

## 光合成・光呼吸・CO<sub>2</sub>補償点の種間差異

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## 論 文

## Comparison of Photosynthesis, Postillumination CO<sub>2</sub> Outburst, and CO<sub>2</sub> Compensation in Poplar Varieties, Sunflower, and Bean

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FURUKAWA, Akio: Comparison of photosynthesis, postillumination CO<sub>2</sub> outburst, and CO<sub>2</sub> compensation in poplar varieties, sunflower, and bean *J. Jap. For. Soc.* 57: 268~274, 1975 Photosynthesis, postillumination CO<sub>2</sub> outburst, the CO<sub>2</sub> compensation points, and dark respiration in leaves of four varieties of poplar (*Populus euramericana* Hardtwalden, *P. nigra* × *maximowizii*, 2n & 4n, *P. maximowizii* × *trichocarpa*) were compared with those in sunflower (*Helianthus annuus*) and bean (*Vigna sesquipedalis*) leaves. The maximum rate of net photosynthesis (NP<sub>max</sub>) in sunflower leaves, estimated by the algebraic method, was 1.13 to 1.63 times greater than in leaves of poplar varieties. The magnitude of the initial CO<sub>2</sub> outburst (PIB-1) in sunflower leaves was 6 mg CO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>, which was 2- to 4-fold greater than that in leaves of poplar varieties. Bean leaves had 2 to 4 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> of PIB-1. The CO<sub>2</sub> compensation points in poplar varieties and in sunflower and bean were 50~57 and 44~50 ppm, respectively. Sunflower leaves had a mean gross photosynthetic rate of about 40 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>, and poplar leaves had 23~33 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>. The rate of gross photosynthesis in bean leaves was about 30 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>. Results indicated that leaves of poplar varieties photosynthesize at rates similar to those herbaceous species of sunflower and bean.

古川昭雄: 光合成・光呼吸・CO<sub>2</sub>補償点の種間差異—ポプラクローンとヒマワリ・ミトリササゲとの比較 *日林誌* 57: 268~274, 1975 ヒマワリ (*Helianthus annuus*) の最大純光合成速度はポプラ4品種 (*Populus euramericana* Hardtwalden, *P. nigra* × *maximowizii*, 2n & 4n, *P. maximowizii* × *trichocarpa*) のそれの 1.13~1.63 倍であった。ヒマワリの光呼吸速度 (PIB-1) は 6 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> で、ポプラ4品種の 2~4 倍であった。ミトリササゲ (*Vigna sesquipedalis*) の光呼吸速度は 2~4 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> であった。また、ポプラの CO<sub>2</sub> 補償点は 50~57 ppmCO<sub>2</sub>, ヒマワリ, ミトリササゲの CO<sub>2</sub> 補償点は 44~50 ppmCO<sub>2</sub> であった。総光合成速度はポプラ4品種で 23~33 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>, ヒマワリで 40 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>, ミトリササゲで 30 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> であった。以上の実験結果は、ポプラの光合成速度は C<sub>3</sub> 型の草本植物の光合成速度と同程度であることを示している。ポプラの高い生長速度は高い光合成速度によるものと考えられる。

### I. Introduction

Some herbaceous species, such as *Saccharum*, *Zea mays*, *Amaranthus*, or *Atriplex*, show very high rates of photosynthesis, and have the new photosynthetic CO<sub>2</sub> fixation pathway known as the C<sub>4</sub>-dicarboxylic acid pathway (14, 17, 18, 23, 24). Those species with the C<sub>4</sub>-dicarboxylic acid pathway will be referred to as the C<sub>4</sub> species. In general, the C<sub>4</sub> species have very low CO<sub>2</sub> compensation points and no detectable rates of CO<sub>2</sub> evolution in the light (1, 7, 26). The C<sub>4</sub> species are known to

have 2- to 3-fold greater rates of net photosynthesis than the C<sub>3</sub> species at high light in normal air (1, 7). The C<sub>3</sub> species are those species with the CALVIN cycle for photosynthetic CO<sub>2</sub> fixation. The C<sub>3</sub> species have relatively low rates of photosynthesis, high CO<sub>2</sub> compensation points between 40 and 60 ppm, and high rates of CO<sub>2</sub> evolution in the light (1, 6, 7).

