Photorespiration and Its Effect on Dry Matter Production

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Currently, higher plants can be divided into two groups according to the mode of photosynthetic dark reaction. Rice, soybean, wheat and many crops are called C_3 plants becaues they fix CO_2 through the Calvin cycle and produce a C_3 acid as a primary product. On the other hand, maize, sugarcane and many tropical grasses are called C_4 plants because they fix CO_2 by C_4 dicarboxylic acid pathway[6].

The efficiency of photosynthesis differs considerably between these two types of plants. In general, the photosynthesis of C_3 plants is lower than those of C_4 plants. One of the major causes for the lower efficiency of photosynthesis of C_3 plants may be due to the active photorespiration which is seemingly a reverse reaction of photosynthesis releasing considerable amount of CO_2. Usually, the amount of carbon loss through photorespiration accounts for 30 to 50% of apparent photosynthesis.

Thus, the regulation of photorespiration may possibly bring about the enhanced dry matter production of C_3 plants through the enhanced photosynthetic efficiency.

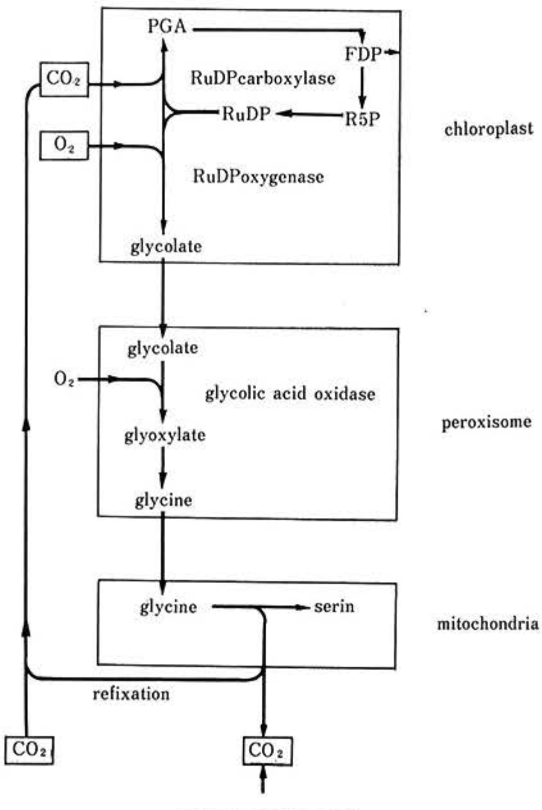


Fig. 1. Photorespiration pathway proposed by Tolbert et al.

Pathway of photorespiration

In 1955, Decker found out the CO_2 burst in darkness just after illumination and predicted the presence of high CO_2 evolving process in a light[5]. Thereafter, many reports presented the evidences that photosynthetic tissues of C_3 plants had a special CO_2 evolving reaction which differed from the ordinary dark respiration. Photorespiration is completely light dependent because the substrate for photorespiration is glycolate supplied directly from photosynthetic Calvin cycle. Besides, photorespiration proceeds only under oxidative condition. According to Tolbert, glycolate is produced from ribulose di-phosphate (RuDP) catalized by the RuDP oxygenase[11] in the chloroplast. Glycolate is transported to the peroxisome and is oxidized to produce glycine. Then glycine transferred to the mitochondria produces serin and CO_2 (Fig. 1). The positive biological role of photorespiration has been doubted and photorespiration is now frequently regarded as wasteful reaction, since the growth experiment in low O_2 environment suggested that plant could do without photorespiration[1].

On the other hand, C_4 plants do not show photorespiration apparently. The lack of photorespiration of C_4 plants have been explained by the anatomical and biochemical compartmentation which is creating an inhibitory environment of photorespiration, although there are some uncertainties and controversies. The leaves of C_4 plants have well developed chlorophyllous bundle sheath cells besides the mesophyll tissue which is the main tissue doing photosynthesis in C_3 plants. This anatomical differentiation of two specialized photosynthetic cells has close relationship with biochemical sequences of C_4 photosynthesis. The C_4 photosynthesis involves two sequential, but spatially-separated, carboxylation reactions. The first carboxylation reaction which is catalized by PEP carboxylase occurs specifically in mesophyll tissue and produces C_4 acids. These C_4 acids are transported to bundle sheath cells and decarboxylated. The released CO_2 is fixed by the second carboxylation catalized by RuDP carboxylase. In bundle sheath cells of C_4 plants, the same photosynthetic pathway as that of C_3 plants (Calvin cycle) would be operating. Therefore, photorespiration pathway itself is known to exist. Photorespiratory CO_2 evolved in bundle sheath cells might be trapped by the efficient PEP carboxylation in the surrounding mesophyll tissue.

