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Differential Light Responses of Photosynthesis by Triazine-resistant and Triazine-susceptible *Senecio vulgaris* Biotypes[1]

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JODIE SIMS HOLT, ALAN J. STEMLER, AND STEVEN R. RADOSEVICH
Department of Botany, University of California, Davis, California 95616

ABSTRACT

Studies were conducted to determine a physiological basis for competitive differences between *Senecio vulgaris* L. biotypes which are either resistant or susceptible to triazine herbicides. Net carbon fixation of intact leaves of mature plants was higher at all light intensities in the susceptible biotype than in the resistant biotype. Quantum yields measured under identical conditions for each biotype were 20% lower in the resistant than in the susceptible biotype. Oxygen evolution in continuous light measured in stroma-free chloroplasts was also higher at all light intensities in the susceptible biotype than in the resistant biotype. Oxygen evolution in response to flashing light was measured in stroma-free chloroplasts of both biotypes. The steady-state yield per flash of resistant chloroplasts was less than 20% that of susceptible chloroplasts. Susceptible chloroplasts displayed oscillations in oxygen yield per flash typically observed in normal chloroplasts, whereas the pattern of oscillations in resistant chloroplasts was noticeably damped. It is suggested that modification of the herbicide binding site which confers *s*-triazine resistance may also affect the oxidizing side of photosystem II, making photochemical electron transport much less efficient. This alteration has resulted in a lowered capacity for net carbon fixation and lower quantum yields in whole plants of the resistant type.

Senecio vulgaris L. populations resistant to *s*-triazine herbicides were first reported by Ryan (23) and later by Radosevich and Appleby (18). Since then, extensive studies on the mechanism of resistance indicate that differential uptake, translocation, or metabolism of atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-*s*-triazine] or simazine [2-chloro-4,6-bis(ethylamino)-*s*-triazine] are not responsible for differences in herbicide sensitivity between resistant and susceptible biotypes of *S. vulgaris* (19, 20). Further studies with other weed species which have developed resistance to triazine herbicides have confirmed these findings (8, 17).

Atrazine and other triazine herbicides are known to inhibit photochemical electron transport and O_2 evolution (PSII) in chloroplasts (2). Binding of triazines to a high-affinity site on the chloroplast thylakoid membranes is related to inhibition of electron transport (26). The specific binding site is thought to be a protein associated with the electron carriers of PSII which are blocked by the inhibitors (26). In binding studies with uniformly ring-labeled [^{14}C]atrazine, susceptible chloroplasts showed strong [^{14}C]atrazine binding, whereas no specific [^{14}C]atrazine binding was found in resistant chloroplasts (15). Studies with isolated chloroplasts and stroma-free thylakoid membranes of both susceptible and resistant weed biotypes indicate that triazine resistance occurs because of a chloroplast membrane alteration at the level of the PSII complex (1, 21).

A protein modification at the herbicide binding site on the thylakoid membrane is believed to account for the loss of atrazine binding and, therefore, lack of inhibition of electron transport in the resistant biotype (15, 21). Little is known about the effects of such a modification of the atrazine binding site on photosynthesis in the resistant biotype in the absence of herbicide.

The susceptible biotype of *S. vulgaris* was more vigorous and produced more seed than the resistant biotype in noncompetitive situations. It was also more competitive than the resistant biotype when various ratios of each biotype were grown together under constant density (3). Furthermore, few resistant *S. vulgaris* plants are found in natural populations unless repeated applications of atrazine or simazine were made in successive years (6, 23). The study reported here was conducted to determine a physiological basis, in the absence of herbicide, for the competitive advantage of the susceptible biotype over the resistant biotype of *S. vulgaris*. Photosynthesis of both *S. vulgaris* biotypes in terms of whole plant carbon dioxide fixation, whole plant quantum yields, and O_2 evolution from isolated chloroplasts in continuous and in flashing light was compared.

MATERIALS AND METHODS

Plant Material. Seeds of both susceptible and resistant biotypes of *S. vulgaris* L. were germinated in soil in peat pots on heating trays. At the cotyledon stage (approximately 10 days from sowing), seedlings were transplanted into 10-cm pots. Plants were grown in a temperature-controlled greenhouse with natural lighting, supplemented in winter by a bank of six Westinghouse warm-white fluorescent lights to give a photoperiod of 13 h. Light intensity ranged from 25 nE cm^{-2} s^{-1} to a maximum of 120 nE cm^{-2} s^{-1} during the 13-h photoperiod. Mean daily maximum and minimum temperatures of 29 and 18 C, respectively, were recorded during the time in which the study was conducted. Plants were watered daily with half-strength Hoagland solution.