Photosynthetic rates in deciduous tree species are generally known to be lower than those in herbaceous species. According to HESKETH (15), photosynthetic rates of oak and maple were lower than

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10 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> while that of orchardgrass (C<sub>3</sub> species) was over 20 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> under the intense light intensity. It is very interesting that he observed the rate of photosynthesis of near 50 mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup> in sunflower (C<sub>3</sub> species) at 300 ppmCO<sub>2</sub>. This photosynthetic rate was similar to that in maize (C<sub>4</sub> species). Photosynthetic rates in tree species of poplar and mulberry were also compared with those in herbaceous species of sunflower and maize by USHIJIMA and TAZAKI(27). They demonstrated similar results, i. e., tree species had lower photosynthetic rates than herbaceous species, and maize had the highest one.

This paper reports the results of experiments designed to test whether poplar leaves are inferior in photosynthetic rates to herbaceous C<sub>3</sub> species for high photorespiratory rates. Net photosynthetic rates as well as the postillumination CO<sub>2</sub> outburst and the CO<sub>2</sub> compensation points as the magnitude of photorespiration were determined in four varieties of poplar and in sunflower and bean for herbaceous C<sub>3</sub> species. To eliminate estimation error from measuring technique or apparatus, the author measured the CO<sub>2</sub> gas exchange of every plant species in the same assimilation chamber and under the same conditions.

## II. Materials and Methods

### *Air circulation system*

The carbon dioxide concentration was controlled by mixing air with CO<sub>2</sub>-free air. CO<sub>2</sub>-free air was prepared by passing air through tubes filled with soda lime or ascarite. Air was passed in succession through an air tank(380 liter), and through the coiled glass tubing placed in the stabilized temperature bath. Air at bath temperature was then led into the leaf chamber and out by a HARTMANN & BRAUN air pump (Membrane Pumpe 2) to the analyser. The air stream entering into the CO<sub>2</sub> analyser was dried by magnesium perchlorate. The precise method for determining the concentration of CO<sub>2</sub> in air was carried out using a HARTMANN & BRAUN infrared CO<sub>2</sub> analyser (URAS-1). The difference in the CO<sub>2</sub> concentration between the ingress and the egress air multiplied by the air flow rate gives the rate of CO<sub>2</sub> uptake or evolution in mgCO<sub>2</sub>dm<sup>-2</sup>hr<sup>-1</sup>. Incident light beams were provided by means of flood-type lamps (National Reflamp 500 W) and were filtered through water filter of 10 cm deep to absorb heat. The intensity of light was changed by varying voltage supplied to lamps and checked by a Toshiba photometer (Model SPI-5) at the surface of the leaf. Water temperature in the bath was controlled by using a Sharp thermo-module (Model TE-14) with a thermistor controller. The

leaf chamber was constructed by polyethylene with a removable lucite lid (3 mm thick) to accommodate the leaf. Its dimension was 15 cm in diameter and 0.6 cm in depth. The transparent lid was attached to the compartment with silicone grease.

### *Method for determining CO<sub>2</sub> gas exchange*

A detached poplar leaf was placed in the assimilation chamber with its petiole immersed in a small glass vial containing distilled water. The top lid was fitted to the compartment and the whole chamber was submerged in the water bath. After the preliminary illumination period with aeration (about 1 hour), photosynthesis was detected. When it was desirable to measure the rate of CO<sub>2</sub> evolution in the light, air was instantly exchanged into CO<sub>2</sub>-free air. Then the rate of CO<sub>2</sub> evolution into CO<sub>2</sub>-free air in the light could be measured.

A conventional method of closed circulating system was employed to determine the CO<sub>2</sub> compensation point. A closed system consisted of an assimilation chamber containing a leaf, a drying column filled with magnesium perchlorate, two diaphragm pumps for circulating air, and URAS-1. The closed system was rigorously tested to be sure there was no leakage.

### *Experimental materials*

Cuttings of poplar varieties were stocked at 5°C for at least 3 months before planting to break dormancy. In April, cuttings were potted in fertilized soil and were grown in the glass house under the field conditions. Four varieties of poplar cuttings, LK-83 (*Populus euramericana* Hardtwalden), NM-101, 2n & 4n (*P. nigra* × *maximowizii*, 2n & 4n), and OP-44 (*P. maximowizii* × *trichocarpa*), were supplied by Kameyama Breeding Station. of the Oji Institute for Forest Tree Improvement Sunflower (*Helianthus annuus*) and bean (*Vigna sesquipedalis*) were also grown in pots in the glass house from early June to July.