Factors affecting photorespiration

The important environmental factors affecting photorespiration are light, temperature, O_2 and CO_2 as shown in Fig. 2. High temperature and high light intensity increase photorespiration remarkably. Photorespiration rate decreases linearly with the lowering of atmospheric O_2 concentration because O_2 is indispensable for producing glycolate in the process of photorespiration. Photorespiration is most active around the ordinary atmospheric CO_2 concentration and high CO_2 suppresses photorespiration. This is because photorespiration and photosynthesis may share one of the photosynthetic intermediate as the substrate. The increase of CO_2 concentration enhances the incorporation of that photosynthetic intermediate to photosynthesis. This may cause the decreased amount of the substrate to be used by photorespiration.

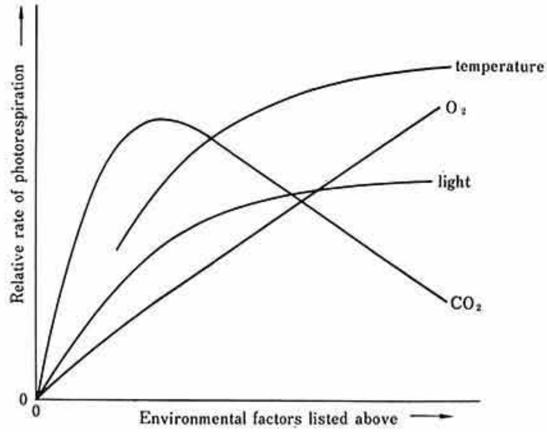


Fig. 2. Diagramatic expression of the effect of environmental factors on photorespiration rate

Some physiological factors are known to affect photorespiration rate. Robinson and Gibbs reported that the concentration of several photosynthetic intermediates of Calvin cycle affect photorespiratory activity[9]. Salin and Homan reported that photosynthesis of young leaves of tobacco, lemon and orange did show a little response to oxygen concentration[10]. This fact seems to indicate that young leaves of those C_3 plants do not show photorespiration.

Table 1. Effect of low oxygen concentration on dry matter production of rice plant, var. Tanginbozu

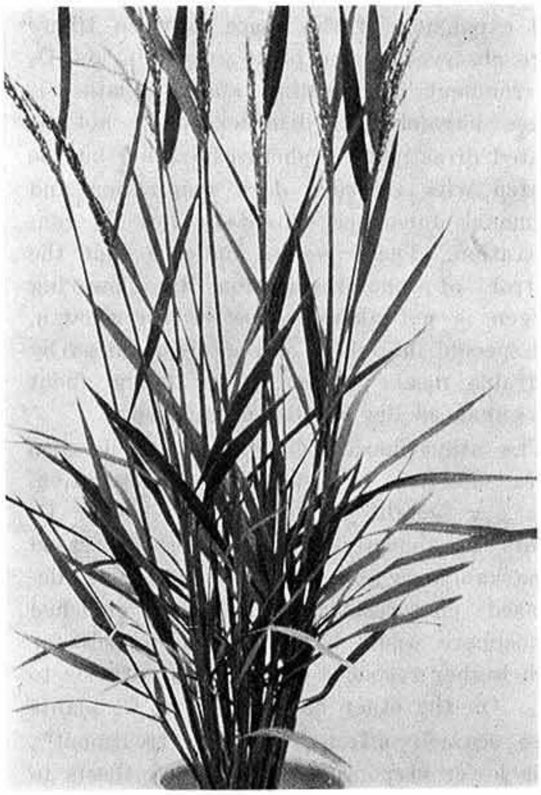
Treatment	Initial dry weight (g)	Final dry weight (g)					Dry weight increase (g)	
		LB	LS	R	E	Total	W	Wc
Control	28.70	6.07	11.90	4.21	12.43	34.61	5.91	8.76(100)
3% O_2	29.90	8.24	25.10	5.19	4.83	43.36	13.46	13.46(154)

Notes: Initial dry weight was estimated from the relationship between dry weight and fresh weight. Effect of CO_2 concentration difference on dry weight increase between control and 3% O_2 plot was corrected on the supposition that the dry weight increase of rice plant was proportional to CO_2 concentration.