Gas Exchange. Plants used for gas exchange measurements were 30 to 60 days old from the time of seed sowing. Plants were well-watered in the morning before experiments were begun. An open-system gas exchange apparatus, described in detail by DeJong (4), was used for measurements of light dependence curves. The assimilation chamber was a 770-cm^3 water-cooled circular brass box in which a fan was installed to ensure rapid mixing and maximum boundary layer conductances. A young, fully expanded, attached leaf was inserted into the leaf chamber. Light was supplied by a 1,500-w mercury vapor metal arc lamp. Response of net photosynthesis to light flux was measured by exposing the leaf initially to maximum irradiance (approximately 200 nE cm^{-2} s^{-1}). A series of wire-mesh screens was used to lower incident flux density in 10 or more steps to complete darkness. Vapor pressure deficits of 5 to 10 mbar, leaf chamber temperatures of 25 C, and ambient CO_2 concentrations of 330 to 360 μl/l were held constant during measurement. Calculations of rates of photosynthesis were

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made from CO_2 flux measurements as described by Jarvis (7). Light response curves were obtained from five individual plants of each biotype.

Photosynthetic rates at low light intensities for quantum yield determination were measured on attached single leaves with an open system gas exchange apparatus described in Robichaux and Pearcy (22). The gas analyzer used for our experiments was a Horiba Instruments IR CO_2 analyzer (model VIA-500R), and light for both photosynthetic and absorptance measurement was provided by a 2.5-kw short arc xenon lamp (Christie Electric Corp.). Light absorptance values (400–700 nm) were determined for the same leaves used in photosynthetic measurements using an integrating sphere (16) and a quantum sensor (Lambda Corp. LI-190S). Conditions and procedures were the same as those used to measure light dependence of photosynthesis, except that incident light intensities ranged from 30 to 0 nE cm^{-2} s^{-1}. Curves were replicated four times for each biotype. These data were pooled and a linear regression was performed to fit a response line to the data. Quantum yield values (slope of line) from the pooled regressions were compared using a two-tailed F-test.

O_2 Evolution in Continuous Light. Chloroplasts were isolated from susceptible or resistant biotypes of 5-week old *S. vulgaris* as described by Stemler (24). Extracts were kept on ice in the dark while experiments were conducted.

Measurements of O_2 evolution in continuous light were made using the Clark-type electrode apparatus described by Stemler (24). Photon flux density was measured with a quantum sensor (Lambda Corp. LI-190S), and neutral density filters were used to attain a range of intensities from 350 to 0 nE cm^{-2} s^{-1} for the light response curve. The sample holder contained 4 ml reaction mixture [10 mM NaH_2PO_4 buffer (pH 6.8), 10 mM NaCl, 5 mM $MgCl_2$, 100 mM sorbitol, 0.5 mM $K_3Fe(CN)_6$, 10 mM methylamine), and 40 μg Chl/ml for both the resistant and the susceptible biotypes. Samples were initially anaerobic. Light response curves were replicated four times for each biotype.

O_2 Evolution in Flashing Light. Broken chloroplasts from both *S. vulgaris* biotypes were extracted as described by Stemler (24). Either fresh or frozen and thawed grana were used; similar results were obtained with either preparation.

The apparatus used for measuring O_2 evolution in response to brief light flashes was similar to that described by Joliot and Joliot (9). The polarizing and monitoring circuit was constructed from a diagram kindly supplied by Dr. Paul Jursinic (12). Signals were recorded on a Hewlett Packard oscillographic recorder (model 74024). Flash illumination was from a Xenon lamp (General Radio Stroboslave type 15 39-A). The light was focused with a large condensing lens. The triggering circuit for the flash lamp was built here. The lamp gave saturating flashes; inserting a Balzers 80% neutral density filter between the lamp and the sample caused no change in the oscillatory pattern or in the steady-state flash yield of O_2.

