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The Effect of Light and Temperature on Competition between Atrazine Susceptible and Resistant *Brassica rapa*

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Biotypes of *Brassica rapa* susceptible (S) and resistant (R) to atrazine were grown in competitive replacement series in all possible combinations of two light levels and three temperature regimes in controlled growth cabinets. Photosystem II function was investigated in all conditions by fluorescence-induction techniques. There were no significant differences in the dry weight of the two biotypes when grown in pure stands. In pure stands both biotypes produced more biomass under the high light level. Under high light both biotypes yielded more biomass at high temperature; in low light they did so at medium temperature. Under high light conditions at high and medium temperatures the susceptible biotype had a greater photon yield and relative competitive ability than the resistant due to the greater vulnerability of triazine-resistant biotypes to photoinhibition. However, surprisingly, the resistant biotype was the better competitor, and had a higher photon yield, in the high light/low temperature regime. In low light no photoinhibition was expected and indeed there were no significant differences in any fluorescence parameters between the resistant and susceptible biotypes. Nevertheless, there were differences in the whole plant performance; the susceptible biotype was a better competitor at low and medium temperatures, but the resistant biotype was better at high temperature. Relatively small variations in both light and temperature, well within the range encountered during British summer time, can have large effects on the relative competitiveness of triazine R and S biotypes in this species with implications for the spread of resistance genes through semi-natural communities. In light of predicted climate changes, interactions between climate and resistance should be studied across a wider range of herbicide types and weed species.

Key words: *Brassica rapa*, chlorophyll fluorescence, competition, light, navew, temperature, triazine resistance.

INTRODUCTION

The rapid increase in herbicide resistant weed species, now numbering over 100 (Warwick, 1991), is becoming an increasingly difficult and expensive agronomic problem (LeBaron, 1991). The most widespread resistance is that to s-triazine herbicides; 55 species in North America, Europe, Australasia and Asia have been reported to have s-triazine resistant biotypes (Warwick, 1991).

Triazine herbicides (including atrazine) are photosynthesis inhibitors which act by binding to one of the chloroplast thylakoid membrane proteins, Q_b (Pfister and Arntzen, 1979), thus blocking electron transport through photosystem II. In most cases, resistance to triazine herbicides has been shown to be due to a single point mutation in the chloroplast gene, *psbA*, altering the herbicide binding polypeptide (D1) of the Q_b protein and thus preventing the herbicide from binding (Hirschberg and McIntosh, 1983). The mutation causes an up to ten-fold reduction in the rate of electron transport (Bowes, Crofts and Arntzen, 1980), often resulting in reduced growth and vigour of resistant (R) compared with susceptible plants (S) (e.g. Gressel and Ben-Sinai, 1985; Holt, 1988; Leroux, 1993). The mutation also affects the sensitivity of the photosynthetic apparatus to environmental variables such as light and temperature (e.g. Hart and Stemler, 1990*a*, *b*; Fuks, van Eycken and Lannoye, 1992). However, the link between electron transport, photosynthetic rate and whole plant performance is weak (Hall and Rao, 1994). Despite large differences in photosynthetic parameters, differences in whole plant performance between R and S biotypes may be only slight (e.g. Warwick and Black, 1981) or absent (e.g. Jansen *et al*., 1986; Schönfeld *et al*., 1987), and little is known about the influence of different environmental conditions on the whole plant performances of R biotypes.

In populations exposed to triazine herbicides the R biotype is obviously more fit than the S. Whether resistant phenotypes can otherwise persist in a weed population, how long a population can remain resistant after herbicide application has stopped and whether resistant phenotypes can spread into and become established in weed populations not previously exposed to the herbicide, will depend not only on agricultural practice, but also on the relative fitness of the two biotypes in the absence of herbicide (Gressel and Segel, 1990; Maxwell, Roush and Radosevich, 1990). This relative fitness has significant implications for the choice of herbicide resistance management strategies and is of considerable agronomic interest (Warwick and Black, 1994). The relative fitness of R and S biotypes also has important ecological implications for the impact of the escape of herbicide resistance from transgenic crops (Darmency and Gasquez, 1990). In order to successfully address these issues, particularly in the light of predictions of future

