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Genotypic Variation in Carboxylation of Tomatoes[1]

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ABSTRACT

The gas exchange characteristics of 24 genotypes of *Lycopersicon esculentum* Mill. and one of *L. minutum* were measured with an infrared gas analyzer and dew point hygrometer in an open system. Net carbon exchange (NCE) and transpiration rate were measured at 50, 100, 150, and 300 μl l^{-1} CO_2, and a regression of NCE *versus* internal lead [CO_2] estimates was calculated. The slope of the regression curve at the CO_2 compensation point was used as the measure of carboxylation efficiency (CE). Significant genotypic differences for CE were obtained. Differences in CE did not appear to be due to differences in diffusive resistance defined as the sum of the boundary layer resistance (r_a) and the stomatal plus cuticular resistance (r_l). There was no correlation ($r = -0.07$) between ($r_a + r_l$) and CE. Within groups with nonsignificantly different means for ($r_a + r_l$) there were genotypes with extremes for CE.

The zero CO_2 intercept has been used as an indication of photorespiration. Application of this method revealed a strong inverse relationship between CE and the intercept value, indicating either that photorespiration is related directly to CE or that this method is unreliable for estimating photorespiration. The fact that the variation in CE occurs at light saturation suggests that the observed differences in CE and rates of NCE are determined either by: (*a*) the concentration and/or kinetic properties of the photochemical reaction centers and associated electron transfer components as they affect the supply of NADPH and ATP and consequently the levels of Calvin cycle intermediates; or (*b*) the concentration and/or kinetic properties of ribulose 1,5-diphosphate carboxylase.

Many crop plants seldom, if ever, reach their total potential for high productivity because the components of maximum production are not combined in a single genotype. Breeders have not used this potential since it cannot be recognized or measured easily. The productivity of many crops can be increased dramatically through understanding of the genetic potential for improvement in fundamental processes that limit yield. An excellent genus for finding and exploiting such potential is *Lycopersicon*, because of its great diversity and the extensive genetic data base. For these reasons, we have initiated a series of studies on photosynthesis in tomatoes.

Genotypic variability in photosynthetic rates has been reported for a number of crops, *e.g.* soybeans (8), bean (15), tobacco (28), peanut (20), and oats (7). We know of no such information for tomato, so the present work was done to assess the extent and nature of variability in its photosynthetic gas exchange characteristics.

MATERIALS AND METHODS

Seeds of one accession of *Lycopersicon minutum*, which has high solids content (21), and 24 genotypes of *L. esculentum*, varying in growth habit, leaf morphology, Chl content, fruit solids content, and/or RuDPcase activity (1), were germinated on slants, selected, and transplanted after 7 days into 3.8-liter plastic pots filled with soil. Three seedlings transplanted/pot were thinned 10 days later to one plant/pot on the basis of uniform size. The plants received a 16-hr (30 C) day and 8-hr (18 C) night in a growth chamber with a PAR[3] of 450 μeinsteins m^{-2} sec^{-1}. The plants were watered as needed, and fertilized weekly with 0.5 g of 10-10-10 (N, P, K).

Assimilation Measurements. Approximately 30 days after sowing, the gas exchange characteristics of the attached terminal trifoliate of the sixth leaf which was three-fourths to fully expanded was measured in an open gas exchange system at a light intensity of 1100 μeinsteins m^{-2} sec^{-1}. Five replicates of each genotype were measured by admitting in turn four CO_2 concentrations (50, 100, 150, and 300 μl l^{-1}) into the leaf chamber at 32.1 C air chamber temperature. Steady state gas exchange rates were attained in 10 to 15 min at the initial [CO_2] and 7 to 10 min for subsequent decreased [CO_2]. These equilibration times made it possible to run two genotypes (10 plants) per day. Preliminary studies indicated no differences in photosynthetic rate with time of day or leaf age over several days.

After photosynthetic measurements, leaf area was determined with a Hayashi-Denko automatic photoelectronic area meter (Model AAM-5), and Chl was determined at 645 and 663 nm in 80% acetone extracts and calculated on the basis of the MacKinney-Arnon equations (2).