O_2 evolution was measured by first allowing a thin layer of chloroplast extract placed on the electrode to equilibrate in the dark at 25 C for 10 min. O_2 yield was measured in response to 3-μs light flashes at 1-s intervals. For comparison between biotypes, yields were normalized to an average steady-state yield of O_2 (after 25 flashes) for each biotype. The reaction mixture contained 100 mM sodium phosphate buffer (pH 7.0), 100 mM NaCl, and either 0.285 mg Chl/ml for the resistant biotype or 0.103 mg Chl/ml for the susceptible biotype. Experiments were replicated, using a new sample, six times for each biotype.

RESULTS

Gas Exchange. Light responses of whole plant photosynthesis of the susceptible and resistant biotypes of *S. vulgaris* are shown in Figure 1. The susceptible biotype had higher photosynthetic rates than did the resistant biotype at all light intensities. The

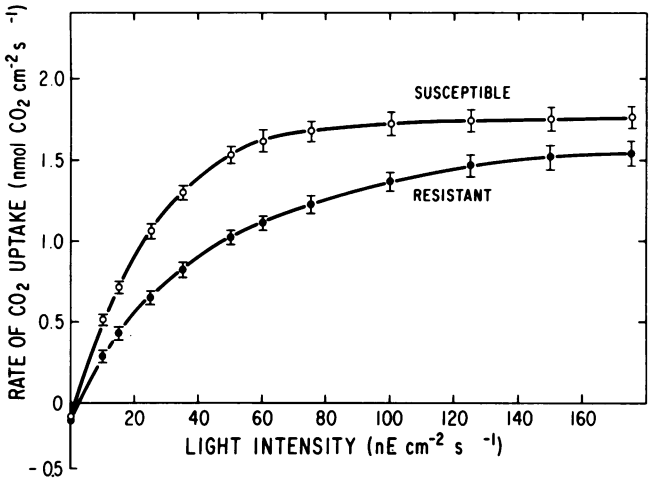

FIG. 1. The light response of photosynthesis of atrazine-susceptible and -resistant biotypes of *S. vulgaris* L. in the absence of herbicide. Each point is an average of measurements from five individual plants. Each vertical bar depicts 1 SE above and 1 SE below the mean.

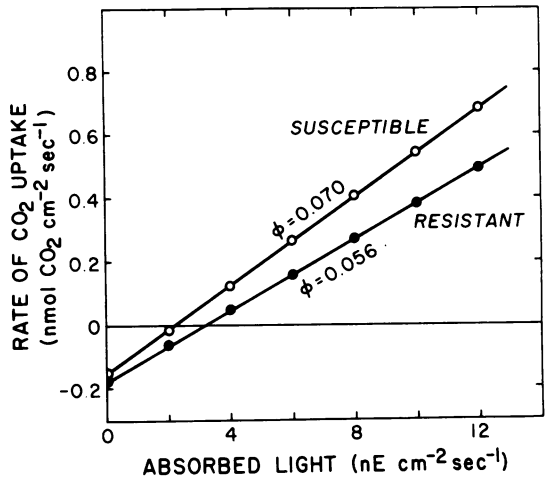

FIG. 2. The rate of CO_2 uptake *versus* absorbed quantum flux (incident quantum flux × leaf absorptance) in susceptible and resistant biotypes of *S. vulgaris* L. Quantum yield (ϕ) = slope of curve. Standard errors about the regression points were ≤0.03 (susceptible) and ≤0.07 (resistant). Curves were generated from a pooled linear regression for each biotype. Differences in quantum yields between biotypes were highly significant ($P < 0.01$).

maximum rates of photosynthesis measured were 1.77 nmol CO_2 cm^{-2} s^{-1} for the susceptible biotype and 1.54 nmol CO_2 cm^{-2} s^{-1} for the resistant biotype. Differences in net carbon fixation between the two biotypes were most pronounced at light intensities below 75 nE cm^{-2} s^{-1}. The half-saturation light intensity for the susceptible biotype was 20 nE cm^{-2} s^{-1}, whereas resistant plants had a more gradual response and reached half-saturation at 32 nE cm^{-2} s^{-1}. At similar conditions of illumination, water supply, temperature, CO_2 concentration, and leaf development, the photosynthetic capacity of susceptible plants was markedly higher than that of resistant plants.

