Photosynthetic Properties and Cross-Resistance to Some Urea Herbicides of Triazine-Resistant *Conyza canadensis* Cronq (L.)

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A comparison of the photosynthetic activities, chloroplast ultrastructures and sensitivities to some urea herbicides of atrazine-resistant (R) and suspectible (S) biotypes of *Conyza canadensis* Cronq (L.) (horseweed) in the rosette stage showed that: 1) The light-intensity dependences of the rates of CO_2 reduction in intact leaves of the R and S plants are very similar. 2) The rate of the Hill reaction of the R chloroplasts at 25 °C is 15–20% lower at all light intensities than that of the S chloroplasts. 3) The rates of the Hill reactions of the R and S chloroplasts exhibit different temperature-dependences. The activation energy for the S chloroplasts in the temperature range 10–40 °C was found to be 15.3 kJ mol^{-1}. For the R chloroplasts, the discontinuity in the Arrhenius plot was found at around 20 °C; the activation energy was 20.1 kJ mol^{-1} at below 20 °C, and decreased to 8.2 kJ mol^{-1} at higher temperatures. 4) The R plants have a better adaptive capacity than the S plants at low temperatures. 5) The chloroplast ultrastructure in the R plants was not reminiscent of that of plants grown under low light intensity. 6) The R biotype exhibited cross-resistance to chlorbromuron and metobromuron, and tolerance to linuron. The R and S biotypes, however, were equally sensitive to diuron. The results permitted conclusions on the properties of the triazine-resistance and urea cross-resistance.

Introduction

Resistance to atrazine in plants was first reported by Ryan in 1970 [1]. The appearance of triazine-resistance at the chloroplast level has been demonstrated in nearly 38 weed species [2].

Wide-ranging efforts have since been made with different techniques to identify and characterize the physiological nature and biochemical background of the resistance in weeds [2, 3]. Recent research results suggest that triazine-resistance is very probably due to a modification of the herbicide-binding site [4–6], leading to the less effective binding of triazine herbicides on the herbicide-binding Q_B protein [7–9]. It is generally accepted that triazine-resistance in weeds originates from a single amino acid change, possibly modifying the structure and properties of the 32 kDa herbicide-binding Q_B protein [10]. The differences in the lipid and pigment compositions of the thylakoids and the ultrastructural differences between the R and S biotypes are secondary alterations, probably resulting from the reduced electron transport rate from photosystem II in the R biotypes [2, 11, 12].

A triazine R *Conyza canadensis* population was first encountered in Switzerland [3]. The appearance of a triazine R population of *C. canadensis* in Hungarian vineyards is well documented [13, 14]. We have previously investigated the chemical composition and physical state of chloroplast lipids of triazine R and S biotypes of *C. canadensis* [15]. In field experiments, we found that chlorbromuron was ineffective against the triazine R biotype of *Conyza*. This population was extremely resistant to atrazine and exhibited cross-resistance to some urea herbicides at the chloroplast level [14].

Abbreviations: atrazine, 6-chloro-N-ethyl-N′-(1-methylethyl)-1,3,5-triazine-2,4-diamine; diuron, N′-(3,4-dichlorophenyl)-N,N-dimethylurea; linuron, N′-(3,4-dichlorophenyl)-N-methoxy-N-methylurea; chlorbromuron, 3-(4-bromo-3-chlorophenyl)-1-methoxy-1-methylurea; metobromuron, N′-(4-bromophenyl)-N-methoxy-N-methylurea; Q_A, primary quinone electron acceptor of photosystem II; Q_B, secondary quinone electron acceptor; PS II, photosystem II; F_i and F_m, fluorescence intensities at 40 ms and 1 s, respectively, in fast fluorescence induction measurements; P and T, initial and terminal levels of fluorescence, respectively, in slow fluorescence induction measurements; DCPIP, 2,6-dichlorophenol indophenol; Chl, chlorophyll; R, herbicide-resistant biotype; S, herbicide-susceptible biotype.

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The present study involves a comparative analysis of the photosynthetic capacities and chloroplast ultrastructures of triazine R and S biotypes in the rosette-forming developmental stage of *C. canadensis* exhibiting cross-resistance to some urea herbicides.

Materials and Methods

Plant material

R and S biotypes of *C. canadensis* plants in the rosette stage were collected near Kecskemét in Hungary. The plants were then grown in soil at 25 °C under laboratory conditions with a 16 h light and 8 h dark regime, illuminated with warm-white fluorescent light of 10 Wm^{-2} intensity for an additional two months. Plants were watered daily and received half-strength Hoagland solution once a week. Five-to-six-month-old plants in the rosette stage were used for the experiments.