From preliminary observations, three genotypes differing in gas exchange characteristics (Ottawa 67 [0 67], VF 145-7879 [7879], and LA 959) were selected for observations of the effect of leaf rank, temperature, and light on photosynthetic rate. The procedure was as described above except in the leaf rank experiment, where leaves 4 to 8 were measured as each approached or attained full expansion; and in the temperature and light-saturation experiments, where two replications per genotype were measured.

Because space was limited in the growth chamber, four different experiments were conducted to screen 25 genotypes. Measurements were made on November 13 to November 20, 1973;

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[3] Abbreviations: PAR: photosynthetically active radiation (400–700 nm); NCE: net CO_2 exchange; CE: carboxylation efficiency = $\Delta NCE/\Delta[CO_2]$ at [CO_2] where NCE equals zero; r_a: boundary layer resistance; r_l: Σ stomatal resistance plus cuticular resistance; RuDPcase: ribulose 1,5-diP carboxylase; Γ: CO_2 compensation point.

December 6 to December 12, 1973; February 7 to February 16, 1974; and July 2 to July 7, 1974. Variable maturation times account for the range in measurement dates for each experiment. Included in each experiment as internal references for comparisons were two genotypes (0 67 and darkgreen Manapal [*dg/dg*] [*dg* Man]).

Apparatus for Assimilation Measurements. Assimilation was measured with attached leaves inserted into the assimilation chamber of a flow-through (open) gas exchange system (Fig. 1). The body of the assimilation chamber was black anodized aluminum with a floor of narrow fins to facilitate heat transfer. A Rotron Whisper Fan, 6 w of dissipation, was mounted horizontally to force air downward onto the finned chamber floor, up around all four walls, over the leaf, and back into the fan. Fan speed was variable and was set to minimize boundary layer resistance. The chamber volume, less than 1800 cm^3, accepted leaves up to 15 × 16 cm.

The leaf was held in place by two nylon nets with a petiole extending through a slot between the chamber body and Plexiglas lid. The edges of the slot were covered with closed-cell foam rubber, which sealed the point of leaf insertion.

The entering air flow was regulated at 2 liters min^{-1} and measured with an electronic mass-flow meter (Flow Technology, Model NFC), while the exit line flow was regulated with a needle valve at 0.25 liters min^{-1}, giving a positive chamber pressure of about 0.3 cm of Hg. This resulted in outward flow at any points of minor leakage. Temperature was controlled with water-cooled Peltier thermoelectric heat exchange modules bolted to the bottom surface of the chamber. Full advantage of the variable cooling and heating capabilities of the Peltier modules is achieved with a bipolar proportional thermistor controller designed and built in this laboratory. Air temperature can be maintained with a short term stability of ± 0.05 C over the range of 10 to 45 C. Three measurements of temperature were taken for each leaf with thermocouple junctions made from 0.08-mm enamel-insulated iron and constantan wire. The thermocouples were mounted on supports so as to be easily adjusted for good thermal contact with the underside of the leaf.