In Figure 2, the photosynthetic responses of both biotypes to low light intensities are shown. From these slopes as well as the initial portion of Figure 1, it is apparent that the quantum yield of the susceptible biotype is higher than that of the resistant. Average values were 0.070 mol CO_2/mol absorbed photons for the susceptible biotype and 0.056 mol CO_2/mol absorbed photons for the resistant biotype, a difference of 20%. Light absorptance values averaged 83.2 ± 0.7% and 83.7 ± 0.6% for the susceptible

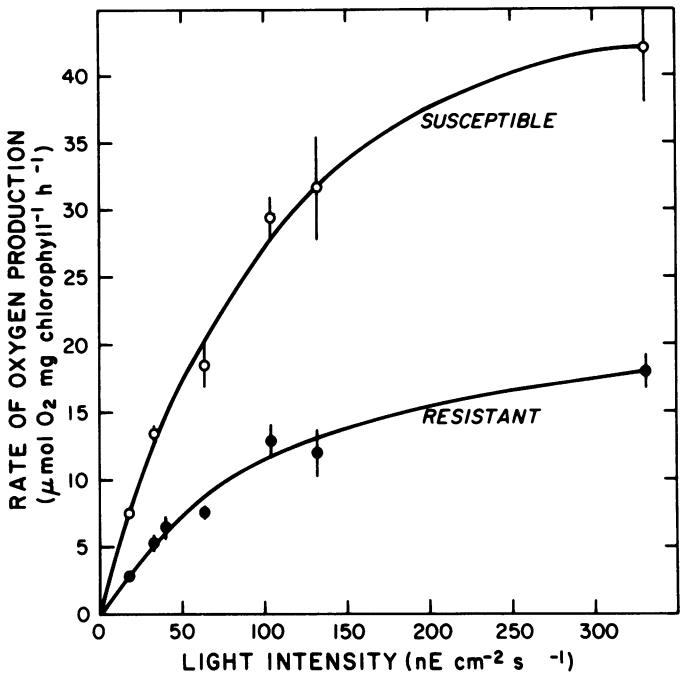

FIG. 3. The rate of O_2 evolution as a function of light intensity in *S. vulgaris* L. chloroplasts, measured in continuous light. Reduced light intensities were attained with neutral density filters. The reaction mixture contained 10 mM NaH_2PO_4 buffer (pH 6.8), 10 mM NaCl, 5 mM $MgCl_2$, 100 mM sorbitol, 0.5 mM $K_3Fe(CN)_6$, 10 mM methylamine, and 40 μg Chl/ml for both the resistant and the susceptible biotypes. Initially, the samples were anaerobic. Each point represents an average of four measurements. Each vertical bar depicts 1 SE above and 1 SE below the mean.

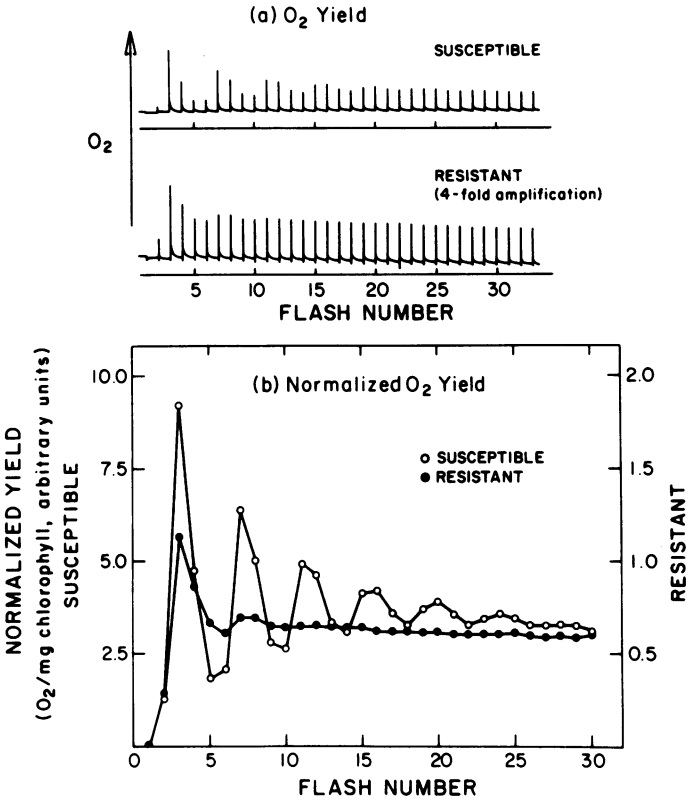

FIG. 4. O_2 evolution in flashing light after 10 min dark equilibration at 25 C, measured in chloroplasts of *S. vulgaris* biotypes. a, representative recorder traces for O_2 evolution yield sequences in the presence of saturating 3-μs flashes at 1-s intervals. b, O_2 yield sequences normalized to an average steady-state yield of O_2 for each biotype as a function of flash number, derived from a. The reaction mixture contained 100 mM sodium phosphate buffer (pH 7.0), 100 mM NaCl, and either 0.285 mg Chl/ml for the resistant biotype or 0.103 mg Chl/ml for the susceptible biotype. Values in b were corrected for differences in Chl concentration and recorder sensitivity settings between biotypes in a. The experiments were replicated six times; however, error bars for standard errors are smaller than the plotted points.

