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COMPARISON OF PHOTOSYNTHESIS IN NORMAL AND TRIAZINE-RESISTANT *Brassica*

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In spaced field plantings, triazine-resistant types of *Brassica campestris* L. and *B. napus* L. had a carbon dioxide exchange rate (CER) 28% lower in 1983 and 25% lower in 1984 than normal (triazine-susceptible) types. In plots simulating agronomic spacings in 1984, the difference between CER in normal and resistant types was 17% for *B. campestris*, 14% for *B. napus* and 13% for *B. juncea* L. Differences were apparent throughout the season and were not associated with any particular stage of growth. Resistant progeny from reciprocal crosses between resistant and susceptible plants of *B. napus* exhibited reduced CER at all levels of photosynthetically active radiation and at all temperatures. There was no significant difference between plant types for chlorophyll *a*+*b* content or chlorophyll *a*/*b* ratio. Shoot dry weight, stomatal resistance and specific leaf weight were higher in the normal types, but there was no difference between types in either relative growth rate or net assimilation rate. The reduced biomass was not therefore linked to reduced CER.

Key words: Carbon dioxide exchange rate, herbicide, oilseed, rapeseed

[Comparaison de la photosynthèse chez des variétés de *Brassica* normales et résistantes à la triazine.]

Titre abrégé: Photosynthèse chez les *Brassica* normales et résistantes à la triazine.

Des variétés de *Brassica campestris* L. et de *B. napus* L. résistantes à la triazine, cultivées en plantations par pieds isolés, présentaient un taux d'échange du CO_2 (CER) inférieur de 28% en 1983 et de 25% en 1984 à celui des variétés normales (sensibles à la triazine). Dans des parcelles simulant l'espacement cultural, en 1984, la différence observée du CER entre les types normaux et résistants était de 17% pour *B. campestris*, de 14% pour *B. napus* et de 13% pour *B. juncea* L. Les différences observées étaient visibles pendant toute la saison et n'étaient pas liées à un stade particulier de la croissance. Les descendants résistants de croisements réciproques entre les plantes résistantes et sensibles de *B. napus* ont laissé voir un CER réduit à tous les niveaux du rayonnement photosynthétiquement utilisable et pour toutes les températures. Il n'y avait pas de différence significative entre les types de plante quand à la teneur en chlorophylle *a*+*b* ou au rapport de la chlorophylle *a* sur la chlorophylle *b*. Le poids sec des tiges, la résistance stomatique et le poids foliaire spécifique étaient plus élevés chez les types normaux mais nous n'avons observé aucune différence, entre les types, quant au taux de croissance relatif ou au taux net d'assimilation. La baisse de la production de biomasse d'était donc pas liée à une réduction du CER.

Mots clés: Taux d'échange du CO_2, herbicide, oléagineux, colza

Can. J. Plant Sci. 67: 457–466 (Apr. 1987)

Triazine herbicide resistance in many species results from a slight modification in a chloroplast polypeptide (Q_B) in photosystem II (Pfister et al. 1981; Hirschberg et al. 1984). The herbicide normally binds to this protein, and the structural change responsible for resistance leads to a loss of this binding capacity. This form of resistance is associated with reduced photosynthetic activity in some, but not all, weed species (Ort et al. 1983; van Oorschot and van Leeuwen 1984). Reduced growth of such biotypes (Marriage and Warwick 1980; Mapplebeck et al. 1982) might be due in part to this lower photosynthetic activity.

Preliminary evidence indicates that photosynthesis is reduced under certain environmental conditions in triazine-resistant *Brassica napus* L. cultivars (Donnelly and Hume 1984) and that triazine resistance in oilseed rape is associated with a reduced yield (Beversdorf and Hume 1984; Grant and Beversdorf 1985). The work presented here was conducted to examine differences between the carbon dioxide exchange rate (CER) in triazine-resistant and susceptible (normal) cultivars of *B. campestris* L., *B. napus* and *B. juncea* L. grown under various environmental conditions. Relationships between CER and growth, and between CER and other physiological characteristics associated with photosynthesis were examined.