Hill reaction measurements

The rate of electron transport was estimated by measuring the light-induced oxygen evolution in continuous light in the presence of $K_3[Fe(CN)_6]$. Chloroplasts were isolated from the S and R biotypes as described by Lehoczki *et al.* [13] and were kept in ice in the dark until the experiments were conducted. The ferricyanide-mediated Hill reaction of the isolated chloroplasts was measured with a Clark (YSI) oxygen electrode in 3.1 ml of reaction mixture containing 0.33 N sorbitol, 50 mM tricine, 5 mM $MgCl_2$, 5 mM NH_4Cl and 0.5 mM $K_3[Fe(CN)_6]$, pH 7.6, and chloroplasts equivalent to 40 μg chlorophyll for both the R and S biotypes. White light from a 650 W tungsten lamp was used, filtered through an 8 cm thick water layer, resulting in a light intensity of 150 mW/cm^2 at the surface of the reaction vessel. A series of neutral density filters were used to attain a range of intensities for light response curves.

The photochemical activities of the chloroplasts were studied in the temperature range 10–40 °C. 0.3 ml chloroplasts stored at 0–4 °C in the dark, was added to the reaction mixture, which was pre-equilibrated to the required temperature, and after a further equilibration period of 2 min the chloroplasts were assayed for Hill reaction activity. The temperature of the reaction mixture was determined with a thermocouple; the accuracy was ±0.5 °C. Correction for the temperature-sensitivity of the Clark electrode was made at each temperature.

The chlorophyll concentration was determined spectrophotometrically according to Arnon [16].

CO_2 fixation

The rate of light-induced CO_2 fixation was studied in detached leaves, in an atmosphere containing $^{14}CO_2$ in a glass chamber with a Hg-blockade, according to the method of Láng *et al.* [17]. Leaves were illuminated with different intensities of white light for 2 min. The maximum intensity of illumination was 60 mW/cm^2. Discs 5 mm in diameter were cut out under a slightly increased pressure and were placed in scintillation vials. The radioactivity of the samples was measured by a liquid scintillation technique with a Beckman LS-100 C instrument. The total or gross photosynthesis was calculated by correction for the rate of dark CO_2 uptake. Fifty discs from different plants and leaves were used for each measurement.

Fluorescence induction of intact leaves

The fluorescence induction curves of the intact leaves were recorded with a laboratory-built apparatus [13]. Prior to the measurements, the detached leaves were floted on phosphate buffer (pH 6.5) solution in a light of 10 Wm^{-2}, with different concentrations of unformulated herbicides. The leaves were kept in darkness for at least 2 h before the fluorescence induction measurements.

Electron microscopy

Segments were excised from leaves of the R and S biotypes, cut into 1 mm^2 pieces, fixed with a glutaraldehyde-paraformaldehyde mixture and postfixed with 1% OsO_4 [18].

The tissue pieces were dehydrated by transferring them through a series of graded ethanol solutions and were embedded in araldite. 80 nm thin sections of palisade and spongy parenchyma were cut and treated with lead citrate before examination in a JEOL 100 B electron microscope [18].

Results

CO_2 fixation by leaves

The light responses of the leaves of the S and R biotypes are shown in Fig. 1. The S biotype had only

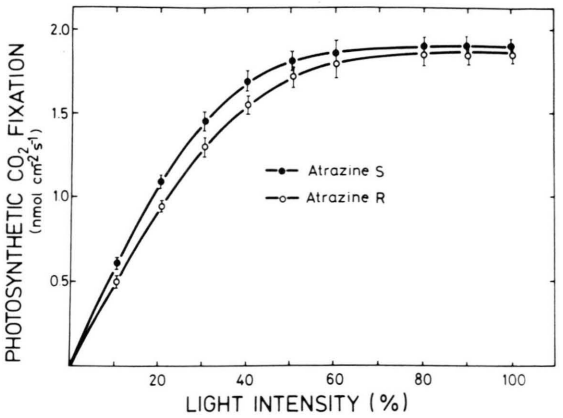


Fig. 1. Mean rates of photosynthetic CO_2 fixation (nmol CO_2 $cm^{-2}s^{-1}$) of intact triazine-resistant (−○−) and, -susceptible (−●−) biotypes of *Conyza canadensis* in relation to light intensity. Each point is an average of measurements from leaves twelve individual plants.

