not be difficult to realize this. The difference in the production and economy between these two types should play an important role in competition between them, and consequently in the distribution of plant species. In this respect it should be remembered that high winter activities remain in *Shiia Sieboldi* and *Cinnamomum Camphora* at Kagoshima, while the summer activities are almost the same as our results (Kusumoto 1957). The leaves of *Cinnamomum* are not much thicker than those of *Zelkova*, but concerning dry matter economy, this may be offset by much low winter photosynthetic activity (Fig. 4 and Kusumoto 1957). In *Lammas* shoots the photosynthetic days for compensation of dry matter are shortened by their high activity up to 9 days, but the duration with this is limited to only a half of that in the normal leaves.

In a plant community not all the leaves can receive full sunlight on account of mutual shading. The total area of openings in canopy through which the sunlight penetrates up to the ground, gives a good measure not only of the light intensity on the forest floor but also of leaf amount. Sky photographs have been taken in *Zelkova* about every two weeks. Early in July the area of the openings in canopy reached a minimum of ca. 13%, and this corresponds to 2.9 in leaf area index (total area of leaves per unit area of land surface), assuming the leaf inclination as 45°. The openings continued in minimum until the middle of September, followed by gradual increase with autumnal leaf falling.

The shade leaf of *Zelkova* showed the maximum photosynthetic activity of 3-5 mg. CO₂/50 cm²/hr., and the respiration of 0.3 mg. CO₂/50 cm²/hr. (June 1955). As the dry weight of the shade leaves was 3-5 mg. per sq. cm. in contrast to 8-9 mg. of the sun leaves, it is expected that on dry weight basis the photosynthesis is in the shade leaves higher than in the leaves even at strong light intensity. Similar results have been confirmed by Tranquillini (1955) in *Pinus Cembra*.

Summary

Seasonal changes of photosynthetic activity of leaves in *Zelkova serrata* (a deciduous tree) and some evergreen trees, were investigated and meaning of concerning dry matter production was discussed.

1. The photosynthetic activity of *Zelkova* increased rapidly up to its maximum value of 5-6 mg. CO₂/50 cm²/hr. later in April and the value persisted for about 2 1/2

months; afterwards the activity decreased slowly until the defoliation in November. The activity maintained itself above a half value of the maximum for about $4\frac{1}{2}$ months of which mean monthly temperatures were above 17° . The photosynthetic activity changed fairly parallel, but only apparently, to the chlorophyll content.

2. In late spring and summer, the courses of change in the photosynthetic activities in evergreen trees, *Shiia Sieboldi*, *Pittosporum Tobira* and *Cinnamomum Camphora*, were more or less similar as that of *Zelkova*. In late autumn the activity fell to a low level, and it continued throughout the winter, and only in *Pittosporum* the activity recovered before the leaf fall in next late spring.

3. The younger stage of leaf is characterized with a higher respiration and compensation point, and with a lower chlorophyll content and photosynthetic activity. These were clearly shown in the leaves of a Lammas shoot which have generally higher activity than those of ordinary shoot.

4. The weight of the leaves of *Shiia* and *Pittosporum* is ca. 180 g./m^2 , while that of *Zelkova* is ca. 90 g./m^2 , hence, to get back these invested capitals the former species must earn about double amount of dry matter. In southern districts this may be easily realized in warmer winter, and which makes the evergreen tree more advantageous in competition with the deciduous tree in natural distribution.

This work was carried out under the guidance of Prof. M. Monsi, to whom we are greatly indebted for valuable help and criticism. Part of this investigation was supported by a grant-in-aid from the Science Research Fund of the Ministry of Education.

References

- 1) Boysen Jensen, P., Stoffproduktion der Pflanzen, Jena (1932). 2) Freeland, R.O., Plant Physiol. 37: 685 (1952). 3) Gabrielsen, E.K., Physiol. Plant. 1: 5 (1948). 4) Ksanaga, H. and Monsi, M., Jap. Journ. Bot. 14: 304 (1954). 5) Kusumoto, T., Bot. Mag. Tokyo 70: 299 (1957). 6) ———, Jap. Journ. Ecol. 7: 126 (1957). 7) ———, Bull. Fac. Educ. Kagoshima U. No. 9: 21 (1958). 8) Monsi, M. and Saeki, T., Jap. Journ. Bot. 14: 22 (1953). 9) Richardson, S.D., Acta Bot. Neerl. 6: 445 (1957). 10) Tranquillini, W., Planta 46: 154 (1955). 11) ———, ibid. 49: 612 (1957). 12) Walter, H., Ber. Dtsch. Bot. Ges. 69: 263 (1956). 13) Willstätter, R. and Stoll, A., Untersuchungen über die Assimilation der Kohlensäure, Berlin (1918).