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# Environmental Responses of the Post-lower Illumination $CO_2$ Burst as Related to Leaf Photorespiration[1]

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## ABSTRACT

**As leaf irradiance is decreased in increments, a single transient $CO_2$ burst is exhibited by $C_3$ plant leaves. This post-lower illumination $CO_2$ burst (PLIB) is sensitive to changes in irradiance, to changes in the concentrations of $O_2$ and $CO_2$, and to temperature. Increasing $O_2$ concentrations above ambient produces a progressively larger PLIB while increasing $CO_2$ concentrations above ambient produces a progressively smaller PLIB. The PLIB, which exhibits many responses to environment common with other methods for measuring photorespiration and photosynthesis, is proposed as a measure of photorespiration in illuminated leaves of $C_3$ plants. Although the PLIB cannot be used as a quantitative measurement of photorespiration, we propose that the PLIB is a rapid, easy, relatively inexpensive, nondestructive method for evaluating photorespiration in intact illuminated $C_3$ leaves in air.**

Leaves of some plants release a burst of $CO_2$ immediately following illumination. This phenomenon was first referred to as a dark $CO_2$ outburst by Decker (6, 7) and is now commonly referred to as PIB.[4] A photo-stimulated dark $O_2$ uptake also appears to be an expression of the same phenomena (13). The PIB was initially interpreted as being a remnant of light respiration (6, 7), and the same interpretation is widely accepted today (3, 15, 21). In relating the PIB to photorespiration, the amplitude of the PIB was shown to be a function of previous light intensity (7, 17, 18), temperature (8), atmospheric $O_2$ concentration (11, 14, 17, 19), atmospheric $CO_2$ concentration (7, 9, 13, 16, 21), leaf age, and photosynthetic $CO_2$ assimilation pathway, *i.e.* $C_3$ and CAM plants exhibit a PIB but most $C_4$ plants do not (10-12, 15, 17-19). In some CAM plants such as pineapple, the PIB is exhibited as two peaks—the first associated with photorespiration, being sensitive to $CO_2$, $O_2$, and light intensity but the second $CO_2$ outburst attributed to decarboxylation of organic acids during CAM (5). Multiple PIB peaks of $CO_2$ release were observed in the earliest $C_3$ plants studied (6, 18), but adequate explanations for the secondary dark $CO_2$ release oscillations are not yet available.

The PIB has been associated with photorespiration although it is observed in the dark after a light to dark transition; however, this phenomenon does not lend itself readily to a quantitative measurement of photorespiration. Perhaps the most widely used detector of photorespiration is the increase in photosynthetic rate measured near 2% $O_2$ *versus* 21% $O_2$ (21) but this measurement includes other $O_2$-dependent processes such as pseudocyclic electron transport and direct $O_2$ inhibition of photosynthesis. Some other methods of estimating photorespiration include the $CO_2$ compensation concentration, biochemical analyses of photorespiration intermediates such as glycine and serine (4), and mass spectrophotometric analyses usually employing isotopes of $O_2$ and carbon (21). In general, these methods require either special equipment or have some limitation in widespread usage although all have been useful in contributing to our current understanding of photorespiration.

Biochemically, it is commonly accepted that photorespiration occurs during photosynthesis in the presence of $O_2$ when the enzyme RuBP carboxylase functions as RuBP oxygenase. In its oxygenase capacity, it adds $O_2$ to RuBP to produce P-glycolate and ultimately amino acids, glycine and serine, as transitory intermediates en route to completing the photosynthetic carbon oxidation cycle. The balance between carboxylation and oxygenation in leaves shows similar responses as does the PIB to environmental parameters such as $O_2$, $CO_2$, and light intensity.

We recently reported (20) a transitory release of $CO_2$ from illuminated leaves when the illumination intensity was suddenly reduced. This post-lower illumination $CO_2$ burst appeared to be a relatively simple means of measuring photorespiration at specific illumination intensities (20). These studies were conducted to document this hypothesis. In the initial work, a release of $CO_2$ was detected following a lowered illumination of intact geranium leaves, and the peak appeared to have an origin related to photorespiration because of its light intensity dependency. Our attention was directed toward conducting a more thorough characterization of the $CO_2$ burst which occurred each time the illumination intensity was reduced from a higher to a lower level (Fig. 1 in Ref. 20). The purpose of this manuscript is to describe the appearance of the maximum PLIB and to evaluate the responses of the PLIB to light intensity, temperature, $O_2$, and $CO_2$. Intact leaves on mature healthy plants are used with geranium as the primary test plant but the PLIB is partially described in other plants to show its occurrence.