and resistant biotypes, respectively. Therefore, the differences in photosynthesis between biotypes were not due to differential leaf absorptance, but to differences in the photosynthetic apparatus itself. These values for quantum yields are consistent with published values for young leaves of other C_3 species which were grown under high light intensity in a greenhouse (14).

O_2 Evolution in Continuous Light. O_2 evolution by isolated chloroplasts as a function of light intensity, measured in continuous light, is shown in Figure 3. The susceptible biotype had higher rates of O_2 production than the resistant biotype at all light intensities. The difference between biotypes was greater than 2-fold at all light intensities; however, the difference was greatest at low light (18 nE cm^{-2} s^{-1}) and decreased with increasing light. The difference between biotypes at identical light levels and greater difference at low light indicate that fewer reaction centers are operating in the resistant biotype than in the susceptible biotype.

O_2 Evolution in Flashing Light. A model of O_2 evolution in PSII for normal systems was presented in detail by Kok *et al.* (13) and Joliot and Kok (10). The model depicts four photoreactions which induce four increasingly oxidized states of a light-trapping center ($S_{0\to 4}$). Each photoreaction corresponds to the addition of one positive charge to the O_2-evolving mechanism and the transfer of 1 electron to intersystem intermediates, with all components cooperating to produce 1 O_2 molecule:

$$S_0 \xrightarrow{h\nu} S_0' \xrightarrow{\text{dark}} S_1 \xrightarrow{h\nu} S_1' \xrightarrow{\text{dark}} S_2 \xrightarrow{h\nu} S_2' \xrightarrow{\text{dark}} S_3 \xrightarrow{h\nu} S_3' \xrightarrow{\text{dark}} S_4$$

$$3S_4 \xrightarrow{\text{dark}} S_0$$

$$2H_2O \longrightarrow O_2 + 4H^+ + 4e^-$$

Dark reactions (turnovers) ($S_n' \xrightarrow{\text{dark}} S_{n+1}$) convert nonphotoactive states to photoactive states and are accompanied by the reoxidation of the photochemical electron acceptor ($Q^- \to Q$).[2] In the $S_4 \to S_0$ process, 1 oxygen molecule is liberated.

In accord with this model, oscillations in the O_2 yield sequence of chloroplasts in response to flashing light, after a period of dark adaptation, follow a characteristic 4-step cycle which was clearly displayed by the susceptible biotype of *S. vulgaris* (Fig. 4a). The resistant biotype showed a damping of the sequence of oscillations in O_2 yield. In Figure 4b, O_2 yield was plotted as a function of flash number. Values for O_2 yield from Figure 4a were normalized to the average total steady-state yield of O_2 for each biotype. The two different ordinates in Figure 4b (0 to 10 for susceptible, 0 to 2 for resistant, arbitrary units) indicate that the total O_2 yield per mg Chl and the steady-state yield for resistant chloroplasts induced by 1-s-interval light flashes was less than 20% that of susceptible chloroplasts. Apparently, under a flash regime, as in low levels of continuous light, fewer reaction centers are evolving O_2 in resistant chloroplasts than in susceptible chloroplasts of *S. vulgaris*.

Parameters of charge accumulation in O_2 evolution occurring after a dark period are presented for each biotype in Table I. α represents the percentage of the light traps not converted by a flash ("misses"), and γ represents the percentage of the traps

[2] Abbreviations: Q amd Q^-; oxidized and reduced states, respectively, of the primary electron acceptor of PSII (Quencher).

Table I. *Kinetics of Charge Accumulation in Photosynthetic O_2 Evolution of Biotypes of S. vulgaris L.*

Values for transition probabilities were calculated from non-normalized O_2 yields in response to 3-μs flashes of saturating light at 1-s intervals, after 10 min dark equilibration at 25 C. The experiments were replicated six times. Standard deviations are presented.