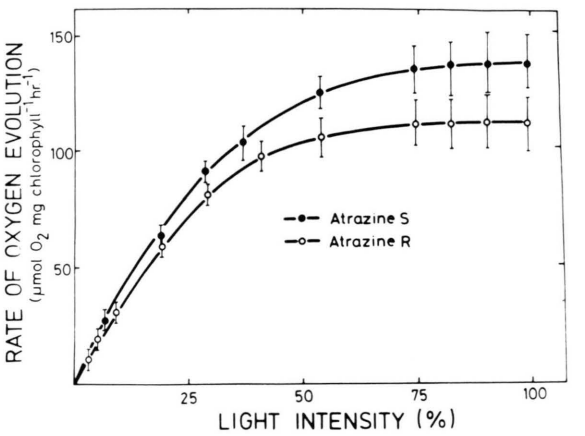


Fig. 2. The rate of O_2 evolution (nmol O_2 $mgchl^{-1}h^{-1}$) as a function of light intensity in *Conyza canadensis* chloroplasts, measured in continuous light. Each point represents an average of five measurements.

a slightly higher photosynthetic rate at all light intensities. The maximum rates of photosynthesis were found to be 1.91 ± 0.05 and 1.86 ± 0.08 nmol CO_2 $cm^{-2}s^{-1}$ for the S and R biotypes, respectively. However, the light intensity-dependences of the rates of CO_2 fixation in intact leaves of the R and S biotypes on a chlorophyll basis were practically the same.

Hill reaction in continuous light

Fig. 2 shows that the rate of the Hill reaction of the R biotype at 25 °C was slightly lower at all levels of irradiance than that of the S biotype. The difference between the two biotypes was not greater than 20% at high light intensities.

The small difference between the biotypes expressed on a chlorophyll basis at identical light levels indicates that reaction centres of PS II are operating more effectively in the R biotype of *C. canadensis* than in the R biotype of *Senecio vulgaris* [19, 20].

Effect of temperature on photosystem II activity

Photosystem II activity as a function of temperature was compared in chloroplasts isolated from the R and S plants. At 25 °C, the activities of the ferricyanide-mediated Hill reaction were 120 ± 30 and 100 ± 20 μmol O_2 (mg Chl)$^{-1}h^{-1}$ for chloroplasts from the S and R biotypes, respectively. Fig. 3 shows the relationship between the temperature and the

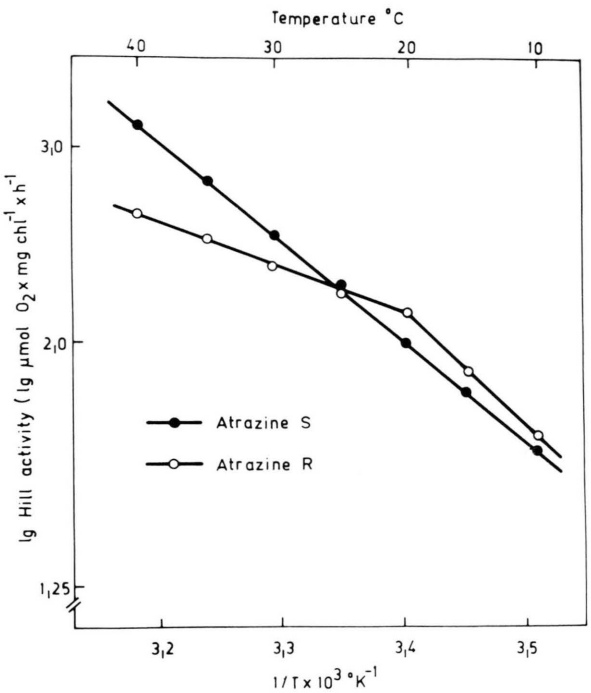


Fig. 3. Arrhenius plot illustrating the temperature dependency of the rate (1 g μmol O_2 $mgchl^{-1}h^{-1}$) of the Hill reaction (ferricyanide reduction at saturating light intensity for atrazine-resistant (−○−) and, -susceptible (−●−) chloroplasts of *Conyza canadensis*.

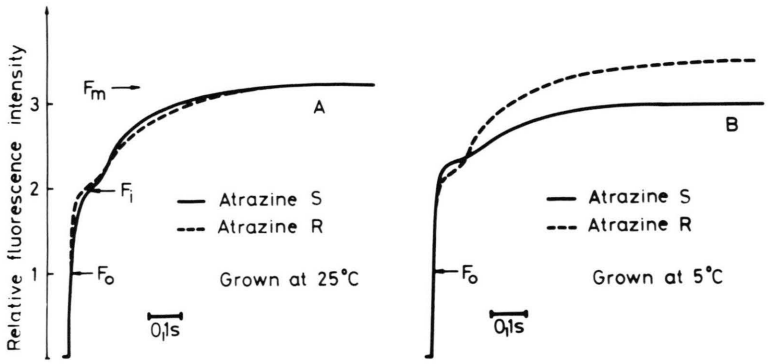


Fig. 4. Fast fluorescence induction curves of atrazine-resistant and, -susceptible *Conyza canadensis* growing at 5 °C and 25 °C temperature. The characteristic points of the curves are indicated.