In most experiments, newly matured leaves were obtained from potted poplar plants in July. The detached sunflower and bean leaves were taken from nodes 4 to 6, numbering from the top of plants.

The leaf area was determined by copying the configuration of the leaf with sensitive paper (Kokuyo, Violet). The shape of the leaf was cut from paper and weighed. From the relation between the paper weight and the known area, the leaf area could be determined. The leaf dry weight was determined after 24 hours at 105°C.

## III. Results and Discussion

### *Net photosynthesis in poplar varieties and sunflower at various light intensities*

The high rate of photosynthesis of  $27 \text{ mgCO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  was obtained in LK-83 at  $25^\circ\text{C}$ ,  $25 \text{ K lux}$ , and  $340 \text{ ppmCO}_2$  (Fig. 1). Photosynthetic rates in other poplar varieties were 20 to  $25 \text{ mgCO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ . These high rates of photosynthesis were accomplished when the air flow rate was  $5.0 \text{ liter/min}$ . The rate of net photosynthesis in sunflower was  $33 \text{ mgCO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  under the same conditions (Fig. 1). Hence it appears certain that the rate of photosynthesis in poplar varieties was not noticeably lower than that in sunflower.

The author has previously reported the low rate of photosynthesis of about  $8 \text{ mgCO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  in NM-101,  $2n(9)$ . This low rate of photosynthesis should be mainly dependent on the low rate of air flow ( $0.5 \text{ liter/min}$ ). It is well documented that the photosynthetic rate is greatly influenced by the

aerating velocity, which is an important limiting factor for the photosynthesis measurement (11). Actually, when the air flow rate was  $0.5 \text{ liter/min}$ , photosynthetic rates in four varieties of poplar were 7 to  $8 \text{ mgCO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  (Fig. 1). Accordingly, the previously reported low rate of photosynthesis in poplar would conceivably be derived from the insufficient supply of  $\text{CO}_2$  caused by the low rate of air flow.

For the critical comparison of photosynthetic rates among species, the estimation of net photosynthetic rates at the infinite light intensity was carried out using algebraic method. Photosynthesis can be written by:

$$P = bI / (1 + aI) \quad (1)$$

where  $P$  is the sum of net photosynthesis and dark respiration, and  $I$  is the light intensity. Since