The comparison of dry weight increse between plots in parenthesis was made by taking dry weight in control plot as 100.

LB: leaf blade, LS: leaf sheath and stem, R: roots, E: ears, Wc: dry weight increase after CO_2 effect corrected.

Control



3% O_2

Plate 1. Effect of low oxygen concentration on growth of rice plant var. Tanginbozu. Materials were treated with the artificial air containing 3% O_2 for 20 days from the heading stage in outdoor condition. In 3% O_2, barrenness, expansion of the space between tillers and many young shoots were observed.

Improving the photosynthetic efficiency by the regulation of photorespiration

The lowering of the atmospheric O_2 concentration is the most popular way to reduce photorespiration. Dry weight and photosynthetic rate are known to be enhanced significantly when C_3 plant is kept in low O_2 environment. Table 1 indicates that rice plant grown in 3% O_2 during daytime for 20 days showed dry weight increase by more than 50% than that grown in normal air[1]. However, low O_2 concentration induced physiological disorders in some metabolisms such as fertilization and growth. Heavy sterility and expansion of the space between tillers were observed in the plant grown in low O_2 environment at ripening stage (Plate 1). These physiological disorders may not be related directly with photorespiration but be related with retarded dark respiration and hormonal unbalance caused by low O_2 concentration. These results indicate that the control of photorespiration by lowering oxygen is not always effective for growth, but specific inhibition of photorespiration by desirable means would always bring about the enhanced dry matter production.

The atmospheric CO_2 enrichment is also quite effective to reduce photorespiration. The dry weight and photosynthesis of C_3 plants, as shown in Fig. 3, were increased remarkably by CO_2 enrichment. The decreased photorespiration in CO_2 enriched atmosphere would be one of the causes for such higher response of C_3 photosynthesis to CO_2. On the other hand, those of C_4 plants were scarcely affected by such treatment[2]. This lower response of C_4 photosynthesis to atmospheric CO_2 enrichment may partly be ascribed to the apparent lack of photorespiration.

Several trials of chemical control of photorespiration have been conducted. For example, α-hydroxysulfonates, specific inhibitor

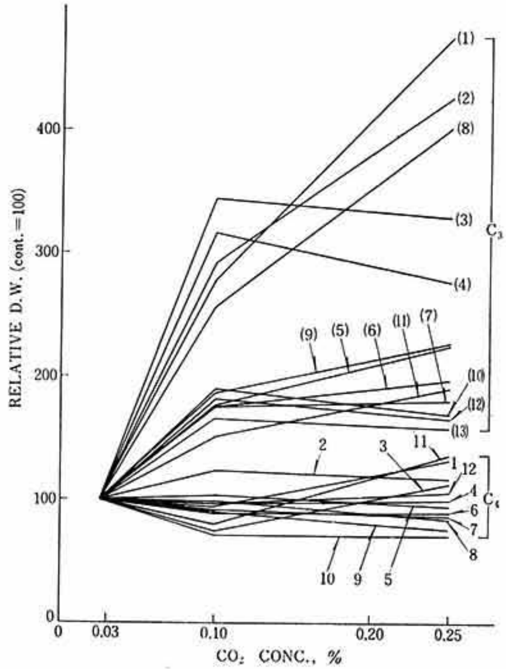


Fig. 3. Differences in the rate of enhancement of dry matter production in response to atmospheric CO_2 enrichment between C_3 and C_4 species. Numbers in the figure show the materials.

of glycolic acid oxidase, reduced photorespiration temporarily in the laboratory experiment with leaf disks. However, when this chemical was applied to the intact plant, it did not enhance the rate of photosynthesis and the dry matter at all because this chemical brought about stomatal closure. Upto now, no practical and specific chemical inhibitors of photorespiration have been reported.