Hill reaction activity in the temperature range 10–40 °C, in which the Hill reaction is dependent on temperature without any thermal denaturation of the chloroplasts. The slope of the Arrhenius plot when ferricyanide was used as oxidant showed no change in this temperature range und gave an apparent activation energy $E_a = 15.3$ kJ mol^{-1} for the reaction for S chloroplasts. For the R chloroplasts, the discontinuity was found at around 20 °C. E_a was 20.1 kJ mol^{-1} at below 20 °C and it decreased to 8.2 kJ mol^{-1} at higher temperature. Similar results (not presented here) were obtained for the photochemical activities of isolated chloroplasts measured by means of the photoreduction of DCPIP.

Effect of temperature on leaf fluorescence induction properties

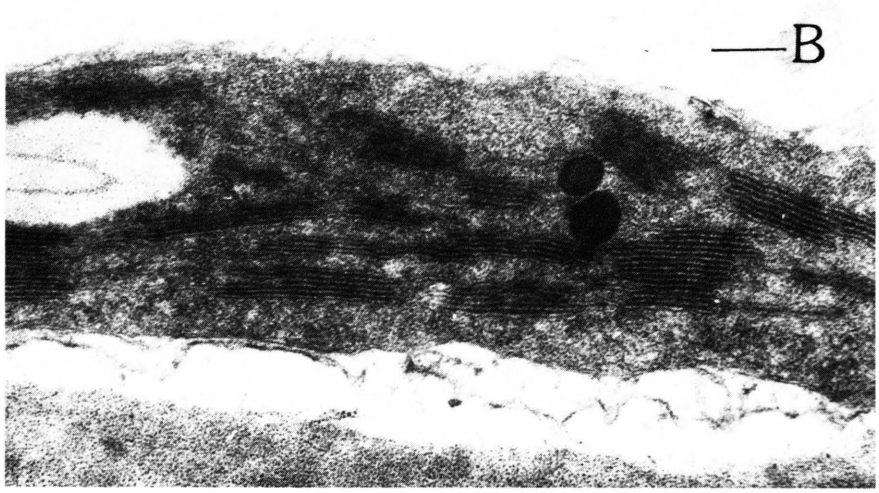
In these experiments, leaf fluorescence induction was measured at room temperature in order to study the effects of cold-adaptation on the electron transport capacity from PS II in plants grown at 5 and 25 °C. The fluorescence transient characteristics kinetics of non-hardened plants (grown at 25 °C) were similar for the R and S biotypes (Fig. 4/a) and the initial rapid rise of the fluorescence to the F_i level was practicaly identical for the two biotypes. The values of the ratio $(F_m - F_i)/F_m$, calculated from the fluorescence induction curves, were 0.352 ± 0.017 and 0.357 ± 0.011 for the R and S biotypes, respectively. The higher F_o and F_i levels and the decrease in the variable fluorescence indicate that the PS II reaction centres and the electron transport from PS II are modified in S plants grown at 5 °C. In contrast, for the R biotype the variable yield fluorescence was practically unchanged (Fig. 4/b).

The low-temperature stress response of the leaves was characterized by the parameter F_R introduced by Hetherington *et al.* [21]. F_R was determined from the tangent to the point of maximum slope of the D-P fluorescence rise, and was found to be 1.8 ± 0.13 and 1.0 ± 0.10 for the R and S biotypes, respectively. These results suggest that at low temperature the R plants have a higher photosynthesis rate than the S ones.

Ultrastructure of chloroplasts in S and R biotypes

Electron micrographs of chloroplasts from the palisade and spongy parenchyma of *C. canadensis* in the rosette stage are shown in Fig. 5 and 6. The ultrastructural characteristics revealed some difference between the S and R biotypes. Chloroplasts from the S biotype contained a greater amount of starch grains, especially in the spongy parenchyma, and exhibited a denser thylakoid network (Fig. 5) than that from the R biotype. Chloroplasts from the R leaves (Fig. 6) lacked starch grains and contained grana stacks with relatively few thylakoids per stack. The relative distribution of the number of thylakoids per stack was determined for both biotypes (Fig. 7). An average of 2–4 thylakoids per grana stack is typical for the R plastids. The chloroplasts from the S biotype had a greater number of thylakoids per grana stack than the chloroplasts from the R biotype (Fig. 6). The occurrence of the 2–4 thylakoids per grana stack is less frequent in the S chloroplasts, especially in the spongy parenchyma, than in the R

Fig. 5. Ultrastructure of chloroplasts from the spongy parenchyma of the triazine-resistant (A) and, -susceptible (B) *Conyza canadensis* leaves. Chloroplasts from the S biotype (B) contained greater amount of starch grains. Bar = 1.0 μm.