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climate change, more information is required on the relative fitness of R and S biotypes in both the vegetative and reproductive phases of growth (Roush, Radosevich and Maxwell, 1990) in a wide range of environmental conditions. In this paper we investigate how some components of photosynthesis and of the relative fitness of R and S biotypes, i.e. vegetative and flower biomass production, in the absence of herbicide, are affected by light availability and ambient temperature. Once separate R and S strains had been acquired, we felt that it was necessary to homogenize nuclear genes between the two strains (R and S characteristics being controlled cytoplasmically), and to investigate several generations. Due to constraints of time and space, we harvested each generation three weeks after germination, when the plants were flowering. Consequently, we did not access the fecundity or fitness of each strain during these experiments. These attributes will be considered in a subsequent paper. For the same reasons we chose strains bred for a short generation time ('fast-plants'). We were only able to acquire one strain each of R and S 'fast-plant' biotypes; it is possible that the nuclear genotypes of other R and S strains might behave in a different way from those reported here.

MATERIALS AND METHODS

Plant material

Seed of atrazine susceptible (S) and resistant (R) *Brassica rapa* bred for short generation time ('fast-plant') was obtained from the Crucifer Genetics Cooperative, University of Wisconsin, Madison. The R and S status of the supplied seed was tested by growing a sample in seed trays until they were a week old then spraying with atrazine solution of $3{\cdot}7 \times 10^{-5}$ M (manufacturer's recommended strength). All the S seedlings were killed, whereas all the R seedlings survived, confirming that the biotypes of the seed were as stated.

To ensure the nuclear genotypes of the two biotypes were as similar as possible, two F_1 generations, each of 500 plants, were raised from bulked seed resulting from controlled crosses made onto 100 each of R and S mothers. This procedure was repeated using 100 each of the F_1 plants as mothers to raise an F_2 progeny with R or S cytoplasmic genomes in which nuclear genomes had been mixed for two generations. The seed of the F_2 plants formed the first experimental generation and some of this seed was also used for the second and third experimental repetitions. Additional F_3 and F_4 seed was raised for the second and third repetitions as described above. Since resistance is determined by a chloroplast gene it is maternally inherited, and so it was assumed that all seed from R plants would be R and all from S plants would be S. This was confirmed at each generation by spraying samples of seedlings with atrazine.

Competition experiments

S and R seeds were sown in a replacement series (de Wit, 1960) containing 0, 25, 50, 75 and 100% R seeds in seed trays (32 cm × 20 cm) at a constant total density of 128 seeds per tray (equivalent to 2000 m^{-2}), in 16 rows of 8 seeds. There has been much debate about the value of replacement series due to density dependence (e.g. Firbank and Watkinson, 1985; Connolly, 1987; Law and Watkinson, 1987; Snaydon, 1991) but other designs have similar problems (Taylor and Aarssen, 1989). Ideally replacement series are carried out at a number of densities, but due to severe space restrictions we were not able to compare different total densities. However, provided that the density used allows competition to occur through much of the life cycle, but permits flowering and fruiting, the replacement series design is a quick and amenable method to analyse the qualitative effects of competition between two components (Taylor and Aarssen, 1989). Grids made from plastic coated garden mesh were used to mark the positions of seeds. In 50% mixtures R and S seeds were planted in alternate rows, in 25/75% mixtures the 25% seed was planted in four rows evenly spaced throughout the tray. Only the central 84 plants were harvested for analysis, the outer layer of 44 plants being discarded to minimize edge effects. At the same time spare seeds were sown in petri dishes and resulting seedlings used to replace any seeds in seed trays that failed to germinate (approx. 5% on average). Six trays of each mixture were sown at a time and one was placed in each of six controlled growth environments encompassing all possible combinations of two light levels and three temperature regimes. In all six environments there was an 18/6 h light/dark cycle and a 5 °C drop in temperature during the dark cycle. The two light levels were 800 μmol m^{-2} s^{-1} (high) and 100 μmol m^{-2} s^{-1} (low); the three temperature regimes were 24/19 °C (high), 21/16 °C (medium) and 17/12 °C (low). Plants were harvested after 3 weeks, at which time they were in full flower, and their vegetative, flower and total-above-ground dry weights assessed. The whole experiment was repeated twice.