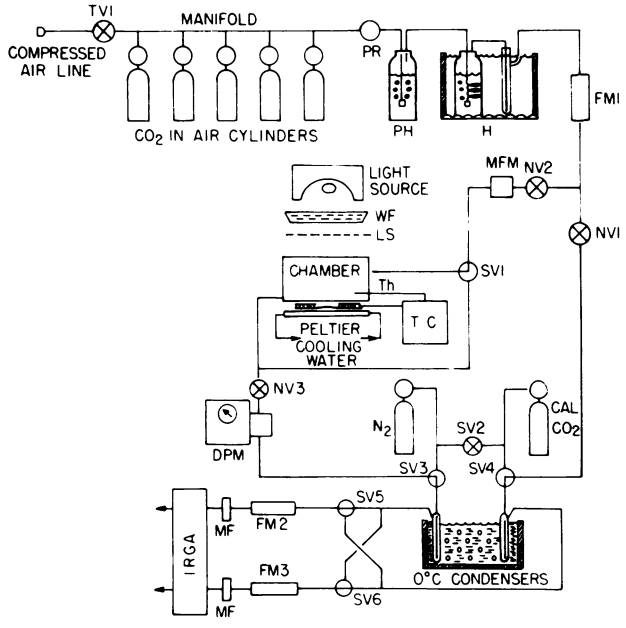

FIG. 1. Schematic diagram of gas exchange apparatus. TV: toggle valve; NV: needle valve; SV: solenoid valve; PR: pressure regulator; PH: prehumidifier; H: humidistat; FM: flow meter; MFM: mass flow meter; Th: thermistor; TC: temperature controller; DPM: dew point meter; MF: filters; WF: water filter; LS: light screens.

The light source was a single 1000-w quartz-iodine lamp, Norelco type FCN, in a fan-cooled Duolite reflector housing with IR filtering. Additional filtering was provided by 4 cm of water. The light source was vertically adjustable to permit fine control of light intensity. Neutral density filters were used for coarse adjustment. A maximum PAR of 1600 μ-einsteins m^{-2} sec^{-1} was achieved with uniformity over the leaf area of ± 5%.

Gas mixtures were obtained from commercially premixed compressed gas cylinders. The incoming gas stream was humidified to saturation in a constant temperature water bath. Both input and output dew points were measured with a single Cambridge dew point hygrometer, Model 880. A bypass line permitted measurement of input dew point without removing the leaf from the chamber.

Differential CO_2 measurements were made with a Beckman IR gas analyzer, Model 315A. Both the measuring and reference gas streams were brought to 0 C dew point by passage through a specially designed condenser with a high surface to volume ratio before entering the IRGA to eliminate differential interference by water vapor. This proved more satisfactory than chemical desiccants.

Data Handling. The raw data (IRGA recorder deflection, dew point in, dew point out, mass flow meter voltage, leaf temperature, input CO_2 concentration, IRGA sensitivity range factor, leaf area, and light intensity) were punched on cards and used with a Fortran IV data analysis program for calculation of the results. The program includes regression formulae for empirically derived corrections to the response of the differential IRGA, eliminating the need for rezeroing and recalibration at each background CO_2 concentration. In addition, the nonlinear calibration curve of the mass flow meter is described by a third order regression equation, and Smithsonian Meteorological tables are internally listed and addressed for conversion of dew points to water vapor concentrations.

The output consists of a table listing net photosynthesis, actual [CO_2] inside the chamber, corrected volume flow rate at standard temperature and pressure transpiration, diffusive resistance to CO_2 of the boundary layer (r_a) and leaf (stomatal and cuticular) (r_l), and the estimated [CO_2] within the substomatal cavity ([CO_2] internal). The last two parameters are calculated from transpirational data, leaf temperature, and the CO_2-H_2O diffusivity ratio (14, 17). A value of 0.32 cm sec^{-1} was obtained for the r_a by measurements of evaporation from a blotter paper leaf replica. Since the correction for partial diffusivity of gaseous flow through the boundary layer (26) was probably minor relative to the genotypic variability in r_a, gaseous flow through the stomata was assumed to be wholly diffusive (23).

Since the data were collected at a number of CO_2 concentrations, the program also punched cards with values of [CO_2] external, [CO_2] internal, NCE, and an identification code. These cards were used in a subsequent program which computed and plotted the second order regression line through the data points for both internal [CO_2] and external [CO_2], and printed the compensation point (x-intercept), the extrapolated zero-[CO_2] value for NCE (y-intercept), NCE at several normalized [CO_2] values, *e.g.* 100, 200, 250 μl l^{-1}, and the slope at the compensation point (CE). This program, in turn, punched cards for subsequent statistical analysis.