MATERIALS AND METHODS

Spaced Plantings

Four genotypes of *B campestris* (Torch, Tobin, Yellow Sarson R500 and DM431) and of *B. napus* (Midas, Westar, Bronowski and DM797) were grown in the field in 1983 and 1984. DM431 and DM797 were triazine resistant and the others were normal. Seed, supplied by the Agriculture Canada Research Station, Saskatoon, was planted on 26 May 1983 and 18 May 1984. Each genotype was sown as a 1-m row with 1 m in all directions between genotypes. The experimental design was a randomized complete block with four replicates. Within rows, plants were thinned to 25-cm spacing. One plant in each row was marked and CER measurements were made on these plants seven times between 29 and 68 d from planting in 1983, and between 38 and 66 d from planting in 1984. Plants were treated with carbaryl to control flea beetles, as required.

Field Plots

A normal and a triazine-resistant genotype of each of *B. campestris* (Tobin and DO531), *B. juncea* (Domo and TRJ83-1507) and *B. napus* (Westar and DM797) were grown in the field in 1984. Plots were established simulating agronomic spacings in a randomized complete block design by the Agriculture Canada Research Station, Saskatoon. CER measurements were made on five randomly selected plants from each of two replicates for each genotype. Four sets of measurements for *B. napus* and three sets for *B. campestris* and *B. juncea* were made between 35 and 51 d from planting.

Reciprocal Crosses

Seed of *B. napus*, produced by reciprocal crossing between single plants of Triton (triazine resistant) and Hanna (normal), was supplied by Dr. W. Beversdorf, Crop Science Department, University of Guelph, Guelph, Ontario. The progeny having Triton as the female parent were triazine resistant whereas those from the reciprocal cross were normal. Spaced plantings were established on 18 May 1984 as described above. The CER measurements were made on all plants four times between 38 and 52 d from planting.

Light curves were generated for the reciprocals in the field using screens of cheesecloth to shade plants on a sunny day in mid-season. Using 0–8 screens, the amount of shade was progressively increased on one replicate within a cross then decreased on the next. In this manner, three plants of each cross were measured under conditions ranging from full sunlight (1800 μmol quanta m^{-2} s^{-1}) to about 100 μmol quanta m^{-2} s^{-1}. The CER was allowed to stabilize (approximately 1 min) at each level of shading before recording CER, cuvette temperature and photosynthetically active radiation (PAR). Average CER for each cross for every 100 μmol quanta m^{-2} s^{-1} below 700 and every 400 μmol quanta m^{-2} s^{-1} above 700 were calculated.

Reciprocals were also grown under controlled environmental conditions. Seeds (one per pot) were planted in 6-inch pots filled with Turface and treated with Nutricote controlled-release fertilizer. Fourteen plants from each cross were grown in a completely randomized design at 20/15°C day/night temperature and a 16-h photoperiod (1000 μmol quanta m^{-2} s^{-1} PAR). At 21 d from planting the plants were subjected to different daily light/temperature regimes. The plants were allowed to acclimatize for 1 d prior to CER, stomatal resistance, chlorophyll, cuvette PAR and cuvette temperature measurements. The regimes used were temperatures of 10, 15, 20 or 30°C combined with high (100%) or low (50%) PAR.

Growth Experiments

Two genotypes of *B. campestris* (Tobin and DM431 — the latter being Tobin with triazine resistance backcrossed into it) were planted in the field in 5-m rows arranged in a randomized complete block design with five replicates on 18 May 1984. Plants were thinned to 10-cm spacings and 24 plants were marked at random in each row for measurement. Four marked plants from each row were harvested each week for 6 wk starting 35 d from planting. CER of two of the plants to be harvested was measured twice during the week prior to harvesting, except week 1 when plants were too small to measure CER.

Fifty plants each of Tobin and DM431 were grown in individual pots under controlled environmental conditions. Seeds were planted as described above and plants were grown in a 16-h photoperiod, 20/15°C light/dark temperatures and 750 μmol quanta m^{-2} s^{-1} PAR. At 16 d from planting, 10 plants of each genotype were harvested. For the next 4 wk CER was measured on 10 randomly selected plants of each genotype and these plants were immediately harvested. The experiment was then repeated at a higher PAR level (1000 μmol quanta m^{-2} s^{-1}). In this experiment there were only four weekly harvests starting at 10 d from planting as the final 10 plants could not be assayed due to equipment failure. Dry weights from the first two harvests of this second experiment were also lost due to a laboratory fire.