For the analysis of competitive interactions the total tray biomass of each biotype was plotted against the percentage the biotype in the mixture. If inter-biotype competition equals intra-biotype competition this plot will result in a straight line. A straight line could also result if the population density was so low that there was no competition. To demonstrate that this was not the case the two biotypes were also grown in monoculture at the densities equivalent to 25, 50 and 75% of the mixtures to provide curves representing no inter-biotype competition. If one biotype is a stronger competitor the monoculture yield curve will lie above the straight line of equal competition; if it is a poor competitor the curve will lie below this straight line. These concave and convex curves are fitted into the formula $y = Ax^b$ where y is the total biomass production of the biotype and x is the proportion of the biotype in the mixture. In the log plots b represents the slope of the line which is found by regression analysis of the double log plot. When a biotype is not influenced by competition $b = 1$, when a biotype is a strong competitor $b < 1$, and when a biotype is a weak competitor $b > 1$ (Jansen *et al.*, 1986).

Fluorescence-induction technique

During the second repetition of the competition experi-

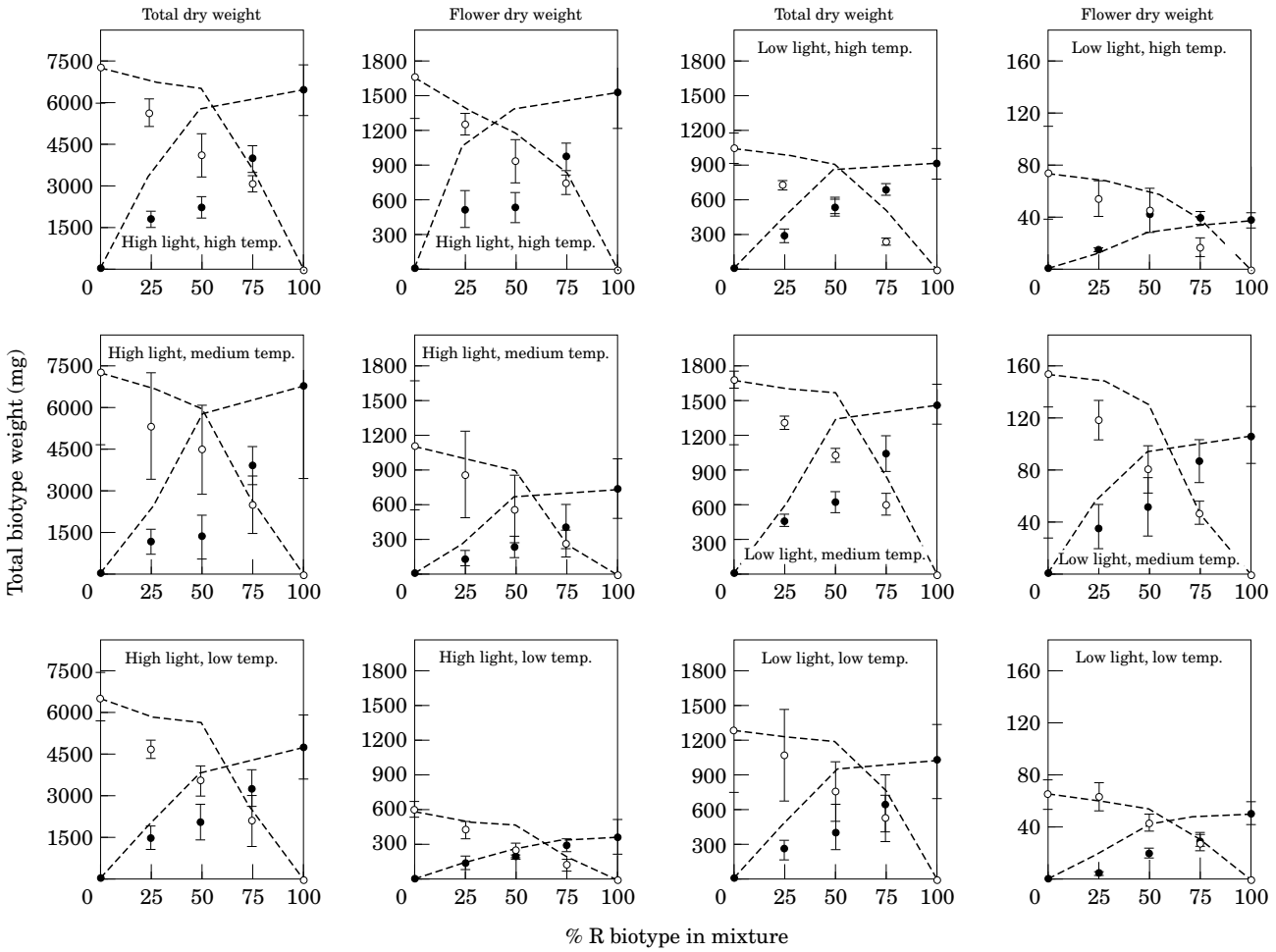

FIG. 1. Biomass production of atrazine R and S biotypes of *Brassica rapa* in replacement series in six combinations of light and temperature. Dashed lines show production of each biotype in single stands at the equivalent mixture density and represent the expected pattern if there was no inter-biotype competition. ○, S biomass; ●, R biomass; Bars show s.e.

