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A Re-evaluation of Soybean Leaf Photorespiration[1]

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ABSTRACT

Recalculations of soybean photorespiration indicate that mean rates are closer to 16.1 than 5.6 milligrams of CO_2 per square decimeter per hour as previously reported. Photorespiration of soybean thus amounts to at least a 30% carbon turnover of light-saturated photosynthesis. Photorespiration showed no significant relationship to net photosynthesis. Negative correlations were found between CO_2 efflux and stomatal resistance as well as between corrected photorespiration and residual intracellular resistance of the leaf to CO_2 uptake.

Dornhoff and Shibles (2) indicated that, of 20 varieties of soybeans tested, no significant differences were found in CO_2 evolution into CO_2-free air in light or in CO_2 compensation concentration. CO_2 evolution was used as an estimate of photorespiration (3, 11). It was concluded that there were no significant differences in photorespiration among the 20 varieties, however. Net photosynthesis and mesophyll resistance did differ significantly. It was postulated (2) that the varietal differences in net photosynthesis were mainly due to differences in diffusive resistances.

Resistances must be taken into consideration to calculate photorespiration accurately. Recalculations were made by using a deviation from equation 8 of Samish and Koller (9).

$$L_{(\mathrm{int})} = \frac{L_{(\mathrm{ext})}\cdot R_{\mathrm{CO_2}}}{r_m} \quad (1)$$

where $L_{(\mathrm{int})}$ = minimal internal photorespiration; $L_{(\mathrm{ext})}$ = CO_2 evolution to CO_2-free air; $R_{\mathrm{CO_2}}$ = total resistance to CO_2 uptake which is equal to the partial resistances in photosynthetic CO_2 uptake from the bulk atmosphere; and r_m = residual intracellular resistances (diffusional, chemical, and photochemical) to CO_2 uptake from the evaporating surfaces of the mesophyll. This equation was further examined and supported by $^{14}CO_2$ studies (10). By the process of summation and averaging:

$$L_{(\mathrm{int})}' = \frac{\sum_{i=1}^{\beta} L_{(\mathrm{int})i}}{\beta} = \frac{\sum_{i=1}^{\beta} \frac{L_{(\mathrm{ext})i}\cdot(R_{\mathrm{CO_2}})_i}{r_{m\,i}}}{\beta} \quad (2)$$

$$R_{\mathrm{CO_2}}' = \frac{\sum_{i=1}^{\beta} (R_{\mathrm{CO_2}})_i}{\beta} \quad (3)$$

$$P' = \frac{\sum_{i=1}^{\beta} (L_{(\mathrm{int})i} + p_{n\,i})}{\beta} \quad (4)$$

$$\frac{L_{(\mathrm{int})}'}{P'}\,\% = \frac{\sum_{i=1}^{\beta} \frac{L_{(\mathrm{int})i}}{p_i} \times 100}{\beta} \quad (5)$$

where the values of P_n', $R_{\mathrm{CO_2}}'$, $L_{(\mathrm{int})}'$, and P' for each cultivar (Table I) represents mean values computed from leaves, the number of which equals β, and P_n = net photosynthesis; P = photosynthesis corrected for photorespiration; and ′ = suffix to distinguish an average.

Photorespiration ($L_{(\mathrm{int})}'$) and photosynthesis (P') values (Table I; both are minimal values) were considerably higher in all varieties than was suggested by average CO_2 efflux rates ($L_{(\mathrm{ext})}'$) alone. The CO_2 exchange values used for recalculations were taken directly from the original individual data of Dornhoff and Shibles (2).

The improved calculations indicate that a considerable portion of photosynthate is used in photorespiration (~30%). These rates are in accordance with findings of Volk (personal communication). These improved calculations also produce adjusted values of photorespiration which may still be minimal, but are considerably greater than the value reported for dark respiration of the soybean variety Wayne (6). This is consistent with other reports (1, 4, 5, 8, 9, 11) that photorespiration rates may considerably exceed dark respiration rates.