Measurements

A Licor 6000 portable photosynthesis system was used to measure CER and stomatal resistance of the reciprocal cross progeny grown indoors. Other CER measurements were made using a portable infrared gas analyzer (Mahon and Hobbs 1981). The second or third fully opened leaf from the apex was measured nondestructively using a fixed area cuvette. Chlorophyll was measured as described by Hobbs and Mahon (1985).

Leaf area (using an area meter from Delta-T devices, Cambridge, England), leaf and shoot dry weights were measured on all harvested plants in the growth experiments.

Analysis

Nested analyses of variance, with time as subtreatments, were performed. Duncan's multiple range test was used for multiple comparisons.

Light curves for spaced plantings in the field were generated by calculating the mean and variance of all CER measurements made during the season between 0 and 500, 501 and 1000, 1001 and 1500, 1501 and 2000, or 2001 and 2500 μmol quanta m^{-2} s^{-1}. Similarly, temperature curves were generated using the parameters 20–25, 26–30, or 31–35°C.

Relative growth rate (RGR) was calculated as $(\ln W_2 - \ln W_1)/(T2 - T1)$ and net assimilation rate (NAR) as $((W_2 - W_1)/(T2 - T1))((\ln L_2 - \ln L_1)/(L_2 - L_1))$ where, for each week ($T2$), W_2 and L_2 are the shoot dry weight and leaf area, and W_1 and L_1 are the shoot dry weight and leaf area of the previous week ($T1$).

RESULTS

No difference in CER was found within species among the normal varieties of *B. campestris* and *B. napus* (Table 1). However, normal types in these species and in *B. juncea* had significantly higher CER than the triazine-resistant types (Tables 1 and 2). This difference was apparent at each measurement time in each year and there was no significant genotype by time interaction.

Progeny from reciprocal crosses between two *B. napus* plants, one resistant and one normal, gave similar results. Mean CER for resistant progeny was 2.21 nmol cm^{-2} s^{-1}, and for normal progeny was 2.66 nmol cm^{-2} s^{-1}, a 17% difference ($P < 0.01$).

In the spaced plantings of *B. campestris* and *B. napus* in both 1983 and 1984, CER was lower in triazine-resistant types at all levels of PAR (Fig. 1). The 1984 measurements did not produce such a smooth curve as those of 1983 as the measurements were concentrated in the 150- to 2000-μmol quanta m^{-2} s^{-1} range through a conscious effort to obtain more readings under higher PAR levels in 1984. The accuracy of the estimate of mean CER at other light intervals was therefore reduced as shown by higher standard errors (Fig. 1). The data from both years indicate a greater difference in CER at higher levels of

Table 1. CER means of space-planted *Brassica* in the field

Genotype	CER (nmol cm^{-2} s^{-1}) 1983	CER (nmol cm^{-2} s^{-1}) 1984
B. campestris		
Torch	2.03*a*	2.64*ab*
Tobin	2.06*a*	2.52*ab*
Yellow Sarson (R500)	2.15*a*	2.82*a*
DM431 (triazine resistant)	1.48*b*	1.80*d*
B. napus		
Midas	2.21*a*	2.62*ab*
Westar	2.19*a*	2.48*b*
Bronowski	2.33*a*	2.55*ab*
DM797 (triazine resistant)	1.63*b*	2.10*c*
Decrease in CER associated with triazine resistance (%)	28	25

a–c Means within a column followed by the same letter are not different at the 0.05 level according to Duncan's multiple range test.