ment *in vivo* fluorescence-induction techniques (Schreiber, Bilger and Neubauer, 1994) were performed on leaves from each biotype in the 50 % mixture trays 2 weeks after sowing. Measurements were made using a pulse amplitude modulated fluorimeter, PAM 2000 (H. Walz, Effelrich, Germany). The minimal fluorescence emitted in the dark adapted state when all PSII centres are fully oxidized (Fo) was determined pre-dawn, using a red-light-emitting diode at a high frequency (1·6 kHz). This stimulating light was of a very low intensity sufficient to detect Fo but not to trigger other phenomena. The apparent minimal fluorescence during illumination (Fo′) was determined in the same way (after rapid reoxidation of PSII centres by far red light) at 4 hourly intervals throughout the day. Maximum fluorescence (Fm) was also measured pre-dawn and at 4 hourly intervals throughout the day (Fm′). This was determined using a higher frequency (110 kHz) saturating actinic white light pulse (6000 μmol m^{-2} s^{-1}). Non-photochemical fluorescence quenching (NPQ) (Bulger and Bjorkman, 1990) and photochemical fluorescence quenching (qP) and photon yield (ΦPSII) (Gentry, Briantais and Baker, 1989) were calculated from these measurements.

RESULTS

Competition experiments

The means of the whole tray total and flower biomass produced by each biotype in each tray for all mixtures and conditions, are shown in Fig. 1. The vegetative biomass mirrored the total biomass very closely (data not shown). The whole tray total, vegetative and flower biomass of pure stands of R and S plants were analysed by three-way analysis of variance (Table 1). Although the mean biomass of the R biotype in pure stands was consistently less than that of the S biotype, this effect was not significant (Table 1), presumably due to large variation in the data. However, light level significantly affected the growth of both biotypes; under high light conditions both biotypes had a much greater total biomass production at all temperatures (Fig. 1). There was also a significant effect of temperature and of light × temperature interaction, but only for flower production. The flower biomass of both biotypes decreased with temperature under high light, whereas under low light flower dry weight of both biotypes was highest at the medium temperature (Fig. 1).