Analysis of variance was conducted for each experiment for each parameter with a computer using a completely randomized design. Comparison of genotypes with 0 67 and *dg* Man was possible for each experiment, but data had to be combined to compare genotypes between experiments. Statistical analysis of variance of 0 67 and *dg* Man over four experiments revealed an average 6.5% difference between experiments, with significant differences between experiments for most parameters except NCE at 100 μl l^{-1} external and internal [CO_2.] To compare genotypes between experiments, a small adjustment was made

on the basis of the lack of detectable genotype x experiment interaction for 0 67 and *dg* Man over the four experiments. The experimental mean deviation of 0 67 and *dg* Man from the overall mean for these lines was used to adjust individual values proportionally for all tomato genotypes. Analysis of variance with a completely randomized design was conducted on the adjusted data, and means were compared by Duncan's multiple range test.

RESULTS AND DISCUSSION

Light Effect. The measure of carboxylation efficiency (27) used in comparing the different genotypes studied was the slope of the regression curve for NCE *versus* CO_2 concentration taken at Γ. The response of CE to increasing light intensity was ascertained for three genotypes, one with high NCE and CE (0 67), one with intermediate NCE and CE (7879), and one with low NCE and CE (LA 959). The response of CE to increasing light intensity (Fig. 2) was similar for 0 67 and 7879, with saturation occurring at 1600 μeinsteins m^{-2} sec^{-1}. In contrast, LA 959 saturated at 700 μeinsteins m^{-2} sec^{-1}, a significantly lower intensity. Similar variations in light saturation for photosynthetic electron transport (24) and CO_2 conductance into leaves (5, 15) have previously been reported. Genotypic differences in CE among the three representative lines were significant at all light intensities, and, although ideally all comparisons in CE should be made at saturating intensities, it is assumed that comparisons at a single intensity likely to be saturating or nearly saturating would be valid. A light intensity of 1100 μeinsteins m^{-2} sec^{-1} was used for all comparisons of genotypes.

Leaf Rank. Comparison of CE for the fourth to eighth leaves above the primary leaves on the main stem showed little variation within each genotype. The differences in CE among genotypes were significant for each leaf. The sixth leaf was routinely used as a compromise between the ease of insertion of the leaf into the chamber and the length of the growth period.

Temperature Effect. The NCE of 0 67 and 7879 were affected similarly by temperature, while that of LA 959 was less affected (Fig. 3). NCE was optimum in response between 25 and 30 C in 0 67 and 7879, but relative comparisons appeared possible at any temperature between 15 and 35 C. Genotypes were compared at 32.1 C to simulate summer field conditions in Davis, Calif.

Genotypic Comparisons. A commonly used parameter for comparison of genotypes is NCE at some specified $[CO_2]$ introduced into a leaf chamber. Variations in actual $[CO_2]$ within the leaf chamber resulting from differences in leaf area or NCE rates of the leaf have frequently been ignored. These variations could lead to inaccurate comparisons among genotypes (Table I). However, for comparison with other reports in the literature, NCE at 300 μl l^{-1} CO_2 input ranged from 10.2 mg CO_2 dm^{-2} hr^{-1} for LA 959 to 26.9 mg CO_2 dm^{-2} hr^{-1} for 0 67, a 2.5-fold difference. NCE at 300 μl l^{-1} CO_2 input reported by Pallas and Samish (20) in the tomato cultivar Marion, grown to comparable age at a light intensity of 255 μeinsteins m^{-2} sec^{-1}, falls within the range of this study. Tanaka *et al.* (25) reported a maximum value of 46 mg CO_2 dm^{-2} hr^{-1} for 'Fikugo No. 2' grown in full sunlight. From data presented by those workers, it is difficult to ascertain whether that high value represents "genotypic" or "physiological variability" due to different light intensities during growth. It is well established in a number of species that NCE at saturating light varies according to the light intensity received by the plant during prior growth (4, 6).