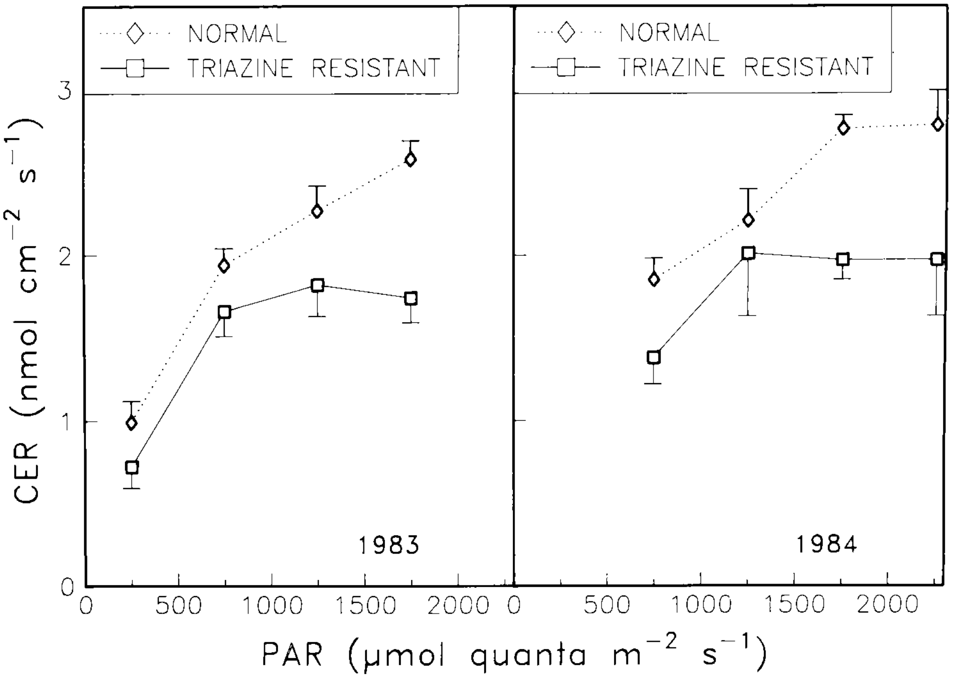

Fig. 1. CER of normal and triazine-resistant space-planted *Brassica*, at different levels of PAR, grown in the field in 1983 and 1984. Bars indicate standard error for each mean.

Table 2. CER values for three different *Brassica* species grown in plots in the field

Normal type CER	Triazine-resistant type CER	Decrease in CER associated with triazine resistance (%)
(nmol cm^{-2} s^{-1})		
	B. campestris	
1.98	1.65*	17
	B. napus	
1.93	1.66**	14
	B. juncea	
2.61	2.28**	13

*,** Differences between normal and triazine-resistant types are significant at the 0.05 and 0.01 levels of probability.

PAR. This may have been due to temperature effects as PAR and temperature were positively correlated in both years (r = 0.809** in 1983; r = 0.582** in 1984). It was only possible to plot CER against temperature for 1984 as temperature measurements were not routinely made in 1983. The temperature curves (Fig. 2) show that CER of triazine-resistant types was lower by a similar amount at each temperature. For the reciprocal crosses, where differences in PAR were rapidly generated by shading with little resulting change in cuvette temperature, differences between triazine resistant and normal progeny also occurred at all levels of PAR (Fig. 3).

Under controlled conditions, triazine-resistant progeny from the reciprocal cross had a lower CER than normal progeny (Fig. 4). The measurements at high PAR (averaging 740 μmol quanta m^{-2} s^{-1} at the cuvette) showed greater difference between types than measurements at low PAR (averaging 390 μmol quanta m^{-2} s^{-1} at the cuvette and the difference was apparently greatest at the high PAR/optimum temperature combi-