The calculated values of photorespiration ($L_{(\mathrm{int})}$) are not significantly different among varieties; ($L_{(\mathrm{int})}$) as a percentage of minimal photosynthesis (P) is not significant either. The lack of significant differences does not necessarily mean that such differences do not exist; refinements in techniques can lower variability. $L_{(\mathrm{ext})}$ is a small value and therefore any small absolute difference between leaves gives a high variance, because with infrared gas analysis the maximal resolution is about 0.5 µl/liter. Secondly, $L_{(\mathrm{int})}$ is calculated from three ex-

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Table I. *Means of CO_2 Exchange Variables for 20 Varieties of Soybeans (Columns 1–5) and Estimates of Photorespiration and Photosynthesis (Columns 7–9) as Recalculated from Original Individual Values According to Equation 1*

Genotype	Photosynthesis Net[1] P_n	CO_2 Efflux to CO_2-free Air[1] $L_{(ext)}'$	CO_2 Compensation Concn[2] Γ	Resistance Mesophyll[3] r_m	Total Resistance to Photosynthesis[3] R_{CO_2}'	Minimal Internal Photosynthesis respiration $L_{(int)}'$	Minimal Photosynthesis[1] P'	$L_{(int)}'$ % of P_i	Remarks
Corsoy	43.4	6.4	37.4	1.58	4.43	18.1	60.4	29.4	Relatively efficient photosynthesizing genotypes
Amsoy	41.6	5.8	36.8	1.62	4.67	19.7	60.4	30.7	
Hark	38.3	5.5	37.9	1.86	5.07	18.4	55.9	28.6	
Harosoy	38.2	5.6	36.4	2.62	5.78	9.7	43.7	21.8	
Illini	36.7	5.2	36.1	1.94	4.92	13.6	53.3	25.9	
Mandarin	36.3	5.6	38.8	2.25	5.44	10.8	46.0	23.8	
Blackhawk	36.1	6.4	41.8	2.17	5.53	20.7	54.5	35.1	
Mukden	35.8	6.5	43.1	1.85	4.74	19.6	59.1	31.7	
PI 86.027	35.3	5.8	41.2	1.92	5.17	16.8	53.6	31.2	
Wayne	35.1	5.3	41.0	1.87	5.66	14.6	48.0	29.6	
PI 68.658	34.8	6.0	42.5	2.07	5.57	17.5	52.3	30.9	
Chippewa	34.7	5.6	42.1	2.31	5.27	12.4	47.9	25.7	
Lee	34.7	4.8	37.7	1.94	5.20	15.6	52.1	28.4	
Manchu	34.2	5.9	41.3	2.24	5.68	16.6	50.3	32.1	
Lincoln	34.1	5.2	39.4	2.16	5.69	14.0	46.9	29.5	
Ford	32.6	5.6	43.6	2.34	5.83	18.3	50.4	33.4	Nonefficient photosynthesizing genotypes
Richland	32.0	5.0	39.3	2.32	5.96	11.9	44.6	27.3	
Hawkeye	31.3	5.5	40.9	3.52	7.32	8.7	34.3	25.1	
PI 68.704	29.6	4.9	43.1	1.71	6.55	17.4	46.1	36.6	
PI 85.019	29.4	4.7	41.7	2.03	6.66	19.2	49.3	39.5	
Mean	35.2	5.6	40.1	2.12	5.56	16.1	51.3	30.1	
Sign	**	NS	NS	*	**	NS	**	NS	

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[1] Net photosynthesis (P_n), CO_2 evolution ($L_{(ext)}'$), minimal internal photorespiration ($L_{(int)}'$), and the minimal photosynthesis (P') are expressed in mg CO_2 dm^{-2} hr^{-1}.

[2] CO_2 compensation concentrations (Γ) are in $\mu l/l$ CO_2.

[3] R_{CO_2}' and r_m are expressed in sec cm^{-1}.

[4] Columns 1–5 taken from Ref. 2.