## MATERIALS AND METHODS

**Plant Material.** One hundred geranium (*Pelargonium* × *hortorum*, Bailey cv Rasmatazz) plants were grown from seed in a

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[4] Abbreviations: PIB, post-illumination $CO_2$ burst; PLIB, post-lower illumination $CO_2$ burst; RuBP, ribulose 1,5-bisphosphate; PN, photosynthesis.

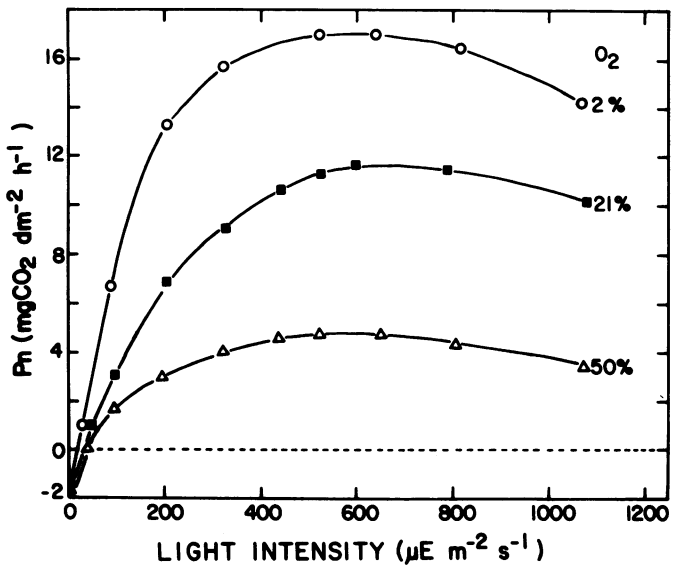


FIG. 1. Rate of photosynthesis, in mg $CO_2$ $dm^{-2}$ $h^{-1}$, of geranium leaves at progressive increases in light intensities from dark to 1100 $\mu$E $m^{-2}$ $s^{-1}$. $CO_2$ concentration was held constant at ~300 $\mu$l/l and $O_2$ concentrations were either 2%, 21%, or 50%.

standard peat:vermiculite (1:1, v/v) mix in 10-cm pots. Plants were watered to saturation when needed and fertilized weekly with a balanced nutrient solution at each irrigation for 10 weeks and were vigorously growing in standard greenhouse at 30 ± 5°C day and 21 ± 3°C night (1). All other plants used in this study were growing in the same greenhouse under similar conditions.

**Measuring Procedure.** The fourth or fifth fully mature geranium leaf from the base was used for all photosynthesis measurements. With all other plants, fully expanded leaves were used. All $CO_2$ measurements were obtained by differential analysis between the $CO_2$ concentration entering and exiting the photosynthesis chamber using a Beckman model 215B IRGA. The circular chamber was sealed gas tight with a rubber 'O' ring and 'putty' at the leaf petiole entrance. An in-chamber quantum sensor (LI-COR 285), thermistor, and low speed (200 rpm) high torque circulating fan resulted in accurate irradiance and temperature measurements and reproducible gas exchange results with a response time of 3 to 5 s. Irradiance intensity was varied by adding or removing cheesecloth. The volume of the system, including the chamber was 145 ml, and gas flow was 1.5 l/min. The gases were premixed at concentrations of 2, 21, 50, and ~100% $O_2$ containing ~300 $\mu$l/l $CO_2$ and 21% $O_2$ containing 300, 430, or 710 $\mu$l/l $CO_2$ with the balance $N_2$.

Leaf areas were measured with a Lambda leaf area meter, and data calculated as previously described (20). The PLIB value in mg of $CO_2$ $dm^{-2}$ $h^{-1}$ was calculated from the peak deflection (20) and is taken as a relative value inasmuch as a steady state likely is never reached. A smaller or larger volume gas exchange measurement system or a change in flow rate would vary the peak height, but our data were collected using the same system so any correction would be constant.