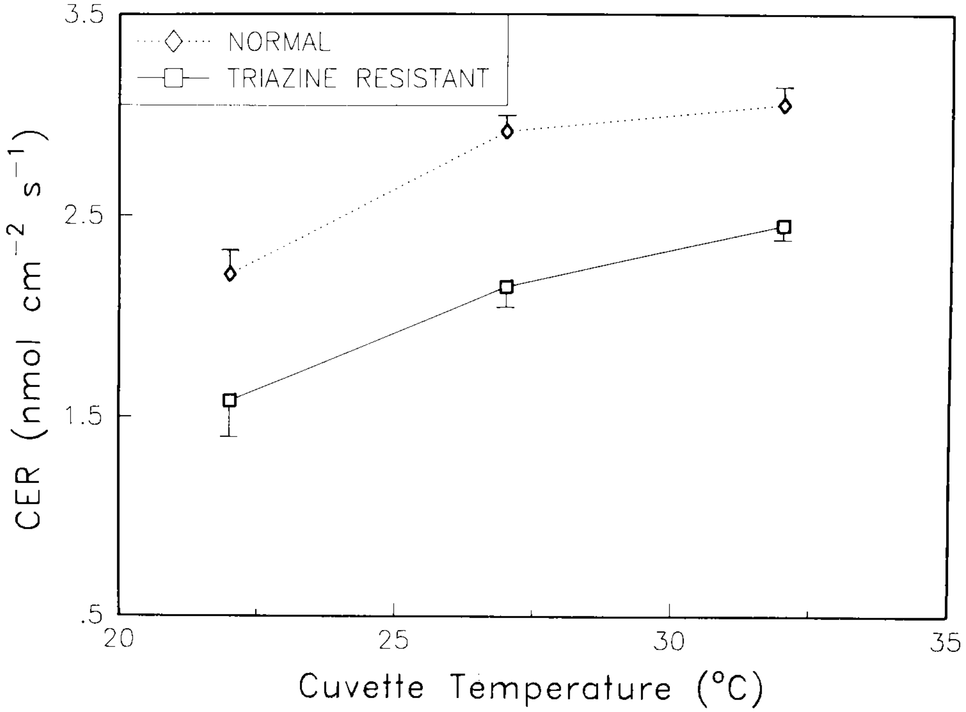

Fig. 2. CER of normal and triazine-resistant space-planted *Brassica*, at different temperatures, grown in the field in 1984. Bars indicate standard error for each mean.

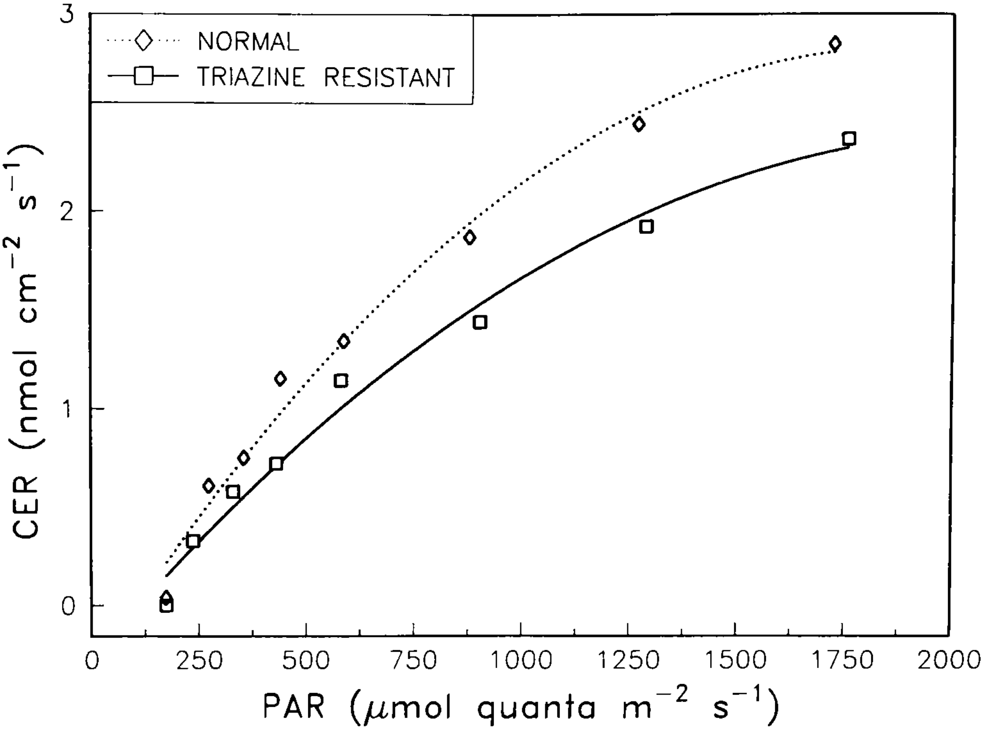

Fig. 3. CER of normal and triazine-resistant *B. napus* progeny from reciprocal crosses, at different levels of PAR, grown in the field in 1984.