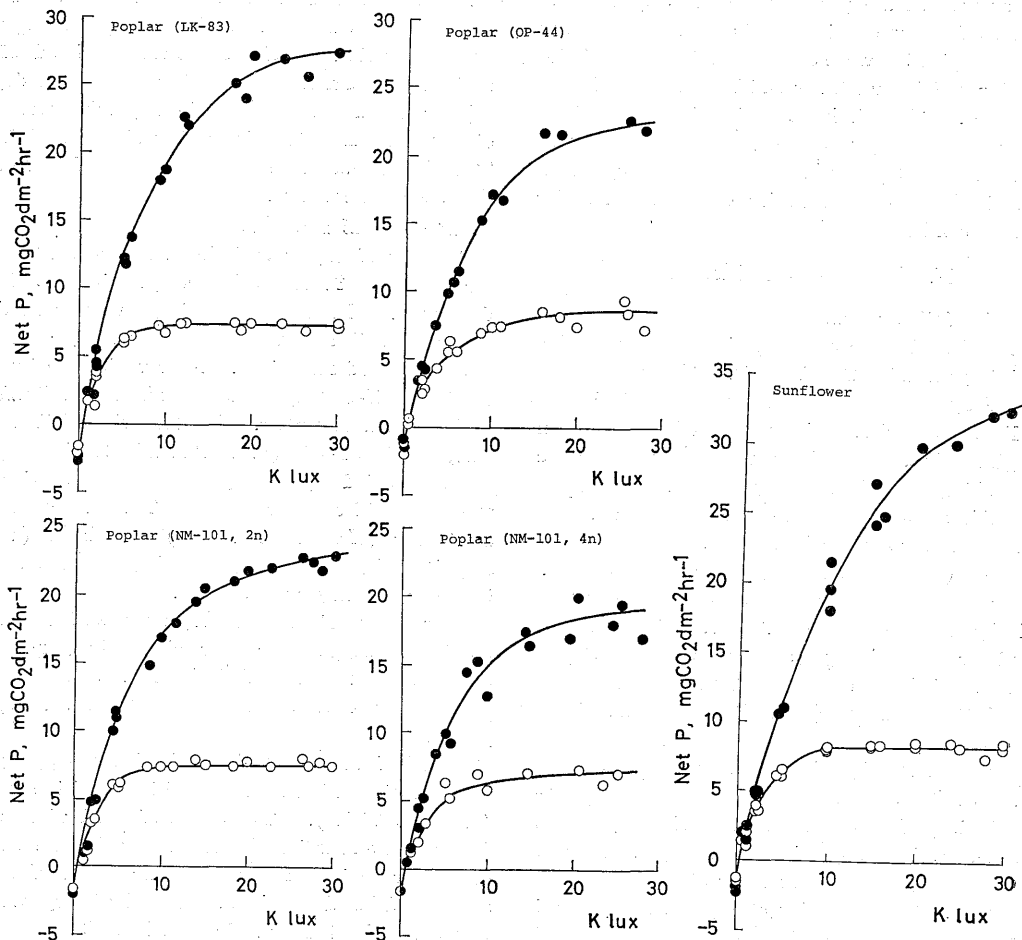


Fig. 1. Net photosynthesis in response to light intensity of a single leaf of poplar varieties and sunflower

The detached leaf was placed in the assimilation chamber with its petiole immersed in water, and photosynthetic  $\text{CO}_2$  uptake was determined at  $340 \text{ ppm CO}_2$ ,  $25^\circ\text{C}$ , and an air flow rate of  $0.5 \text{ liter/min}$  (open circles) of  $5.0 \text{ liter/min}$  (closed circles) by measuring  $\text{CO}_2$  concentrations at the inlet and the outlet of the assimilation chamber.

Table 1. Comparison of  $NP_{max}$  and  $I_{1/2}$  in detached leaves of four poplar varieties and sunflower at 340 ppmCO<sub>2</sub> and 25°C

Species	Flow rate (l/min)	$NP_{max}$ (mgCO <sub>2</sub> ·dm <sup>-2</sup> ·hr <sup>-1</sup> )	$I_{1/2}$ (Klux)
Poplar (LK-83)	0.5	8.9	2.0
	5.0	36.7	8.0
Poplar (OP-44)	0.5	9.5	2.8
	5.0	29.7	8.0
Poplar (NM-101, 2n)	0.5	8.3	2.0
	5.0	30.3	7.4
Poplar (NM-101, 4n)	0.5	8.1	2.0
	5.0	25.4	7.9
Sunflower	0.5	9.8	1.8
	5.0	41.5	8.6

$P$  values have no physiological meaning, the author proposes the revised method for the estimation of the net photosynthetic rate at the infinite light intensity ( $NP_{max}$ ) with an assumption that light has no effect on the rate of dark respiration. Thus:

$$NP_{max} = P_{max} - DR \quad (2)$$

where  $P_{max}$  is the maximum  $P$  in equation (1) when  $I \rightarrow \infty$ . The values of  $a$  and  $b$  were graphically estimated by the method of SHINOZAKI and KIRA(22). The magnitude of  $1/a$  is the light intensity ( $I_{1/2}$ ) where  $P_{max}=1/2$ .

$NP_{max}$  was also influenced by the rate of air flow and 3 to 4 times  $NP_{max}$  was obtained in every species at 5.0 liter/min in comparison with that at 0.5 liter/min (Table 1). At the higher air flow rate, sunflower leaves had  $NP_{max}$  of 41.5 mgCO<sub>2</sub>·dm<sup>-2</sup>·hr<sup>-1</sup>, which is greater than any poplar variety. But sunflower was only 1.13 times as great in  $NP_{max}$  as LK-83.

The CO<sub>2</sub> compensation points in poplar, sunflower and bean

The CO<sub>2</sub> compensation points varied in four varieties of poplar between 50 and 57 ppm, but there was no remarkable difference among them. Sunflower had also a similar CO<sub>2</sub> compensation point with a mean of 48.5 ppm. The CO<sub>2</sub> compensation point in bean was 44~48 ppm (Table 2). Thus, the CO<sub>2</sub> compensation points in herbaceous plants were slightly lower than those in poplar varieties.