TABLE 1. *Results of three-way analysis of variance of the effects of temperature, light and biotype on mean biomass production, across three repetitions, of pure stands of R and S* Brassica rapa

	Source	*F*	d.f.	*P*
Total dry weight	Temperature	0·46	2, 24	0·64
	Light	43·70	1, 24	0·001***
	Biotype	0·51	1, 24	0·48
	Temperature × Light	0·29	2, 24	0·75
	Temperature × Biotype	0·06	2, 24	0·94
	Light × Biotype	0·21	1, 24	0·65
	Temperature × Light × Biotype	0·04	2, 24	0·96
Vegetative dry weight	Temperature	0·43	2, 24	0·66
	Light	42·16	1, 24	0·001***
	Biotype	0·46	1, 24	0·50
	Temperature × Light	0·07	2, 24	0·94
	Temperature × Biotype	0·12	2, 24	0·89
	Light × Biotype	0·17	1, 24	0·68
	Temperature × Light × Biotype	0·09	2, 24	0·92
Flower dry weight	Temperature	5·63	2, 24	0·01**
	Light	38·83	1, 24	0·001***
	Biotype	0·60	1, 24	0·44
	Temperature × Light	5·55	2, 24	0·01**
	Temperature × Biotype	0·11	2, 24	0·89
	Light × Biotype	0·32	1, 24	0·58
	Temperature × Light × Biotype	0·08	2, 24	0·93

*** $P < 0·001$, ** $P < 0·01$.

TABLE 2. *Competitive coefficients (b) of S and R biotypes of* Brassica rapa *in each of six sets of conditions derived from the means of three repetitions of the experiment*

			Total dry weight		Vegetative dry weight		Flower dry weight	
Light	Temperature	Biotype	b	*P*	b	*P*	b	*P*
High	High	S	0·61	*	0·61	*	0·57	*
		R	0·89	ns	0·94	ns	0·76	ns
	Medium	S	0·72	*	0·67	*	0·94	ns
		R	1·25	ns	1·25	ns	1·19	ns
	Low	S	0·97	ns	0·95	ns	1·10	ns
		R	0·80	ns	0·82	ns	0·65	*
Low	High	S	1·01	ns	1·01	ns	1·02	ns
		R	0·80	*	0·81	*	0·43	*
	Medium	S	0·73	**	0·71	**	0·88	*
		R	0·81	ns	0·82	ns	0·79	ns
	Low	S	0·65	*	0·66	*	0·63	*
		R	0·99	ns	0·98	ns	1·79	*

Values greater than 1 indicate poor competitors, values less than 1 indicate good competitors. *P* values indicate significant deviation from 1, *, $P < 0·05$, **, $P < 0·01$, ns not significant.

The dashed lines in Fig. 1 represent the values for each biotype grown separately at the equivalent mixture densities, i.e. they represent no inter-biotype competition. The competitive coefficients, calculated from the regression of the double log plot, of the mean biomass production across three repetitions were compared with the expected value of one (i.e. equal competition) by *t*-tests (Table 2). Under high light conditions the S biotype was clearly the stronger competitor both in the high and medium temperature regimes. However, in the low temperature regime the R biotype was the stronger competitor, significantly so in terms of flower weight. In low light conditions the R biotype was the significantly stronger competitor in the high temperature regime in terms of total, vegetative and flower biomass production. However, the S biotype was the significantly stronger competitor at the medium and low temperatures. The only case of a significantly poorer competitor (i.e. a competition coefficient significantly greater than 1), was for flower weight of the R biotype in the low light/low temperature environment.

Competitive coefficients can be tested not only against unity as in Table 2, but also against each other. Three-way

TABLE 3. *Results of three-way analysis of variance of the effects of light, temperature and biotype on competitive coefficients (values of b from Table 3) of* Brassica rapa *from three repetitions of the experiment*

	Source	*F*	d.f.	*P*
Total dry weight	Temperature	0·17	2, 24	0·84
	Light	1·19	1, 24	0·29
	Biotype	4·10	1, 24	0·06
	Temperature × Light	1·75	2, 24	0·19
	Temperature × Biotype	0·76	2, 24	0·48
	Light × Biotype	1·39	1, 24	0·25
	Temperature × Light × Biotype	8·74	2, 24	0·001***
Vegetative dry weight	Temperature	0·25	2, 24	0·78
	Light	0·69	1, 24	0·41
	Biotype	3·38	1, 24	0·08
	Temperature × Light	1·83	2, 24	0·18
	Temperature × Biotype	1·15	2, 24	0·33
	Light × Biotype	1·19	1, 24	0·29
	Temperature × Light × Biotype	6·13	2, 24	0·007**
Flower dry weight	Temperature	2·83	2, 24	0·08
	Light	0·30	1, 24	0·59
	Biotype	0·80	1, 24	0·38
	Temperature × Light	1·73	2, 24	0·20
	Temperature × Biotype	1·91	2, 24	0·17
	Light × Biotype	0·45	1, 24	0·51
	Temperature × Light × Biotype	20·04	2, 24	0·000***