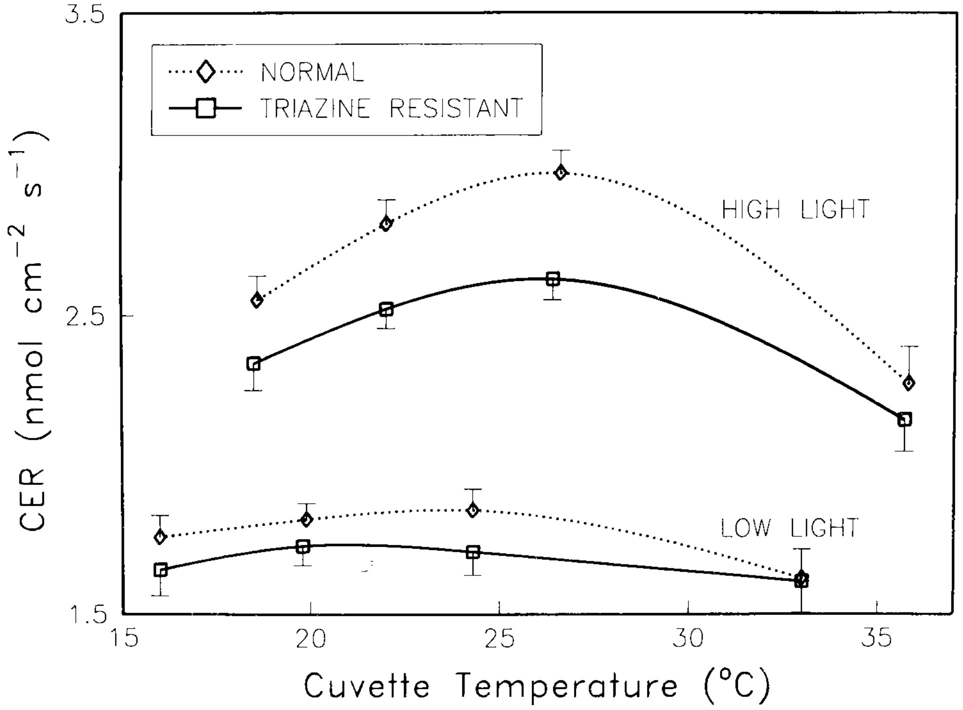

Fig. 4. CER or normal and triazine-resistant *B. napus* progeny from reciprocal crosses at different indoor PAR and temperature regimes. Bars indicate standard error for each mean.

nations. The CER differences between types were 8.5, 11, 13.5, and 5% at the high PAR and 6, 5, 8 and 1% at the low PAR for cabinet temperature settings of 10, 15, 20 and 30°C, respectively.

Final shoot weight was greater in normal types under both field and controlled environmental conditions but RGR and NAR did not differ significantly between triazine-resistant and normal types (Table 3).

Specific leaf weight was higher in the normal types (Table 3), though this was only significant in the indoor (low-light) conditions. The triazine-resistant and normal types did not differ in chlorophyll content or in chlorophyll *a*/*b* ratio (Table 4) but stomatal resistance was lower in the triazine-resistant type (Table 4).

Table 3. Mean values for characteristics of *B. campestris* grown in the field and under controlled conditions

	RGR (week^{-1})	NAR (g m^{-2} wk^{-1})	Specific leaf weight (mg cm^{-2})	Final shoot weight (g)
Field 1984				
Normal	0.59	144	5.65	54.5
Triazine resistant	0.58	108	5.48	25.5
Significance level†	NS	NS	NS	**
Indoor (high light)				
Normal	1.17	101	5.91	12.2
Triazine resistant	1.39	117	5.54	10.8
Significance level†	NS	NS	NS	*
Indoor (low light)				
Normal	1.09	83	4.69	26.1
Triazine resistant	1.22	81	4.21	19.2
Significance level†	NS	NS	**	**

†,*,** Differences between normal and triazine-resistant types are significant at the 0.05 or 0.01 levels of probability, respectively; NS, nonsignificant.

Table 4. Mean values for characteristics of progeny from reciprocal crosses between normal and triazine-resistant ypes of *B. napus* grown under controlled high light conditions

	Triazine-resistant progeny†	Normal progeny‡
CER (nmol cm^{-2} s^{-1})	2.14	2.33**
Chlorophyll $a+b$ (μg cm^{-2})	40.0	38.7
Chloropyll a/b	2.35	2.48
Stomatal resistance (s cm^{-1})	1.11	1.28**

† Progeny from crosses using triazine-resistant type as female.

‡ Progeny from crosses using normal type as female.