## RESULTS AND DISCUSSION

Photorespiration is difficult to measure accurately for the simple reason that, in light, $CO_2$ is being assimilated from the atmosphere and $O_2$ is taken up while at the same time $CO_2$ is evolved from the leaf through both photorespiration and dark respiration and $O_2$ is evolved. Internal gas cycling probably occurs in all green plant tissues, but a quantitative method for measuring this internal leaf gas metabolism is not available. In a study to establish the optimum light intensity for geranium growth and $CO_2$ assimilation via photosynthesis, it was observed that a burst of $CO_2$ occurred from geranium leaves following each progressive light intensity reduction (20). The initial kinetics of the light $CO_2$ burst were somewhat similar to the often reported PIB in darkness (6, 11). Preliminary investigations showed the amplitude of the light $CO_2$ burst varied with both the length of irradiation exposure and light intensity plus $CO_2$ and $O_2$ concentration. It was therefore apparent that the $CO_2$ burst was an environmentally responsive phenomenon and likely was associated with photorespiration (20).

To obtain a better understanding, a systematic environmental study was initiated on the PLIB primarily with geranium plants. The photosynthetic rate of geranium leaves determined in 2, 21, or 50% $O_2$ and ~300 $\mu$l/l $CO_2$ indicated that $O_2$ concentrations did not affect the optimum irradiance intensity for the geranium plant (Fig. 1). The optimum light intensity was approximately 600 $\mu$E $m^{-2}$ $s^{-1}$ in all $O_2$ concentrations. This fact was important in establishing a photosynthetic base for our subsequent PLIB studies. As expected (2), the highest $CO_2$ assimilation was at 2% $O_2$, followed by 21%, 50% (Fig. 1), and essentially zero at ~100% $O_2$ (data not plotted).

Initially in plotting the PLIB in air *versus* successive decreases in illumination intensity, we obtained a positive relationship

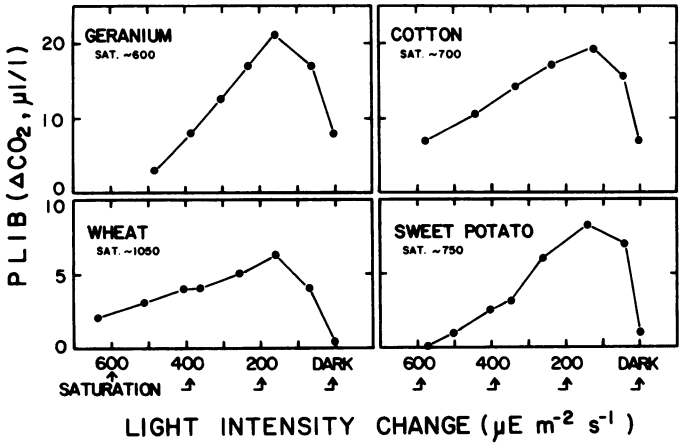


FIG. 2. Determination of the maximum PLIB in $\mu$l/l $CO_2$ evolved with various $C_3$ plants in air. Decreases in irradiance from light saturation to each lower intensity shows the maximum PLIB is generated with a decrease to ~150 $\mu$E $m^{-2}$ $s^{-1}$ with each plant. Note the scales change for the $CO_2$ evolved by each plant and different leaf areas were used in each study.

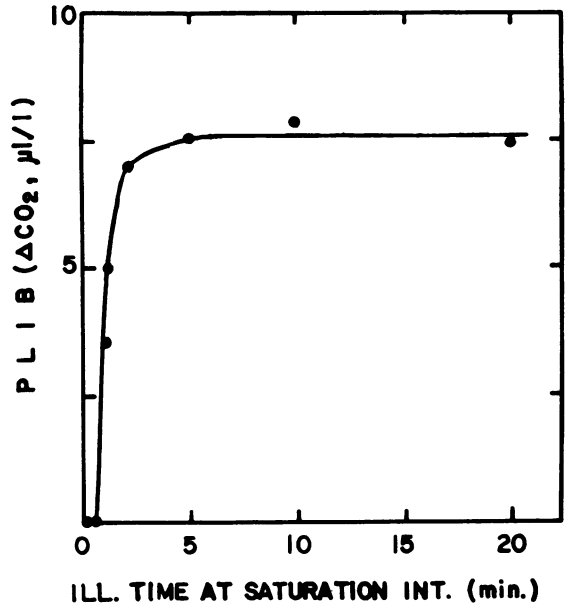


FIG. 3. Duration of illumination at light saturation required to produce a maximum PLIB in geranium leaves in air.