To overcome the variations in external $[CO_2]$ mentioned above, $[CO_2]$ was varied and a regression of NCE on $[CO_2]$ was made. Genotypes were compared either at normalized $[CO_2]$ (both external and internal) or for certain characteristics of the regression curve, such as slope. Genotypic differences were

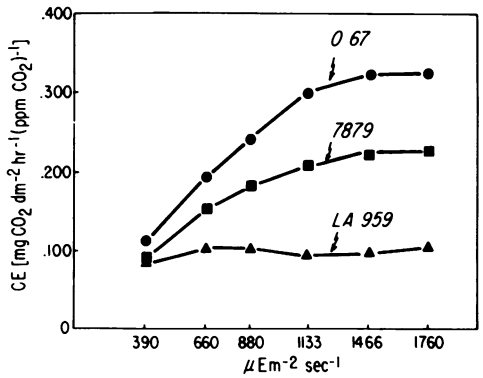

FIG. 2. Light-saturation curve for carboxylation efficiency (CE) of representative high, intermediate, and low genotypes.

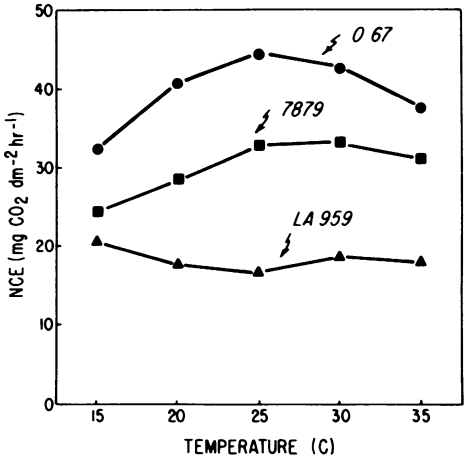

FIG. 3. Influence of leaf temperture on P_{net} at 250 μl/l CO_2 (external) for representative high, intermediate, and low genotypes.

significant ($P = 0.01$) for each parameter observed. Slope at Γ (CE) (Table I) rather than NCE at a certain $[CO_2]$ was used in genotype comparisons to avoid any bias due to differences in Γ. (Curves with high Γ could give reduced NCE values at 100 μl l^{-1} CO_2 despite high CE.) There was a 3-fold difference in CE between extreme genotypes.

Genotypic variation in NCE in oats (7) and soybeans (8) has been attributed to differences in diffusive resistance. Statistically significant differences among genotypes were obtained from $(r_a + r_l)$ (Table II). Within nonsignificantly different groups there were genotypes with extreme CE values, indicating that $(r_a + r_l)$ may not account for the most important genotypic differences in CE. Among the genotypes with large $(r_a + r_l)$ means are included genotypes with large CE values. The lack of a significant correlation ($r = -0.07$) between $(r_a + r_l)$ and CE also indicates a lack of causal relationship between these two factors.

The effect of estimation and removal of $(r_a + r_l)$ to yield the internal $[CO_2]$ was observed by comparing the NCE at 100 μl l^{-1} external and internal $[CO_2]$ (Table III). NCE was greater for 100 μl l^{-1} internal $[CO_2]$ than at 100 μl l^{-1} external $[CO_2]$ because of removal of $(r_a + r_l)$ in the former (22). That NCE is not related to genotypic variation for diffusive resistance is further indicated by the fact that internal and external $[CO_2]$ have similar groups of means that are not significantly different.

Genotypic variation in NCE in tobacco (28) has been attributed to photorespiration differences. It has been suggested that Γ can be related to the magnitude of photorespiration (9), and screening for genotypic variation based on differences in the magnitude of Γ has been attempted (19). Although large differ-