** Differences between normal and triazine-resistant types are significant at the 0.01 level of probability.

DISCUSSION

The lower CER in triazine-resistant types of the three *Brassica* species was apparent under most temperature and PAR regimes in plants grown in the field or in controlled environment conditions (Figs. 1–4). Although leaves are not the primary photosynthetic organs throughout plant growth in *Brassica* (stems and pods playing major roles in the later growth stages (Chapman et al. 1984)), differences in the leaf CER were maintained throughout the season and were not restricted to a particular physiological age of plant or leaf.

A single base substitution in the chloroplast gene coding for Q_B protein in photosystem II has been found to be associated with triazine resistance in *Amaranthus hybridus* and *Solanum nigrum* (Hirschberg et al. 1984). The resulting structural change apparently reduces triazine binding ability. Wild turnip probably has a similar mechanism of resistance (Ali and Souza Machado 1984) and it was this resistance that was transferred to commercial *Brassica* (Beversdorf et al. 1980). In the control of photosynthesis, it has been shown that photochemical capacity (the maximum rate at which a leaf can convert a nonlimiting supply of light energy to chemical product) can be co-limiting with intracellular CO_2 concentration under light-saturated conditions (Terry and Farquar 1984). It is possible, therefore, that the reduction in CER found here, and in the triazine-resistant biotypes of many weed species (Ort et al. 1983; van Oorschot and van Leeuwen 1983), was due to a reduction in photochemical capacity associated with a change in the Q_B protein. However, although Bowes et al. (1980) showed that electron transfer between the primary quinone acceptor in photosystem II (Q_A) and Q_B was 10 times slower in triazine-resistant chloroplasts of pigweed (*A. retroflexus*), the rate of electron transfer from Q_A to Q_B is not usually the rate-limiting step and isolated chloroplasts from triazine-resistant and normal types of *A. hybridus* had equivalent rates of whole-chain electron transfer (Ort et al. 1983). Hence, the slower electron transfer from Q_A to Q_B cannot directly account for the lower CO_2 reduction rates under all conditions.

Ort et al. (1983) suggested that there may be genetic differences other than triazine resistance between the biotypes examined and that these could be the underlying cause of reduced CER in the triazine-resistant types. Although the F_1 progeny of reciprocal crosses between normal and resistant individuals examined here also showed differences in CER (Figs. 3 and 4), such crosses still do not preclude the existence of multiple differences in the chloroplastic genome.

Ducruet and Lemoine (1985) found that triazine-resistant plants had a greater increase in fluorescence at high temperatures than did normal plants. This was ascribed to greater heat sensitivity in the photosystem II electron transfer linked to triazine resistance. Heat effects may, in part, explain greater differences in CER between types at higher levels of PAR in the field (Fig. 1) as PAR was correlated to temperature. However, the CER differences in the field did not appear to increase at higher temperatures (Fig. 2), nor would such temperature effects explain the indoor results where the greatest difference in CER between types was found at optimum temperature (Fig. 4) under high levels of PAR.

Other explanations for the differences between the CER in the triazine-resistant and normal types could not be found. There were no significant differences in chlorophyll $a+b$ or in chlorophyll a/b ratio as had been found in wild turnip (Burke et al. 1982). Stomatal resistance was higher in normal types (Table 4) and was not differentially affected by temperature at high levels of PAR in the same way that CER was. There was some difference noted between specific leaf weight in the two types, which may have accounted for CER differences (Table 4). However, the higher specific leaf weight in normal types may have been due to increased starch build-up in plants with higher CER.

Shoot dry weight was lower in the triazine-resistant types, both in indoor and field trials (Table 3). In pea, genetic differences in CER have been found to be correlated to RGR and NAR (Hobbs and Mahon 1982; Mahon 1982) but, in the *Brassica* species studied here, RGR and NAR were not significantly different in the two types. Hence, it could not be demonstrated that reduced CER was correlated with lower shoot dry weight through a reduction in these growth parameters.

The shoot weight of the triazine-resistant types was lower than that of the normal types at the initial harvest time in each growth experiment. Consequently, final shoot weight was lower in resistant types even though RGR and NAR did not differ. This early difference in shoot dry weight could be due to seedling differences, such as earlier seedling emergence, as found in several weed species (Mapplebeck et al. 1982) or due to CER differences being of greater importance in the very early stages of seedling growth. Further examination of early growth might be useful as this may elucidate the cause of the overall decrease in plant performance associated with triazine resistance.

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