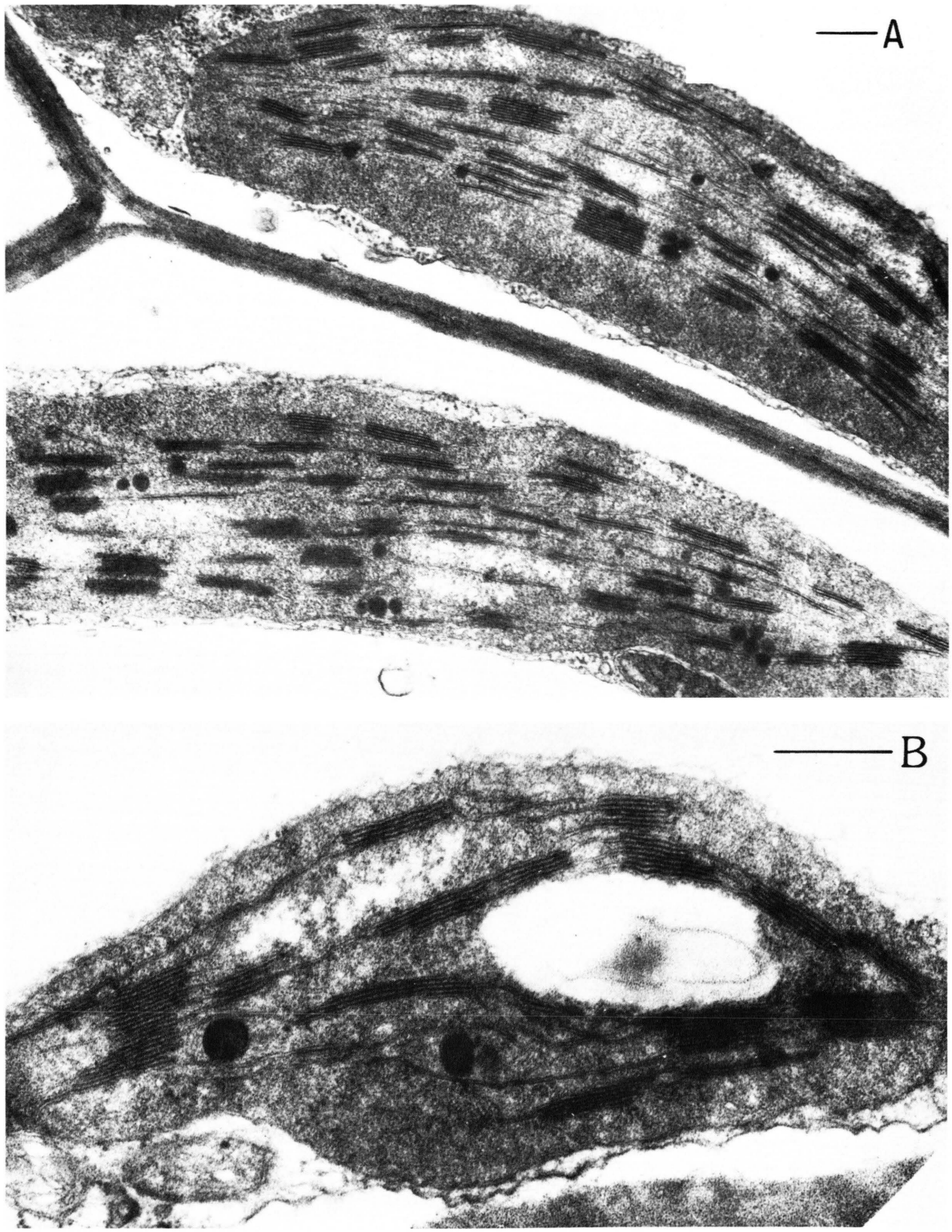


Fig. 6. Ultrastructure of plastids from the palisade parenchyma of the triazine-resistant and, -susceptible *Conyza canadensis* chloroplasts from R leaves (A) lacked starch grains and contained grana stacks with relatively few thylakoids. The chloroplasts of the S biotype (B) exhibited denser thylakoid network than those from the R biotype. Bar = 1.0 μm.