Table I. *Variation among Genotypes for NCE and CE*

CE[1] rank	Genotype	CE [mg CO_2 dm^{-2} hr^{-1} (ppm CO_2)$^{-1}$]	CE rank	Genotype	NCE at 300 µl l^{-1} CO_2 (mg CO_2 dm^{-2} hr^{-1})
1	LA 986	0.334	2	0 67****	26.9
2	0 67****	0.300	9	0 67*	25.1
3	Manapal***	0.295	3	Manapal***	24.9
4	Manapal*	0.295	6	0 67**	24.8
5	LA 783	0.294	7	Manapal**	24.2
6	0 67**	0.287	5	LA 783	24.1
7	Manapal**	0.276	10	0 67***	24.1
8	LA 876	0.275	4	Manapal*	23.8
9	0 67*	0.269	1	LA 986	22.2
10	0 67***	0.264	11	Manapal****	22.0
11	Manapal****	0.263	8	LA 876	21.6
12	2-237	0.257	12	2-237	21.5
13	*L. minutum*	0.252	18	PI 270414	21.2
14	K-83043	0.251	19	0 66	21.0
15	2-2311	0.239	21	R839-1	20.3
16	3-319	0.237	27	1339	20.2
17	2-491	0.236	17	2-491	20.1
18	PI 270414	0.228	14	K-83043	20.1
19	0 66	0.223	13	*L. minutum*	19.9
20	2-505	0.218	22	Cavalier	19.1
21	R 839-1	0.216	15	2-311	18.9
22	Cavalier	0.213	20	2-505	18.9
23	3-83	0.200	29	7879	18.3
24	LA 336	0.189	26	3-345	179
25	LA 1094	0.188	24	LA 336	17.9
26	3-345	0.182	16	3-319	17.9
27	1339	0.176	23	3-83	17.7
28	VF 36	0.170	28	VF 36	16.8
29	7879	0.160	25	LA 1094	16.6
30	LA 1098	0.134	30	LA 1098	10.4
31	LA 959	0.090	31	LA 959	10.2

Duncan's multiple-range test: means sharing same line are not significantly different at 1% level.

(*) Asterisks in genotype designations for Manapal and 0 67 indicate experiment number.

[1] Slope of response curve of NCE versus internal [CO_2] taken at the CO_2 compensation point).

ences in CE were observed among the genotypes, the differences in Γ were relatively small. Notable exceptions were LA 1098 and LA 959, which had significantly greater Γ and lower CE than the other genotypes. These results suggest that screening based on Γ has little likelihood of success. Careful consideration of models such as that of Lommen *et al.* (18) suggest that Γ is a complex integral function of the rates of the carboxylation reactions of photosynthesis and the decarboxylation reactions of respiration and photorespiration as well as diffusive resistance between the various sites within the leaf where these reactions occur.

The zero CO_2 intercept obtained by extrapolation of the

Table II. *Leaf Resistance to CO_2 Diffusion*

CE rank	Genotype	Leaf resistance[1]
		(sec cm^{-2})
13	*L. minutum*	2.25
23	3-83	2.16
15	2-311	2.08
30	LA 1098	2.01
25	LA 1094	1.96
24	LA 336	1.93
22	Cavalier	1.88
14	K-83043	1.80
17	2-491	1.73
28	VF 36	1.70
16	3-319	1.69
20	2-505	1.68
7	Manapal**	1.68
29	7879	1.67
8	LA 876	1.67
26	3-345	1.66
1	LA 986	1.66
31	LA 959	1.64
10	0 67***	1.56
4	Manapal*	1.54
11	Manapal****	1.54
5	LA 783	1.47
21	R 839-1	1.46
2	0 67****	1.45
9	0 67*	1.44
18	PI 270414	1.43
3	Manapal***	1.43
19	0 66	1.43
27	1339	1.36
6	0 67**	1.31
12	2-237	1.23

Duncan's multiple-range test: means sharing same line are not significantly different at the 1% level.

(*) Asterisks in genotype designations for Manapal and 0 67 indicate the experiment number.

[1] Boundary layer (r_a) plus stomatal and cuticular (r_l) resistance.