The low photorespiratory characteristics could easily be introduced into plants with high photorespiration by crossing if there is varietal differences in photorespiration within a given C_3 species. Since the rate of photorespiration is strongly dependent on the photosynthetic activity, the ratio of photosynthetic rate in 3% O_2 to that in normal air (P_3/P_{21}) is often taken to show the relative intensity of photorespiration. In rice varieties, high positive correlation between photosynthetic rate in normal air and that in low oxygen was obtained and only

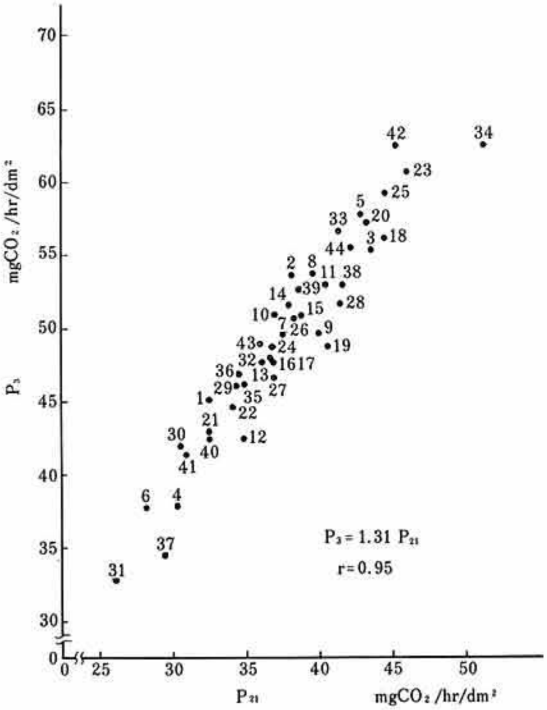


Fig. 4. The relationship between photosynthetic rate in normal air (P_{21}) and that in 3% oxygen (P_3) of 44 rice varieties. Photosynthesis was measured in 0.03% CO_2 with 60 klux and at 28°C (leaf temperature). Numbers in the figure correspond to the varieties.

little variations were observed in the ratio of P_3/P_{21}[3] (Fig. 4). The carbon dioxide compensation point (CCP) is usually considered to be in parallel with the rate of photorespiration. This value in C_3 plant is about 50 ppm while near zero ppm in C_4 plant. In many varieties of wheat, oat and soybean, the low CCP like those of C_4 plants was not observed[8]. These results suggest that there might be only few varieties with specifically lower photorespiration relative to photosynthesis. Thus, the reduction of photorespiration by crossing seems to be pessimistic as far as rice plant, wheat, oat and soybean are concerned. On the other hand, the varietal difference in photorespiratory rate was reported in a few species such as *Lolium*[13] and tobacco[14]. These reports seem to indicate that genetic control of photorespiration by crossing might be possible in some species.

The incorporation of low photorespiratory characteristics of C_4 plants into C_3 plants by genetic manipulation would be one of the most desirable way to reduce photorespiration because C_4 pathway is the only system to reduce photorespiration occurring naturally. Björkman et al. observed that hybrids between *Atriplex patula* (C_3 plant) and *A. rosea* (C_4 plant) did not show low photorespiration although some of them had similar leaf structure and biochemical traits with C_4 parent[4]. Not only the leaf morphology and biochemical traits, but also the appropriate coordination of each reaction steps in time and space would be required to accomplish C_4 photosynthesis in those hybrids. Fundamentally C_3 plants often produce small amount of C_4 acids in a definite condition and the guard cells of C_3 plants show C_4 photosynthesis[12]. Besides the conversion of photosynthetic dark reaction from C_4 to C_3 types within a species has been reported[7]. These facts indicate that all plants may have the genetic potential to produce all the kinds of enzymes related to C_3 and C_4 photosynthesis and to perform both types of photosynthesis, although the activity and the amount of each enzyme differ considerably. To increase the agronomic yield further by regulating photorespiration, it would be necessary to clarify conditions how C_4 photosynthesis could be accomplished as well as to find out techniques to regulate photorespiration pathway specifically.

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