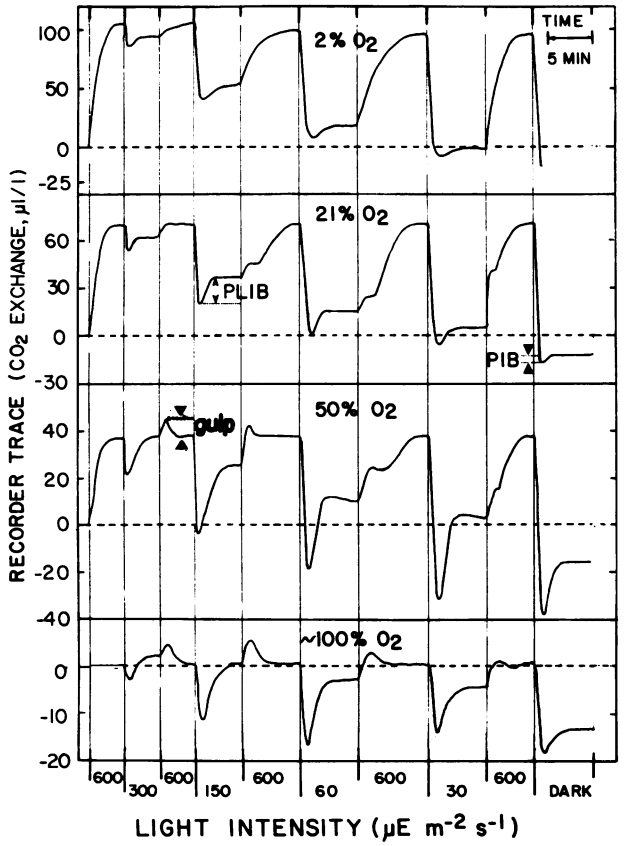


FIG. 4. Recorder traces of changes in uptake or release of $CO_2$ by geranium leaves, not corrected for various leaf areas or system gas flow rates, showing photosynthesis and kinetics of the PLIB at various light intensities in 21%, 50%, or ~100% $O_2$ at ~300 $\mu$l/l $CO_2$. Note the scale changes for different $O_2$ concentrations. The light intensity was returned to saturation, 600 $\mu$E $m^{-2}$ $s^{-1}$, between each subsequent decrease in light intensity. The PLIB, PIB, and the $CO_2$ gulp are identified.