Parameter	Biotype	
	Susceptible	Resistant
α (misses)	0.10 ± 0.004	0.23 ± 0.011
β (single hits)	0.86 ± 0.005	0.66 ± 0.012
γ (double hits)	0.03 ± 0.005	0.09 ± 0.005
$S_0^{(0)}$ [a]	0.24 ± 0.016	0.27 ± 0.005
$S_1^{(0)}$	0.76 ± 0.016	0.73 ± 0.005

[a] $S_0^{(0)}$ and $S_1^{(0)}$ represent fractions of the reaction centers in the S_0 and S_1 states, respectively, after 10 min dark equilibration at 25 C.

which are photochemically converted more than once during a flash ("double hits"). Both of these events are assumed to occur randomly in all reaction centers. β represents the percentage of single complete photoconversions per flash ("single hits"), and equals $1 - \alpha - \gamma$. $S_0^{(0)}$ and $S_1^{(0)}$ represent the percentages of the O_2-evolving complexes found in each of these states after 10 min dark adaptation. These values were obtained from calculations based on yields of flash numbers 1 through 9 (Fig. 4a) using the matrix multiplication technique described by Thibault (25) (see also ref. 11).

As we expected from the "typical" sequence of oscillations in flash yield (Fig. 4a), the susceptible chloroplasts exhibited the O_2 yields of a normal system as described by Forbush *et al.* (5). Their reported 10% misses and 5% double hits for spinach chloroplasts are similar to an α value of 10.0% and a γ value of 3.5% for susceptible *S. vulgaris* chloroplasts. Resistant chloroplasts responded differently than those of the susceptible biotype to the same type of flashing light. Resistant chloroplasts had an α value of 23.5% and a γ value of 9.9%. Corresponding percentages of single hits (β) are 86.5% for the susceptible and 66.6% for the resistant chloroplasts. Under the flash regime, the reduced number of reaction centers which continue to operate in the resistant chloroplasts do so in an abnormal fashion.

Preillumination experiments (5) indicate that the most likely distribution of the *S*-states in the dark is an equilibrium at 25% $[S_0]$/75%$[S_1]$. Both susceptible and resistant *S. vulgaris* biotypes have a $[S_0]/[S_1]$ ratio after dark adaptation close to 25:75% (Table I). Because of the similar dark *S* distribution of the two biotypes, the large miss and double hit values of the resistant biotype may help account for the rapid damping to steady-state O_2 yield after only nine flashes.

DISCUSSION

Comparison of the O_2 yields in broken chloroplasts from the two biotypes reveals consistently higher yields in susceptible than in resistant chloroplasts. There is a greater than 2-fold difference in yield between biotypes in continuous light and a 5-fold difference in flashing light. This indicates that the resistant biotype, with fewer reaction centers operating at any given time, is less photoefficient, compared to the susceptible biotype.

The larger percentage of misses occurring in resistant chloroplast reaction centers (23.5%) than in susceptible chloroplasts (10.0%) can account for a portion of the difference in O_2 flash yields between the two biotypes. However, this doubling of the miss percentage is not enough to account for the 5-fold decrease in the number of reaction centers working in resistant chloroplasts under a flashing light regime. The reasons for the occurrence of misses and double hits in the O_2-evolving centers of chloroplasts are not well understood.

An alteration occurring on the reducing side of PSII may be partially responsible for the large O_2 yield difference between susceptible and resistant *S. vulgaris* chloroplasts. The resistance phenomenon is thought to be due to a genetic alteration of the inhibitor binding site, which affects the transfer rate of Q^- to the secondary electron acceptor of PSII. Pfister and Arntzen (15) reported Chl fluorescence data indicating the presence of a higher concentration of reduced Q (Q^-) in dark-adapted chloroplasts of resistant weed biotypes compared to susceptible weed biotypes. The larger amount of reduced Q present in resistant chloroplasts before a light flash could limit the number of charge separations and result in a miss inasmuch as the reaction center Chl (P680) and the acceptor Q both must be in the proper oxidation state for an electron to be transferred.