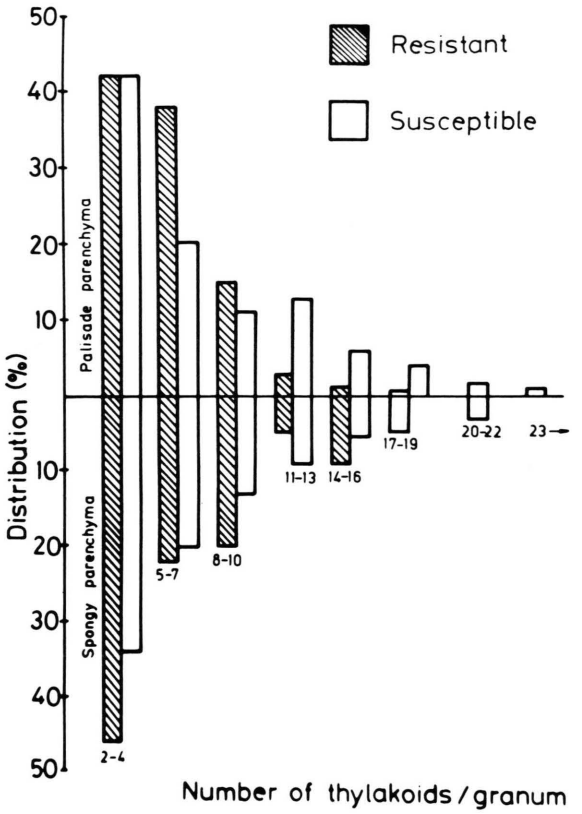


Fig. 7. Distribution of lamellae/granum in atrazine-resistant and, -susceptible chloroplasts originated from palisade and spongy parenchyma of *Conyza canadensis* leaves. Each line on the histogram indicates the distribution of thylakoids in grana stacks of varying size.

biotype. Our results indicate that an appreciable on of the thylakoids is not characteristic in R *C. canadensis* in contrast to other weed species, as described previously for R biotypes of *Brassica campestris* [22], *Chenopodium album* and *Amaranthus retroflexus* [12] and for atrazine-adapted plants [11, 23–25]. The average diameter of the grana was 400 ± 15 μm in the R chloroplasts, and 350 ± 10 μm in the S ones. In herbicide-adapted plants and in plants grown at low light intensities, the larger grana stacks are typical [24]. We concluded, therefore, that the ultrastructure of the chloroplasts in the R biotype of *C. canadensis* in the rosette stage of development is not reminiscent either of that of other R plants or of those of plants grown under low light conditions, or of those of herbicide-adapted plants [23–25].

Cross-resistance to urea herbicides in intact leaves of triazine R C. canadensis

We earlier determined the resistance factors of *C. canadensis* at the chloroplast level to atrazine and some urea herbicides by measuring the ferricyanide-mediated Hill reaction [13, 14].

Cross-resistance to some urea herbicides has been observed in the triazine R chloroplasts in the early flowering state of development [14]. In the present study we have characterized the photosynthetic capacities of the R and S plants in the presence of urea herbicides by fluorescence induction measurements on intact leaves. These investigations revealed that chlorbromuron, metobromuron and linuron were equally effective in inhibiting reoxidation of Q^- in S leaves whereas in R leaves only diuron caused inhibition (Fig. 8). It has been demonstrated that

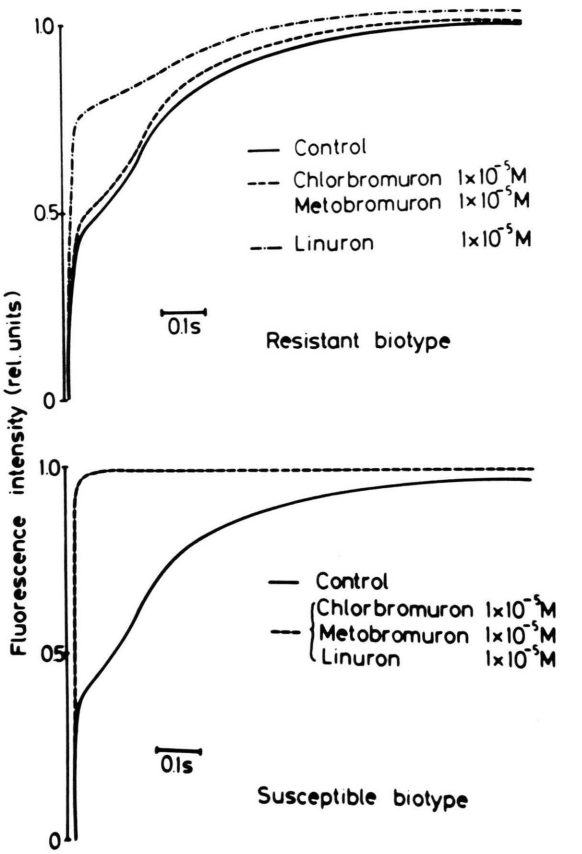


Fig. 8. Chlorophyll fluorescence induction of excised triazine and urea cross-resistant *Conyza canadensis* leaves infiltrated with chlorbromuron, metobromuron and linuron.