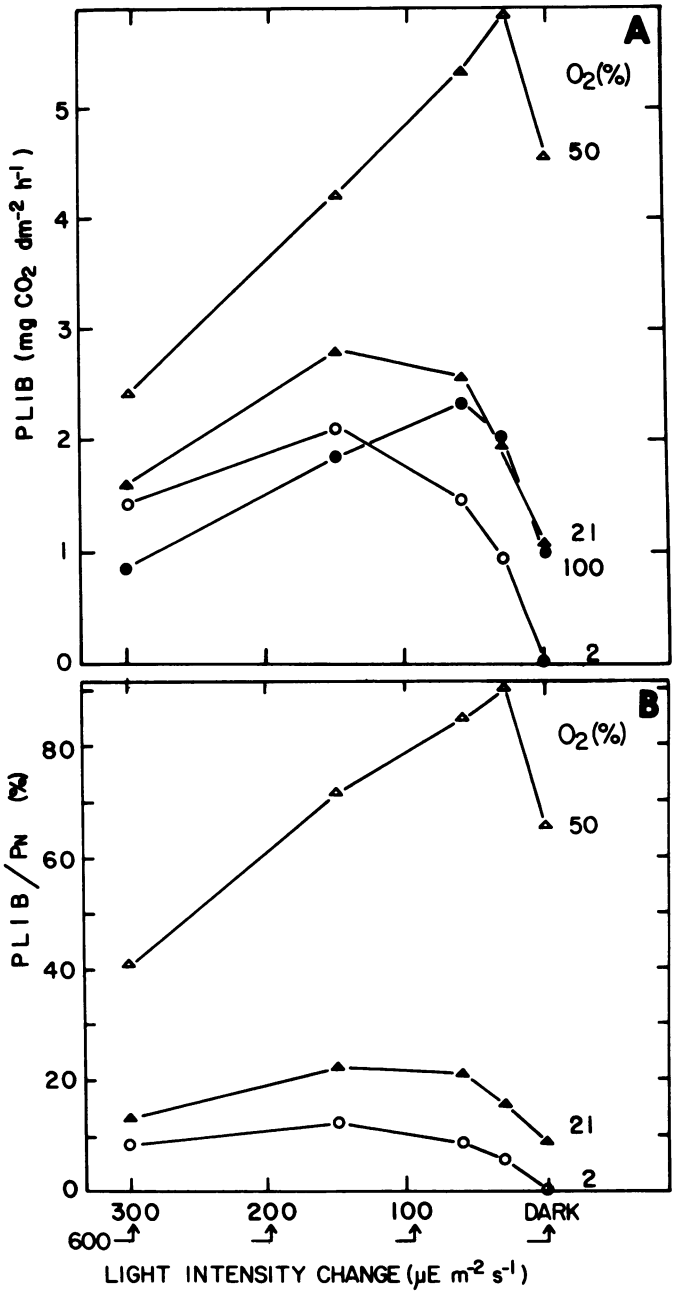


FIG. 5. (A), Calculation of the maximum PLIB with various light intensity changes or in darkness from 600 $\mu$E $m^{-2}$ $s^{-1}$ in mg of $CO_2$ $dm^{-2}$ $h^{-1}$ from exchange data as illustrated in Figure 4. (B), Calculated ratios of the PLIB (from Fig. 5A) to photosynthetic rate in 2, 21, and 50% $O_2$ at sequential decreases in light intensity through darkness from 600 $\mu$E $m^{-2}$ $s^{-1}$.

with no apparent light saturation (20). However, in a more systematic study, we soon learned that the maximum PLIB was observed by irradiating leaves near light saturation and then quickly decreasing the light to a lower intensity. Figure 2 illustrates the results of this work with four $C_3$ plants. In each plant, dropping the light intensity from its photosynthesis saturation intensity to near 150 $\mu$E $m^{-2}$ $s^{-1}$ resulted in the maximum PLIB in air. Also shown in Figure 2 is the classic PIB (the dark data in each frame) which clearly is severalfold less than the maximum PLIB with each plant species.

As we were learning how to obtain a maximum PLIB value, we asked, how long does a leaf need to be illuminated at

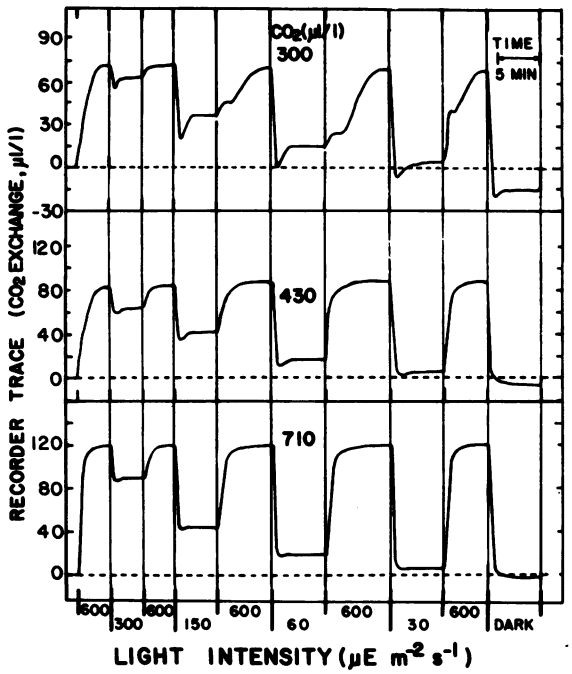


FIG. 6. Recorder traces at various light intensities of changes in uptake or release of $CO_2$ with attached geranium leaves similar to Figure 4 except the $CO_2$ concentration was either 300, 430, or 710 µl/l, each at 21% $O_2$. Also note the scales change in each frame and the data are not corrected for leaf area and system flow rate differences.