The CO<sub>2</sub> compensation points of healthy and green leaves are basically different for C<sub>4</sub> and C<sub>3</sub> species (1,7). In those species with a significant photorespiration, C<sub>3</sub> species, the CO<sub>2</sub> compensation points are 40~60 ppm in air containing a normal concentration of O<sub>2</sub>, 21%, and at 25°C, while C<sub>4</sub> species have 0~5 ppm. The CO<sub>2</sub> compensation point of maize grown in our glass house during the summer months was 5 ppm. Because of the high activity of photosynthetic refixation of the evolved CO<sub>2</sub>, C<sub>4</sub> species lack photorespiration and have very low CO<sub>2</sub> compensation points(8). However, there are

Table 2. Comparison of PIB-1, PIB-2, dark respiration, and CO<sub>2</sub> compensation in leaves of four poplar varieties, sunflower, and bean at 25°C and an air flow rate of 1.0 liter/min. PIB-1, PIB-2, and dark respiration were determined after the measurement of net photosynthesis and CO<sub>2</sub> compensation points at 25 Klux

Species	Dark respiration			CO <sub>2</sub> compensation point
	PIB-1	PIB-2	respiration	
	mgCO <sub>2</sub> ·dm <sup>-2</sup> ·hr <sup>-1</sup>			ppmCO <sub>2</sub>
Poplar (LK-83)	1.58	2.06	1.18	55
	1.52	3.04	2.12	52
Poplar (NM-101, 2n)	2.18	3.46	1.96	54
	2.74	2.36	1.37	50
Poplar (NM-101, 4n)	1.18	3.30	1.97	52
	1.09	2.44	1.52	50
Poplar (OP-44)	2.76	2.10	1.66	55
	3.14	1.62	0.98	57
Sunflower	6.20	2.64	1.24	47
	6.32	2.04	1.28	50
Bean	4.03	2.18	1.40	44
	2.02	1.68	1.10	48

only a few report about the CO<sub>2</sub> compensation points in tree species. MOSS(20) reported that Norway maple (*Acer platanoides*) has the CO<sub>2</sub> compensation point of 145 ppm, and has a very low rate of photosynthesis. However, the author could not obtain such a high CO<sub>2</sub> compensation point in maple (*Acer micranthum*). The CO<sub>2</sub> compensation point in maple was 54 ppm (FURUKAWA, unpublished results). The author also measured the CO<sub>2</sub> compensation points of more than 50 tree species. All had the CO<sub>2</sub> compensation points below 80 ppm, and 70% of these species were below 60 ppm (55±3 ppm). Low compensation points below 40 ppm could not be found. Likewise, little variation occurred in compensation points of CO<sub>2</sub> in poplar varieties listed in Table 2, 53.1±2.5 ppm. CHEN *et al.*(5) reported the CO<sub>2</sub> compensation point of 52 ppm in cowpea (*Vigna sinensis* L.), and GOLDSWORTHY and DAY(13) reported 50±0.8 and 62.2±1.9 ppm in tobacco and Pelargonium, respectively. Furthermore, MOSS(21) reported 52±2 and 55±2 ppm in wheat and barley genotypes, respectively. Thus, the CO<sub>2</sub> compensation points of tree species may essentially be the same as those of herbaceous C<sub>3</sub> species.

Postillumination CO<sub>2</sub> outburst in poplar, sunflower, and bean

Sunflower had over 6.0 mgCO<sub>2</sub>·dm<sup>-2</sup>·hr<sup>-1</sup> of the initial postillumination CO<sub>2</sub> outburst (PIB-1), while poplar varieties had only 1~3 mgCO<sub>2</sub>·dm<sup>-2</sup>·hr<sup>-1</sup> and bean had 2~4 mgCO<sub>2</sub>·dm<sup>-2</sup>·hr<sup>-1</sup>. Compared with PIB-1, there was no significant difference in the rate of either the second burst (PIB-2) or dark respiration among species tested here (Table 2).

There is no precise method devised to date for the critical estimation of photorespiration. Measurement of photorespiration is rendered difficult, since