Using Chl fluorescence induction transients, Pfister and Arntzen (15) demonstrated a slower rate of Q^- reoxidation following a saturating light flash in resistant chloroplasts than in susceptible chloroplasts. The half-time for fluorescence decay, (Q^- reoxidation), was 300 to 700 μs in susceptible chloroplasts of *Ambrosia artemisiifolia* and *Chenopodium album* and ≥10-fold longer (≥3 to 7 ms) in resistant chloroplasts of these species, with a portion of Q^- in resistant chloroplasts remaining in the reduced state for many seconds (15). An alteration of the rate constant for Q^- reoxidation in resistant chloroplasts can account for some of the observed decrease in O_2 yield per flash. However, the 3- to 7-ms half-time for Q^- reoxidation is much shorter than the 1-s spacing of flashes used in our experiments, during which time much of the Q^- should become oxidized. To explain the reduction in O_2 yield in resistant chloroplasts to only 20% of the yield in susceptible ones, 80% of Q^- in resistant chloroplasts would have to remain reduced 1 s after a flash is given. Although the resistant chloroplasts display a monophasic fluorescence decay lasting several seconds, it is not certain that all of the damping of flash yield in resistant chloroplasts can be explained by a reduction in the rate of Q^- reoxidation. Other factors may also be partially responsible for the great differences in O_2 yield per flash and in efficiency of electron transfers (α and γ) between susceptible and resistant *S. vulgaris* biotypes.

The data presented here suggest that the thylakoid membrane alteration which confers resistance may have resulted in a modification, not only on the reducing side of PSII, but perhaps also on the O_2-evolving side. This suggested modification could result in greatly altered electron transfer capability in resistant chloroplasts (shown by the increased percentages of misses and double hits), a greatly altered pattern of oscillations in O_2 yield, and a much lower steady-state O_2 yield under a flashing light regime. However, until further studies are done, a proposed modification of the O_2-evolving apparatus itself must remain tentative.

Gas exchange measured on intact leaves of *S. vulgaris* biotypes reveals striking differences in light-dependent and maximum rates of net carbon fixation and in light intensity at saturation (where CO_2 is limiting). The resistant biotype does not become light-saturated until a high light intensity is reached. At low light intensities, the quantum yields of the two biotypes are different, suggesting an intrinsic alteration in photosynthetic light-harvesting ability in the resistant biotype. This difference in whole plant quantum yields is not of the magnitude of chloroplast level differences (Figs. 3 and 4), perhaps because net photosynthesis includes other whole plant processes, such as dark reactions and photorespiration, which may compensate for, or mask, the lowered light-harvesting ability in resistant plants. Alternatively, the process of thylakoid isolation may magnify in some way the *in-vivo* differences in quantum efficiency between whole plant biotypes. Inefficiencies in the light-trapping reactions, in which many quanta are "wasted," may be responsible for the prolonged light dependence, high intensity required for light saturation, and low-

ered quantum yield in resistant plants.

Our results indicate that, in several facets of light response, resistant chloroplasts of *S. vulgaris* are different from susceptible chloroplasts. Whole plant carbon fixation, which is dependent upon energy generated in the light reactions, differs between biotypes, as does the rate of O_2 production. Although variations in rates of photosynthesis may be due to arrangement and number of stomata, leaf conductances to water and CO_2, and mesophyll conductances to CO_2, the susceptible and resistant biotypes of *S. vulgaris* appear to be similar in these respects (J. D. Sims and S. R. Radosevich, unpublished data). Pfister and Arntzen (15) found no differences between *S. vulgaris* biotypes in leaf pigment content, Chl *a/b* ratios, and photosynthetic unit size. Differences in gas exchange characteristics, therefore, are apparently due to intrinsic inefficiencies in the photosynthetic apparatus of the resistant biotype.

As a recently developed biotype, resistant *S. vulgaris* has not had sufficient time, in an evolutionary sense, to respond to selection pressures which might result in a more efficient organism capable of competing with the susceptible biotype. Given its poor photosynthetic performance, the resistant biotype may never be able to become as successful a competitor as the susceptible biotype. At the cost of lowered vigor, photosynthetic performance, and competitive fitness, triazine resistance is apparently only of benefit to the plant in field situations where triazine herbicides are repeatedly used.

The phenomenon of herbicide resistance is of particular interest in agricultural situations where a buildup of resistance in weeds is likely to have severe agronomic consequences. A greater understanding of the behavior of susceptible and resistant biotypes is crucial in order to understand their relationship in field situations and to predict possible shifts in weed populations in response to various management techniques. Furthermore, the phenomenon of inheritance of resistance needs to be understood more fully as progress is made towards transferring resistance to crop species.

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