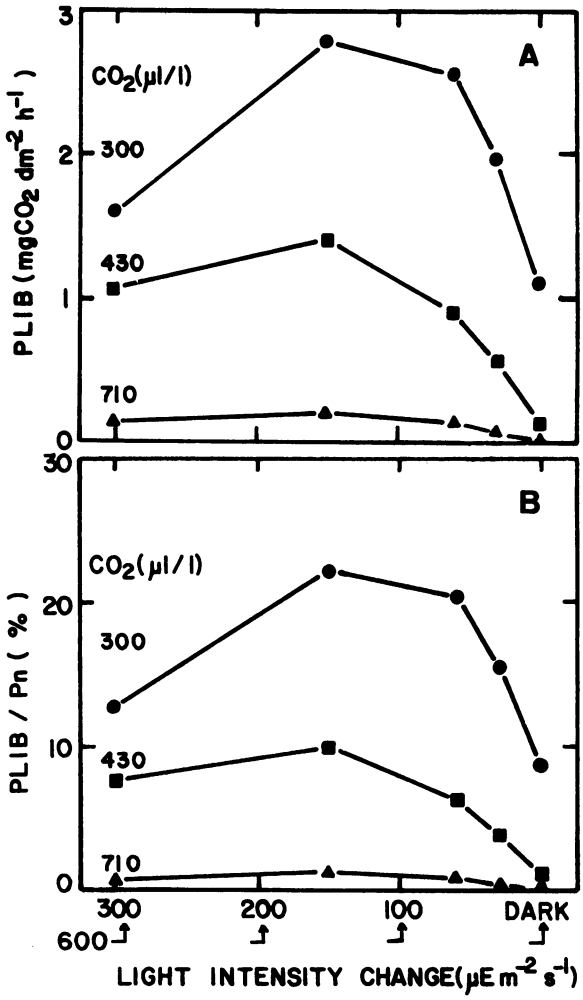


FIG. 7. (A), Effects of $CO_2$ at either 300, 430, or 710 µl/l on the geranium leaf PLIB, in mg $CO_2$ $dm^{-2}$ $h^{-1}$, as the light intensity is decreased from 600 to either 300, 150, 60, 30 µE $m^{-2}$ $s^{-1}$, or dark. Calculated from data as shown in Figure 6. (B), Calculated ratios of the PLIB (from Fig. 7A) to photosynthetic rate in 300, 430, or 710 µl/l $CO_2$ in 21% $O_2$ at each sequential decrease in light intensity.

saturation to obtain the maximum PLIB? Figure 3 shows the results of this study in which geranium leaves were illuminated alternately at 600 µE $m^{-2}$ $s^{-1}$ and then at 150 µE $m^{-2}$ $s^{-1}$ for various time intervals in air. The PLIB was measured each time the illumination dropped to 150 µE $m^{-2}$ $s^{-1}$. The leaf then was illuminated at 600 µE $m^{-2}$ $s^{-1}$ for the times indicated in Figure 3, then back to 150 µE $m^{-2}$ $s^{-1}$. Between 4 and 5 min of illumination at 600 µE $m^{-2}$ $s^{-1}$ was required to reach a plateau and a maximum PLIB. Thus, in subsequent work, leaves were illuminated at a saturating light intensity for at least 5 min prior to measuring the PLIB.

Following these procedures for obtaining the maximum PLIB and using geranium plants with a saturation intensity of 600 µE $m^{-2}$ $s^{-1}$, the PLIB and PIB were generated in ~300 µl/l $CO_2$ and either 2%, 21%, 50%, or ~100% $O_2$ (Fig. 4). Photosynthesis is highest at 2% $O_2$ and decreases to essentially zero at ~100% $O_2$, necessitating different scales for the family of curves shown for each $O_2$ concentration. The PLIB is increased by increasing $O_2$ concentration as is photorespiration, indicating that PLIB and photorespiration are related.

We wish to note there is a '$CO_2$ gulp' immediately following a return of the light intensity to 600 µE $m^{-2}$ $s^{-1}$ which was detected as a 'hip' at 21% $O_2$, somewhat more pronounced at 50% $O_2$, and more so at ~100% $O_2$ (Fig. 4). As we will see later in Figure 6, high $CO_2$ eliminates the $CO_2$ gulp. An adequate explanation of this $CO_2$ gulp is, at this time, not in evidence but is under investigation.

For a more precise comparison of the PLIB at different $O_2$ concentrations and light irradiance changes, the maximum amplitude from recorder traces of the PLIB at different irradiance intensity changes were converted to mg $CO_2$ $dm^{-2}$ $h^{-1}$ and plotted in Figure 5A. At 50% $O_2$ and ~300 µl/l $CO_2$, a decrease in irradiance from 600 to ~25 µE $m^{-2}$ $s^{-1}$ showed the largest PLIB, although PLIBs were present at all post-illumination intensities (Fig. 5A). We conclude from these PLIB data (Fig. 4 and 5) that the rate of photorespiration as measured by the PLIB is not a constant at all light intensities and, in air, the maximum PLIB is near 150 µE $m^{-2}$ $s^{-1}$ post-illumination intensity.