photosynthetic refixation of the evolved  $\text{CO}_2$  occurs simultaneously, so as to partially or completely mask the process. The flux of  $\text{CO}_2$  from the respiratory site should be refixed at the boundary layer of the leaf surface and at the photosynthetic site, chloroplast. The rate of refixation at the boundary layer is reduced by the rapid flow rate of air over the leaf surface(11). PIB-1 is also affected by the rate of air flow (FURUKAWA, unpublished results). This predicts that the evolved  $\text{CO}_2$  be refixed at the laminae boundary layer by the prolonged uptake of  $\text{CO}_2$  in the dark. Other methods for the measurement of photorespiration are also affected by the rate of air flow. The method developed by ZELITCH(28), who measured the rate of release of recently fixed  $^{14}\text{CO}_2$  in the light in  $\text{CO}_2$ -free air, was also influenced by the air flow rate. It appears that photosynthetic refixation can affect and lower the estimate of photorespiration rate measured by any method. However, PIB-1 should give a fairly accurate estimate of the rate of photorespiration. It may be adequate to suggest that the rate of refixation may be rapidly inactivated by extinguishing the light. Then the influence of photosynthetic refixation to PIB-1 should be less than that of the rate of  $\text{CO}_2$  evolution measured in the light. With this in mind, the author measured PIB-1 in various species to compare the rates of photorespiration.

GAASTRA(12) has shown that the diffusion of  $\text{CO}_2$  through stomata and mesophyll can be described by the following equation:

$$NP = ([\text{CO}_2]_e - [\text{CO}_2]_c) / (R_a + R_s + R_m) \quad (3)$$

where  $\text{CO}_2$  concentration is  $[\text{CO}_2]$  in the ambient air;  $[\text{CO}_2]_e$ , at the surface of chloroplast;  $[\text{CO}_2]_c$ .  $R_a$ ,  $R_s$ , and  $R_m$  are diffusion resistances at the boundary layer, stomata, and mesophyll, respectively. If  $[\text{CO}_2]_e = 0$ , and  $-NP$  is replaced by  $NE$ , equation (3) can be rewritten as:

$$NE = [\text{CO}_2]_c / (R_a + R_s + R_m) \quad (4)$$

Then the measured rate of  $\text{CO}_2$  evolution in the light can be explained by  $NE$ , and this suggests that the rate is directly dependent on the total sum of diffusion resistances of  $\text{CO}_2$ .  $R_a$  is controlled by physical characteristics of tested materials, not by physiological ones. The rate of air flow and the leaf width are the limiting factors of  $R_a$ (25). In this experiment, the rate of air flow was 1.0 liter/min and the leaf width was fairly constant among species tested here (the mean leaf area was  $110 \text{ cm}^2$  with a standard error of  $\pm 23 \text{ cm}^2$ ). Then the differences of the measured rates of  $\text{CO}_2$  evolution in the light among species should be independent of  $R_a$ ; i.e., the difference of PIB-1 among species may be independent of the refixation rate

at the laminae boundary layer. Hence it appears that poplar varieties have larger diffusion resistances of stomata and mesophyll than sunflower, and/or photorespiratory activity. Though there is no direct evidence, the former explanation may be reasonable and the diffusion resistance of stomata may be more effective than that of mesophyll(2).

#### Gross photosynthesis in poplar, sunflower, and bean

Some workers define gross photosynthesis as the sum of net photosynthesis and respiration in the dark. But it is questionable to estimate the rate of gross photosynthesis by this method. According to ZELITCH(29), the rate of photorespiration at  $35^\circ\text{C}$  becomes approximately 60% of the rate of gross photosynthesis, while the rate of dark respiration becomes only 10%. A similar result was also observed in poplar plant, and the rate of photorespiration estimated by the extrapolation method was 3.5 times greater than the rate of respiration in the dark at  $25^\circ\text{C}$ (11). Accordingly, the rate of gross photosynthesis should be "net photosynthesis + dark respiration + photorespiration". However, there is no single method to compute the real rate of gross photosynthesis since it is impossible to estimate the real rate of photorespiration. Some methods for measuring photorespiration are proposed by physiologists, but there is no exact method for the measurement of the true rate of photorespiration as discussed in this text. Another problem in estimating gross photosynthesis is whether or not normal dark respiration is present in the light. Some workers proposed the possibility that dark respiration is inhibited in the light(3,16), but other workers demonstrated opposite results(4,19). Although there is no convincing evidence yet for the existence of dark respiration in photosynthetic tissues in the light and there is no critical method for the estimation of photorespiration, the author offers the definition of gross photosynthesis and the method for the estimation of the rate of gross photosynthesis using the  $\text{CO}_2$  gas exchange method.