$[CO_2]$ *versus* NCE response curve has also been used to estimate photorespiration (22). Therefore this parameter was calculated using the NCE versus internal $[CO_2]$, thus eliminating the effects of varying r_l and r_a. Significant differences were obtained (Table IV), with the more efficient genotypes having higher intercepts than the less efficient ones. This is a simple mathematical consequence of the linear extrapolation of lines with different slopes through nearly congruent Γ values. This fact leads to the conclusion either that photorespiration was dependent upon CE or that this method does not reliably estimate photorespiration. Estimating the magnitude of photorespiration by the zero $[CO_2]$ intercept is based on the assumptions

Table III. *NCE at 100 μl l⁻¹ External and Internal [CO_2]*

CE rank	Genotype	External [CO_2] (mg CO_2 dm^{-2} hr^{-1})	CE rank	Genotype	Internal [CO_2] (mg CO_2 dm^{-2} hr^{-1})
2	0 67****	7.18	1	LA 986	11.12
6	0 67**	7.06	5	LA 783	10.55
4	Manapal*	6.82	2	0 67****	10.51
3	Manapal***	6.75	4	Manapal*	10.44
5	LA 783	6.70	6	0 67**	10.39
10	0 67***	6.60	3	Manapal***	10.33
9	0 67*	6.52	10	0 67***	9.83
1	LA 986	6.30	7	Manapal**	9.77
7	Manapal**	6.28	9	0 67*	9.71
18	PI 270414	6.21	11	Manapal****	9.65
11	Manapal****	6.16	13	*L. minutum*	9.09
8	LA 876	5.75	8	LA 876	8.89
12	2-237	5.72	18	PI 270414	8.58
19	0 66	5.50	14	K-83043	8.28
16	3-319	5.47	16	3-319	8.21
17	2-491	5.33	12	2-237	8.17
13	*L. minutum*	5.27	17	2-491	8.10
14	K-83043	5.27	19	0 66	7.82
20	2-505	4.96	20	2-505	7.32
26	3-345	4.81	15	2-311	6.87
21	R 839-1	4.80	21	R 839-1	6.86
27	1339	4.78	26	3-345	6.71
15	2-311	4.36	22	Cavalier	6.46
22	Cavalier	4.32	23	3-83	6.26
28	VF 36	4.18	27	1339	6.25
25	LA 1094	4.18	24	LA 336	6.25
24	LA 336	4.17	25	LA 1094	6.14
23	3-83	4.15	28	VF 36	5.90
29	7879	4.12	29	7879	5.58
30	LA 1098	2.72	30	LA 1098	3.76
31	LA 959	1.30	31	LA 959	1.61

Duncan's multiple-range test: means sharing same line are not significantly different at the 1% level.

(*) Asterisks in genotype designations for Manapal and 0 67 indicate experiment number.

that the CO_2 response curve is linear and that the rate of photosynthesis and the CO_2 concentration do not influence respiration (23). The effects of photosynthesis and CO_2 on the photorespiration are not known (23), although the CO_2 response curve above Γ approaches linearity over the range of [CO_2] used in this study. The validity of the assumption that the CO_2 response curve is linear below Γ has been shown to be questionable by Holmgren and Jarvis (13).

Chlorophyll content differed significantly among genotypes (Table V) and was correlated with CE and NCE ($r = 0.74$). This correlation suggests that there is some relationship between Chl content and CE and NCE despite considerable evidence that increased Chl, *per se*, is not responsible for the higher CE in many species. For example, results at low light intensities with a variety of species have shown that Chl concentration does not further increase NCE (10). Furthermore, Chl mutants of cotton,