$O_2$ plays a role in the light $CO_2$ burst inasmuch as the PLIB amplitude was smaller at 2% $O_2$ and higher at 50% $O_2$ (Fig. 5A). Furthermore, a comparison of the ratio of PLIB to its saturating photosynthetic rate at different $O_2$ concentrations and at various irradiance intensity shows that the PLIB/Pn ratio is higher at 50% $O_2$ compared with other $O_2$ concentrations (Fig. 5B). A reasonably constant PLIB/Pn ratio occurs as irradiance intensity is decreased from 600 to 300, 150, and 60 µE $m^{-2}$ $s^{-1}$ for 21% and 2% $O_2$ but not for 50% $O_2$ (Fig. 5B). This ratio for 2% and 21% $O_2$ is much more constant, and reaches a maximum value near 23%, than the PLIB plotted alone (Fig. 5A), indicating that photosynthesis plays an integral role in the PLIB. Values of PLIB/Pn at 100% $O_2$ are not included because of extremely low photosynthetic rates.

Increased $CO_2$ concentrations, from ~300 µl/l up to 710 µl/l, reduced or eliminated the PLIB (Fig. 6). High $CO_2$ would be expected to reduce or eliminate photorespiration due to shifting RuBP utilization through a carboxylase rather than an oxygenase. This again indicates the PLIB is related to photorespiration; as a result, photosynthetic rates increase with an increase in $CO_2$ to 430 and 710 µl/l at 21% $O_2$ compared to 300 µl/l $CO_2$ (Fig.

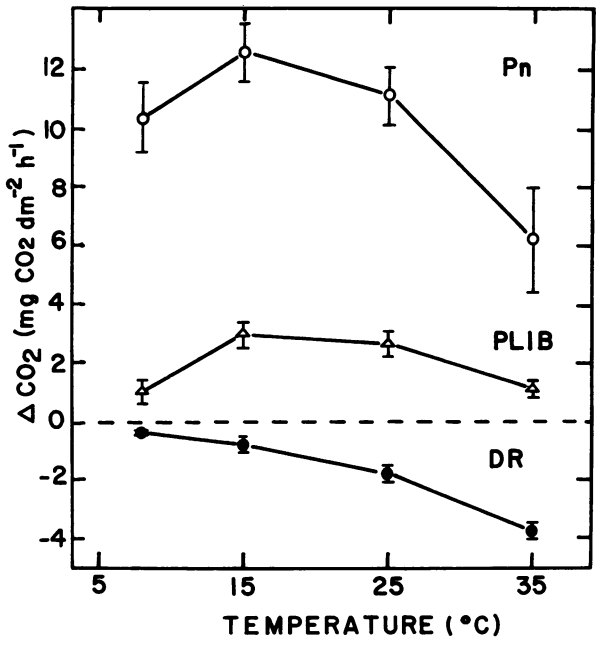


FIG. 8. The influence of leaf temperature on the rate of dark respiration (DR) and photosynthesis *versus* the PLIB measured at 600 $\mu$E $m^{-2}$ $s^{-1}$ *versus* the PLIB measured at 600 $\mu$E $m^{-2}$ $s^{-1}$ *versus* changing to 150 $\mu$E $m^{-2}$ $s^{-1}$ with geranium leaves in air.

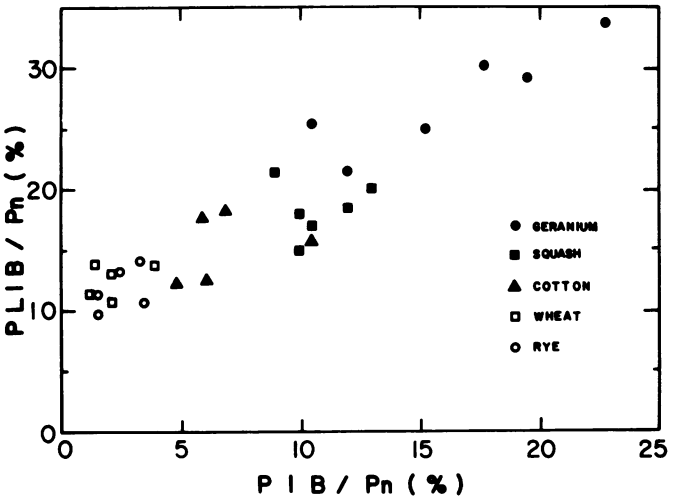


FIG. 9. A comparison of the ratio of the PLIB/photosynthetic rate to PIB/photosynthetic rate in monocot (open symbols) and dicot (closed symbols) plants in air. The coefficient of correlation equals 0.85.