1.10^{-4} M atrazine caused no inhibition of photosynthetic electron transport in R leaves of *C. canadensis* [13]. Linuron inhibited the electron transport, particularly in the leaves of the R biotype, as revealed by fluorescence induction measurements. We examined the electron transport in the presence of herbicides by measuring the slow fluorescence induction recorded in the time range of 3 min (Fig. 9). The control leaves exhibited quenching of the fluorescence from the initial P to a steady-state T level. The R leaves treated with chlorbromuron or with metobromuron displayed similar extents of fluorescence quenching, while the linuron-treated leaves reached a higher steady-state level than R leaves treated with chlorbromuron or metobromuron. We suggest, therefore, that there are intermediate biotypes for linuron-resistance in *C. canadensis*, characterized by their fluorescence induction curve, as described previously for *Chenopodium album* [26–28] and *Poa annua* [26, 29].

These observations indicate that *C. canadensis* that is extremely resistant to triazine (the resistance factor is about 1000 for atrazine) display resistance to chlorbromuron and metobromuron and exhibits tolerance to linuron at the whole plant level.

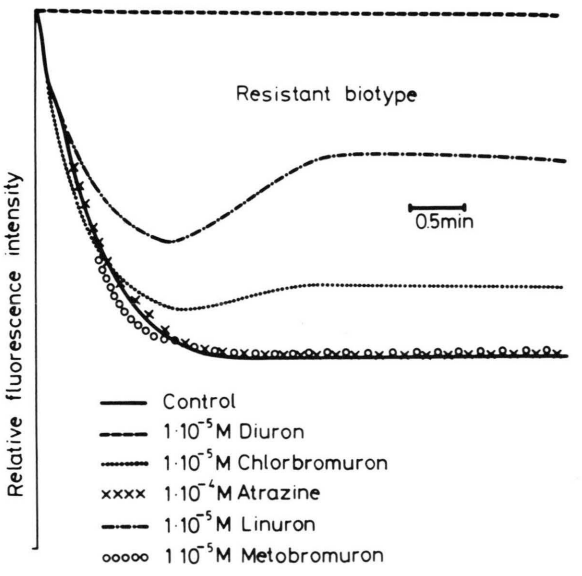


Fig. 9. Slow fluorescence curves of herbicide-resistant *Conyza canadensis* leaves infiltrated with diuron, chlorbromuron, metobromuron, linuron and atrazine.

Discussion

It is generally accepted that a reduction of the photosynthetic efficiency in the chloroplasts of triazine R weeds results in a lowered electron transport efficiency from PS II to PS I in the R biotype, was compared to the S biotype [5, 19, 20, 30–33].

Our studies with triazine R and S biotypes of *C. canadensis* had the aim of characterizing the structural, physiological and biochemical characteristics of the R and S biotypes. Our earlier results [13] and those presented in this paper indicate that the photosynthetic efficiency of R plants of *C. canadensis* does not differ from that of the S plants. The evidence was as follows: The fast fluorescence induction transients of the R and S leaves exhibited only a slight difference in the rapid rise of the initial fluorescence, indicating that the rates of Q_A-reoxidation, the rates of transfer of electrons from Q_A to Q_B, do not differ greatly in the two biotypes. It also indicates that the R biotype of *C. canadensis* has a normal photosynthetic potential. In contrast to some literature data [2, 19, 22] there was no difference in the rates of photosynthetic CO_2 fixation in intact leaves of the R and S biotypes of *C. canadensis*.

Ort *et al.* [34] suggested that the lower rate of light-induced CO_2 fixation in the R biotype is not a direct consequence of the reduced electron transport from Q_A to Q_B, since this step is not the rate-limiting one in the overall electron transport chain. On the other hand, van Oorschot and van Leeuven [35] found no difference in photosynthetic activity between the R and S biotypes of *Polygonum lapathifolium, Poa annua, Solanum nigrum, Chenopodium album* and *Stellaria media*.

Holt and Goffner [36] reported that the PS II activity differences between the R and S biotypes, as concerns the structure and function of the leaves, are probably due to a complex developmental adaptation, which may be only indirectly related to the modified PS II activity in the R plants. Our results suggest that the development of triazine-resistance is not necessarily accompanied by a reduction of photosynthesis in the rosette stage of *C. canadensis*.

In contrast to earlier results [11, 12, 22], the ultrastructure of the chloroplasts from the R biotype is not modified appreciably; this is probably a consequence of the normal photosynthetic efficiency of the R plants. "Shade-type" chloroplasts were not observed.