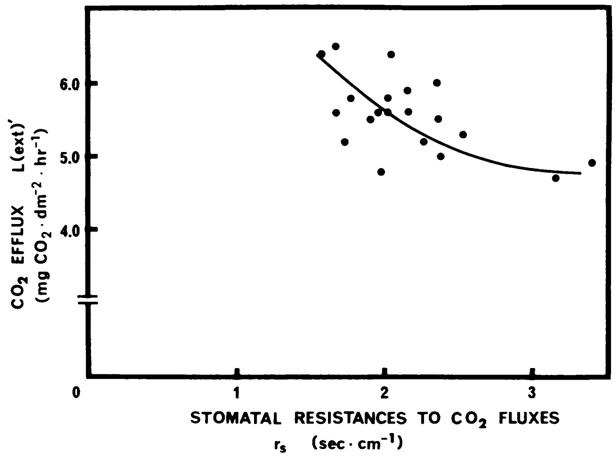
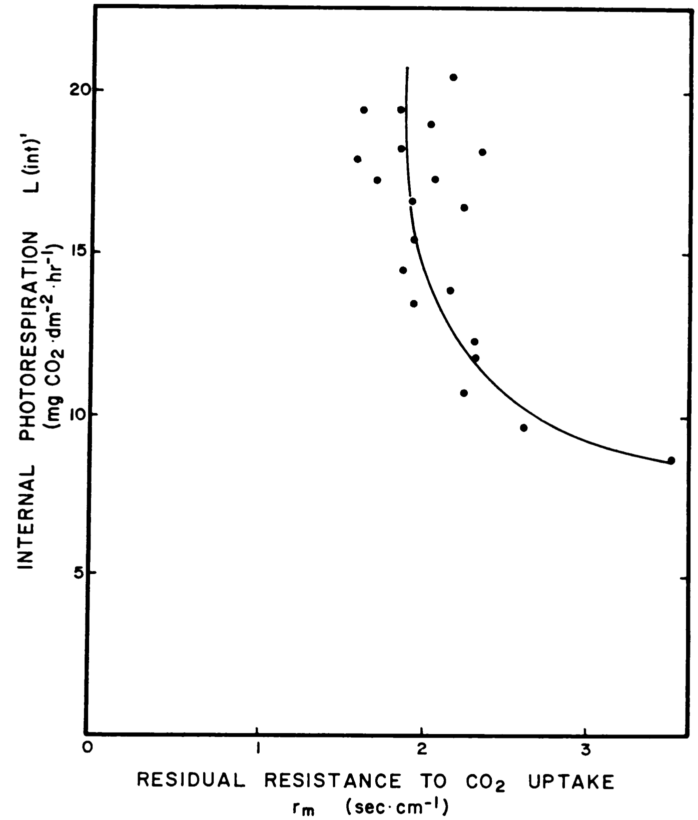


FIG. 1. Measurable CO_2 efflux from leaves ($L_{(ext)}'$) to CO_2-free air as a function of stomatal resistance to CO_2 exchange (r_s). Data from Dornhoff and Shibles (2).

FIG. 2. Minimal internal photorespiration ($L_{(int)}'$) as related to intracellular resistance to CO_2 uptake (r_m). Data from Dornhoff and Shibles (2) and Table I.



perimental variables (R_{CO_2}, r_m, and $L_{(ext)}$); hence, we are dealing with three variances, giving $L_{(int)}$ a very high variance.

The differences among photorespiration values (column 7 of Table I) cannot account for the large differences in net photosynthesis (column 8 of Table I). Thus, the original interpretation of Dornhoff and Shibles (2) that varietal differences in net photosynthesis were not attributable to differences in photorespiration is presently valid. On the other hand, varieties with high stomatal resistance seem to show low rates of net photosynthesis as well as low CO_2 efflux into CO_2-free air (Fig. 1). The implication is that stomatal resistance could be the important factor determining differences in net photosynthesis.

Ogren and Bowes (7) concluded that the rate of photorespiration in soybean is regulated by a limiting factor which may be common to both photosynthesis and photorespiration. They suggested ribulose diphosphate carboxylase activity as the regulating factor. Ribulose diphosphate is thought to be used both by carboxylation in photosynthesis and as a substrate for photorespiration. Their hypothesis is supported by the negative correlation between the internal photorespiration $L_{(int)}$ and the internal resistance to photosynthesis (r_m) as plotted in Figure 2. This could mean that, if stomatal restrictions are eliminated, soybean varieties with high photosynthesis (*i.e.*, having low r_m) also show relatively high photorespiration rates. This idea is contradictory to previous thinking.

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