6).

For more precise comparisons of the PLIB at different $CO_2$ concentrations and irradiation intensities, the changes in the maximum PLIB from recorder traces as in Figure 6, were converted to mg $CO_2$ $dm^{-2}$ $h^{-1}$ and plotted in Figure 7A. The PLIB was largest in ambient atmosphere of ~300 $\mu$l/l $CO_2$ and 21% $O_2$, decreasing at higher $CO_2$ concentrations as does photorespiration. As $CO_2$ concentration was increased, the PLIB amplitude was decreased for all irradiances, which is similar to that expected for photorespiration. This condition of the highest PLIB in an ambient atmosphere compared to $CO_2$ enrichment allows a simple and easy PLIB measurement during routine photosynthetic measurements.

Calculated ratios of PLIB/Pn shown in Figure 7B gave similar curves to those in Figure 7A since the photosynthetic rate was higher and PLIB lower as $CO_2$ concentration was elevated, with the maximum PLIB being about 23% of the rate of photosynthesis in air (Fig. 7B).

Photosynthesis decreased and dark respiration increased in air as temperatures were elevated (Fig. 8). The PLIB *versus* temperature followed the photosynthesis curve again relating the PLIB to photosynthetic rate. With each 10°C increase in temperature, dark respiration approximately doubled while the PLIB was less affected by temperature changes. In ambient air, both the PLIB and photosynthetic rate were low at 8°C and 35°C, again indicating that the PLIB is dependent on the process of photosynthesis.

The amount of photosynthetic inhibition at 21% $O_2$ compared to 2% $O_2$ (Pn at 2% $O_2$ − Pn at 21% $O_2$) is widely accepted as a measure of photorespiration (21). To further test the hypothesis that the PLIB is a measurement of photorespiration, a comparison was made with monocots and dicots between the PLIB and the amount of photosynthetic inhibition by $O_2$. This was a collection of data from various experiments with various rates of photosynthesis; there was a general positive correlation between the PLIB and the degree of $O_2$ inhibition of photosynthesis between these separate determinations (data not shown).

Also as suggested previously (20), the rate of photosynthesis is related to both the PLIB and the PIB. A collection of these data plus photosynthetic rates with various plants shows that they also correlate well (Fig. 9). One can see again that the PLIB/Pn ratio also is greater than the PIB/Pn ratio in this collection of data.

## CONCLUSIONS

From these studies with intact leaves of several $C_3$ plants, but with emphasis upon geranium, we conclude that the PLIB is a reasonable estimation of photorespiration in illuminated $C_3$ plant leaves in air. This conclusion is based upon the following considerations. The sensitivity of the PLIB to $O_2$, $CO_2$, and temperature is similar to other measurements of photorespiration and photosynthesis. The PLIB is not exhibited with a similar environmental sensitivity in $C_4$ plants (20). The PLIB is qualitatively similar to intact leaf substrate levels in that about 280 nmol $CO_2$/mg Chl are released during the transition time of a typical PLIB while the steady state levels of RuBP in intact leaves range from 200 to 400 nmol/mg Chl in air (C. C. Black, unpublished data). The PLIB as a comparative measurement of photorespiration is near 50% of the 2% $O_2$ inhibition method of detecting photorespiration (Z-P. Tu, unpublished data). This $O_2$ inhibition appears to be an overestimation of photorespiration because of other effects of $O_2$ on photosynthesis. The PLIB as a comparative measurement of photorespiration is nearly 2-fold greater than the PIB (Fig. 9), which makes the PIB appear to be an underestimation of photorespiration.

We wish to note that the PLIB occurs in an illuminated leaf as a single transitory peak (Figs. 4 and 6), unlike the PIB which exhibits multiple unexplained peaks (6, 11). Thus, the PLIB is easier to analyze and likely has less components involved in the light than does the PIB during the dark transition. We propose that the PLIB is a closer measurement of photorespiration than other available methods because it is conducted in air during illumination of attached leaves. Certainly, the uncertainties due to darkness and the lack of photochemical electron flow associated with measuring the PIB are eliminated as are the other metabolic effects of $O_2$ involved in measuring photorespiration by the method of $O_2$ inhibition of photosynthesis. Although the PLIB cannot be used as a strictly quantitative measurement, we propose that the PLIB is a rapid, easy, relatively inexpensive, non-leaf-destructive method for estimating photorespiration in attached illuminated $C_3$ leaves in air.

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