The rate of the Hill reaction of the R biotype at 25 °C was only slightly (15–20%) lower at all light levels than that of the S biotype. However, at below 20 °C the R chloroplasts display a higher rate of the Hill reaction than those from the S biotype. Similarly, a difference in temperature optimum was found between the R and S chloroplasts of *Chenopodium album* and of *Brassica campestris* [37]. The 15–20% lower Hill reaction activity of the R thylakoids at 25 °C is probably due to the greater heat-sensitivity of the PS II electron transfer [37]. In support of this conclusion, it is worth mentioning that the R biotype of *C. canadensis* has a better adaptive ability that the S biotype at low temperatures, as revealed by the fluorescence induction measurements. These results indicate that the R plants could be photosynthetically more competent than the S ones at low temperatures.

Numerous studies have compared chilling-resistant and chilling-sensitive plant species and demonstrated that chilling-resistant plants contain more unsaturated fatty acids [38–40]. It was also shown that the R chloroplast lipids contain a higher proportion of unsaturated fatty acids, and the lipid matrix of the thylakoid membranes of the R biotype is more fluid than that of the S biotype. In the liposomes from the S chloroplast lipids, the temperature at which phase separation occurred was around 27 °C, this appearing as a discontinuity in the Arrhenius plot.

In liposomes prepared from polar lipids of the R chloroplasts, the thermotropic phase transition occurred in the temperature range 15–22.5 °C. In consequence, the R thylakoid are less rigid at low temperature, and the higher fluidity of the thylakoids from the R biotype probably causes the greater heat-sensitivity of the PS II function. Darmency and Gasquez [41] reported that the triazine R biotype of *Polygonum lapathifolium* displayed the characteristics of chilling-resistant plants and they pointed out that the consequences of this finding were of importance from ecological and epidemiological points of view.

The cross-resistance to urea herbicides in a triazine R population of *C. canadensis* has been observed in field experiments [14]. Little information is available at present on cross-resistance to herbicide other than triazines [2, 3]. However, evidence is accumulating for varying patterns of cross-resistance in triazine R weeds and especially in different mutant algae [42–46]. Oettmeier *et al.* [46] found cross-resistance to various uracil and urea herbicides in chloroplasts isolated from a triazine R biotype of *Amaranthus retroflexus;* the resistance factors to linuron, bromacil and metribuzin were greater than to the atrazine. An increased tolerance to monolinuron and methabenzthiazuron was reported for atrazine R biotypes of *Brassica campestris* and *Chenopodium album* [47]. The triazine R biotypes of *Phalaris paradoxa* and *Alopecurus myosuroides* exhibited resistance to methabenzthiazuron [48]. The atrazine R biotypes of *Amaranthus hybridus, Chenopodium album, Senecio vulgaris* and *Brassica napus* showed similar patterns of cross-resistance to triazine, triazinone, pyridazinone, uracil and quinazoline herbicides [49]. Resistance to chloroxuron was observed in atrazine-resistant *Chenopodium album* [50]. The triazine R biotype of *C. canadensis* exhibited resistance at the chloroplast [14] and whole plant levels to chlorbromuron and metobromuron, and tolerance to linuron, whereas the R and S biotypes were equally sensitive to diuron.

These results, combined with those on algal mutants, strongly suggest that the herbicide-binding site has a considerable structural and functional flexibility. It has been proposed that three different amino acid residues in the 32 kDa thylakoid membrane protein can be altered independently to produce three different patterns of resistance to s-triazine and urea-type herbicides [10, 44, 51]. Under selective conditions, a single mutation spreads by intermolecular recombination or by gene conversion [51].

It is clear that herbicide-resistance occurs when an alteration in the thylakoid membrane reduces herbicide binding. However, it is not clear whether the binding efficiency of triazines to thylakoid membranes is determined solely by the primery structure of the herbicide-binding protein or by a complex structure consisting of several proteins in the PS II complex, and it is not known either what the role of the lipid microenvironment in the function of herbicide binding is. The discrepancies between studies reporting cross-resistance patterns are probably due to alterations in the chloroplast lipid composition and to an allosteric effect at the herbicide binding site. Thylakoid membranes from the triazine R biotype of *C. canadensis* differ from those from the S biotype not only in herbicide binding, but also in lipid composition [11, 13, 15, 22, 52–56]. From the various results, we earlier reached the conclusion that the lipid matrix is possibly involved in the function of herbicide binding, and we put forward the

hypothesis that the resistance to atrazine may result from an alteration in the herbicide-binding protein itself and in the lipid microenvironment of the Q_B protein. As shown in this work, some of the secondary pleiotropic effects generally accompanying the triazine-resistance of weeds were not observed for the triazine R biotype of *C. canadensis*. From these results it is concluded that the alterations in the lipid and fatty acid compositions of the thylakoid membranes of the R biotype, which occur in order to maintain a normal photosynthetic function and membrane fluidity at different growth temperatures, are of relevance to the problem of herbicide-resistance.

Acknowledgements

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