From the derivation of equation (3) and (4), gross photosynthesis ( $GP$ ) could be written as:

$$GP = NP + NE = [\text{CO}_2]_c / (R_a + R_s + R_m) \quad (5)$$

A far better estimation of  $NE$  may be carried out as follows: plotting the rate of  $\text{CO}_2$  exchange against the ambient concentration of  $\text{CO}_2$  and extrapolating the line to  $[\text{CO}_2]_e = 0$ , one could estimate  $NE$  in  $\text{mgCO}_2\text{dm}^{-2}\text{hr}^{-1}$ ,  $NE$  thus estimated might contain, in part, the rate of  $\text{CO}_2$  evolution derived from dark respiration in the light, if it could occur. So it is of no use to add the rate of dark respiration to  $NE$  for the estimation of gross photosynthetic rate. In some cases, the rate of dark

respiration measured in the dark is larger than  $NE$ , and one is apt to consider that photorespiration is not as large as dark respiration. However, in most instances, lower rate of respiration in the light may be mainly caused by the refixation of the evolved  $CO_2$  by photosynthesis. Therefore, it is essential to decrease the rate of refixation at the boundary layer of the leaf surface by the rapid flow rate of air. This is also the case for the estimation of  $NE$  by the extrapolation method.

Substitution of equation (3) into (5) gives the rate of gross photosynthesis.

$$GP = NP \frac{[CO_2]_e}{([CO_2]_e - [CO_2]_c)} \quad (6)$$

This method is based on the assumption that  $NP$  vs.  $[CO_2]_e$  is linear. However, a linear relation between these two functions does not always exist, so that the rate of gross photosynthesis estimated by this method is underestimated. In poplar leaves, although  $NP$  vs.  $[CO_2]_e$  is not linear, the error introduced by this method is only 4%, and it is convenient to estimate the rate of gross photosynthesis routinely. Thus the author used this method to estimate the rate of gross photosynthesis.

Four varieties of poplar had remarkably high rates of gross photosynthesis with a mean of  $28.0 \text{ mgCO}_2\text{dm}^{-2}\text{hr}^{-1}$ . The maximum was obtained in LK-83 and was  $34.1 \text{ mgCO}_2\text{dm}^{-2}\text{hr}^{-1}$ . Sunflower had the rate of gross photosynthesis of  $37.0 \sim 42.1 \text{ mgCO}_2\text{dm}^{-2}\text{hr}^{-1}$  higher than any variety of poplar, while bean had only  $26.6 \sim 34.6 \text{ mgCO}_2\text{dm}^{-2}\text{hr}^{-1}$  (Table 3). From these results, it can be concluded that poplar plants are not inferior in photosynthetic rates to herbaceous  $C_3$  plants.

A large part of the differences in net photosynthesis between the efficient and the non-efficient species can be explained by the much slower rate of photorespiration that is encountered naturally only

Table 3. Comparison of net photosynthesis and gross photosynthesis in detached leaves of four poplar varieties, sunflower, and bean at  $25^\circ\text{C}$ , 25 Klux, and an air flow rate of 5.0 liter/min

Species	Net	Gross
	photosynthesis	photosynthesis
	$\text{mgCO}_2\text{dm}^{-2}\text{hr}^{-1}$	
Poplar (LK-83)	27.0	31.5
	29.2	34.0
	28.9	34.1
Poplar (NM-101, 2 n)	25.4	30.0
	23.6	27.6
Poplar (NM-101, 4 n)	21.2	24.9
	23.2	27.1
Poplar (OP-44)	19.5	23.2
	18.2	21.5
	20.1	23.2
Sunflower	36.6	42.1
	31.6	37.0
Bean	23.4	26.6
	29.9	34.6

in the efficient species. However, this explanation of the difference in net photosynthesis between the efficient and the non-efficient plants is not always the case. No remarkable difference in the  $CO_2$  compensation points was observed, although the gross photosynthesis was 47% greater in LK-83 than OP-44. Furthermore, although sunflower had a rate of PIB-1 twice as fast as OP-44, sunflower fixed a 80% greater amount of  $CO_2$ , gross photosynthesis, than did OP-44. Accordingly, it could not be always true that lower rate of net photosynthesis in some poplar varieties, such as OP-44, is dependent on higher rate of  $CO_2$  production in the light.

It is commonly known that the growth rate of poplar plant is faster than those species which are popular in Japan. Thus, it is reasonable that poplar has a very high photosynthetic rate, since 90~95% of the dry weight of plants comes from the assimilation of airborne  $CO_2$  during photosynthesis. However, it is not obvious that only poplar plant has a very high photosynthetic rate. There is little data comparing photosynthesis under the same conditions and in the same assimilation chamber. Further analyses of photosynthetic rates in tree species are awaited.

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