Table IV. *CO_2 Compensation Point and Zero [CO_2] Intercept*

CE rank	Genotype	CO_2 compensation point (ppm)	CE rank	Genotype	Zero CO_2 intercept (mg CO_2 dm^{-2} hr^{-1})
18	PI 270414	58.3	1	LA 986	-25.0
11	Manapal****	58.4	2	0 67****	-21.0
10	0 67***	59.2	3	Manapal***	-21.0
6	0 67**	59.3	8	LA 876	-20.9
5	LA 783	59.5	4	Manapal*	-20.7
4	Manapal*	59.8	5	LA 783	-20.2
13	*L. minutum*	60.0	12	2-237	-20.0
9	0 67*	60.0	6	0 67**	-19.9
26	3-345	60.1	15	2-311	-19.7
16	3-319	60.3	7	Manapal**	-19.3
7	Manapal**	60.5	14	K-83043	-18.7
3	Manapal***	60.6	9	0 67*	-18.4
2	0 67****	61.4	10	0 67***	-18.2
19	0 66	61.5	11	Manapal****	-18.0
17	2-491	61.8	17	2-491	-17.8
1	LA 986	62.1	13	*L. minutum*	-17.3
27	1339	62.1	16	3-319	-17.1
28	VF 36	62.4	22	Cavalier	-16.6
20	2-505	62.6	21	R 839-1	-16.2
14	K-83043	62.7	20	2-505	-15.9
8	LA 876	63.4	19	0 66	-15.6
29	7879	63.5	23	3-83	-15.3
25	LA 1094	64.1	18	PI 270414	-15.1
24	LA 336	64.1	25	LA 1094	-14.0
12	2-237	65.4	24	LA 336	-13.5
23	3-83	65.7	26	3-345	-12.2
21	R 839-1	65.8	27	1339	-11.9
22	Cavalier	66.8	28	VF 36	-11.9
15	2-311	67.6	30	LA 1098	-11.4
30	LA 1098	70.6	29	7879	-11.0
31	LA 959	77.6	31	LA 959	- 8.3

Duncan's multiple-range test: means sharing same line are not significantly different at the 1% level.

(*) Asterisks in genotype designations for Manapal and 0 67 indicate experiment number.

pea, soybean, and barley having one-fifth to one-third the Chl content of their wild-type genotypes (3, 11, 16) or lacking Chl entirely (12) have been shown to have either similar or higher NCE per unit of leaf area when saturating amounts of light were used. Species having an 8-fold variation in Chl content have likewise been shown to have a similar NCE (10). The reasons for the discrepancy between those reports and the high correlation between Chl content under light-saturating conditions in the present studies are not understood. It is possible that differences in the number of photochemical reaction centers and associated electron transport components per unit of leaf area determine the observed differences in CE and NCE, and that variation in total Chl in some way reflects these differences in photochemical activity.

Table V. *Chlorophyll Content*

CE rank	Genotype	Chlorophyll content (mg dm^{-2})
1	LA 986	7.91
16	3-319	6.86
12	2-237	6.77
11	Manapal****	6.71
6	0 67**	6.63
18	PI 270414	6.58
19	0 66	6.48
10	0 67***	6.40
3	Manapal***	6.28
4	Manapal*	6.27
26	3-345	6.17
7	Manapal**	6.04
20	2-505	6.02
9	0 67*	6.01
14	K-83043	6.00
2	0 67****	5.96
13	*L. minutum*	5.87
8	LA 876	5.71
22	Cavalier	5.20
5	LA 783	5.17
27	1339	5.14
28	VF 36	5.10
21	R 839-1	5.10
29	7879	4.98
23	3-83	4.95
15	2-311	4.92
24	LA 336	4.36
17	2-491	3.88
31	LA 959	3.66
30	LA 1098	3.57
25	LA 1094	3.02

Duncan's multiple-range test: means sharing same line are not significantly different at the 1% level.
(*) Asterisks in genotype designations for Manapal and 0 67 indicate the experiment number.

Differences in the quantity and/or kinetic properties of enzyme catalyzing the dark reactions of photosynthetic CO_2 metabolism may be another possible source of genetic variability in CE and NCE. Genotypic variation in NCE in soybeans (15) has been attributed to differences in the kinetic properties in Calvin cycle reactions. Tomato has been reported (1) to vary in the quantity and kinetic properties of RuDPcase. Relating Anderson's (1) report to this study by using the same four genotypes[4] reveals there was a positive association between CE and quantity of RuDPcase and a negative relationship between CE and specific activity of RuDPcase. Further studies are needed to determine the basis for genetic variation in CE for all tomato genotypes and the relationship between photochemical activity, Chl content, and photosynthetic CO_2 metabolism.

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[4]

Anderson *et al.* Genotype No.	Present Study Genotype No.
1115	LA 1098
873	LA 986
763	LA 783
863	2-237

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