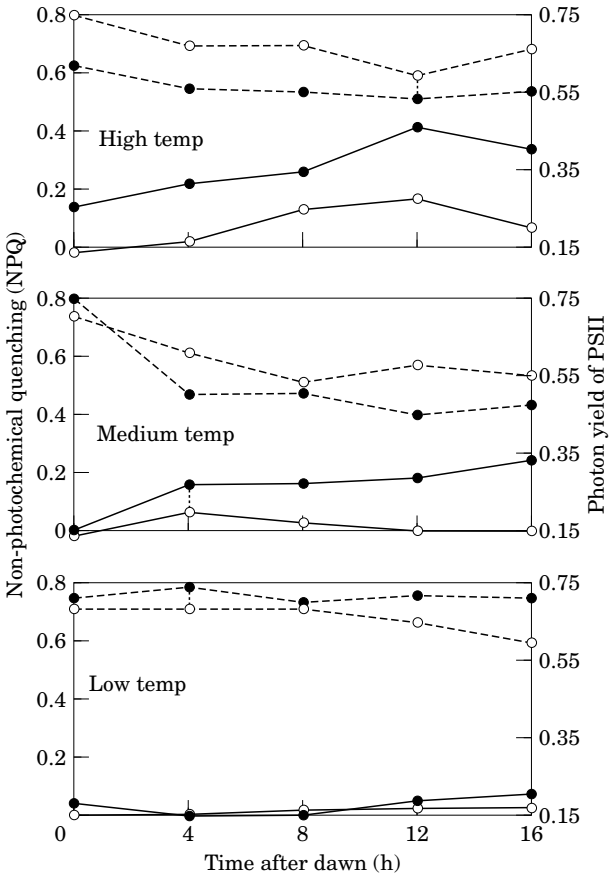

FIG. 2. Non-photochemical quenching (——) and photon yield of PSII (– – –) of atrazine R and S biotypes of *Brassica rapa* in high light and high, medium and low temperature. R and S values at each time point were compared by *t*-tests. Those points which were not significantly different at the 5% level are joined by a dotted line. ○, S biotype; ●, R biotype.

analysis of variance was used to test for effects of light, temperature and biotype on the competitive coefficients i.e. values of *b* from the regression equations (Table 3). None of the main factors had a significant effect, although biotype was almost significant when considering vegetative and total dry weight ($P = 0{\cdot}08$ and 0·06, respectively). However, in all three cases (total, vegetative and flower dry weight) the three way interaction between light, temperature and biotype was highly significant ($P = 0{\cdot}001$, 0·007 and $< 0{\cdot}001$, respectively). This was due to generally low values (indicative of a good competitor) for the S biotype and generally high values (indicative of a poor competitor) for the R biotype, except in high light/low temperature and low light/high temperature regimes, where the opposite was the case (Table 3).

Fluorescence

In the high light conditions, the results from fluorescence analysis support those of the competition experiment. Under high light, and at high and medium temperatures, the R biotype had a significantly greater NPQ than the S biotype, indicating increased dissipation of excess energy via non-photochemical mechanisms and a lower ΦPSII indicating poorer overall PSII efficiency (Fig. 2). In addition, in the highest temperature the R biotype had significantly higher Fo and Fo′ indicating the build up of reduced Qa and thus the increased potential for photoinhibitory damage (Fig. 3). However, in the low temperature where R was the better competitor it had a higher ΦPSII indicating greater photosystem II efficiency than the S biotype in these conditions (Fig. 2). At all three temperatures under low light there was very little difference between the two biotypes in any of the fluorescence parameters measured. This suggests that the small, but significant, differences in competitive ability are due to factors other than photosystem II function.

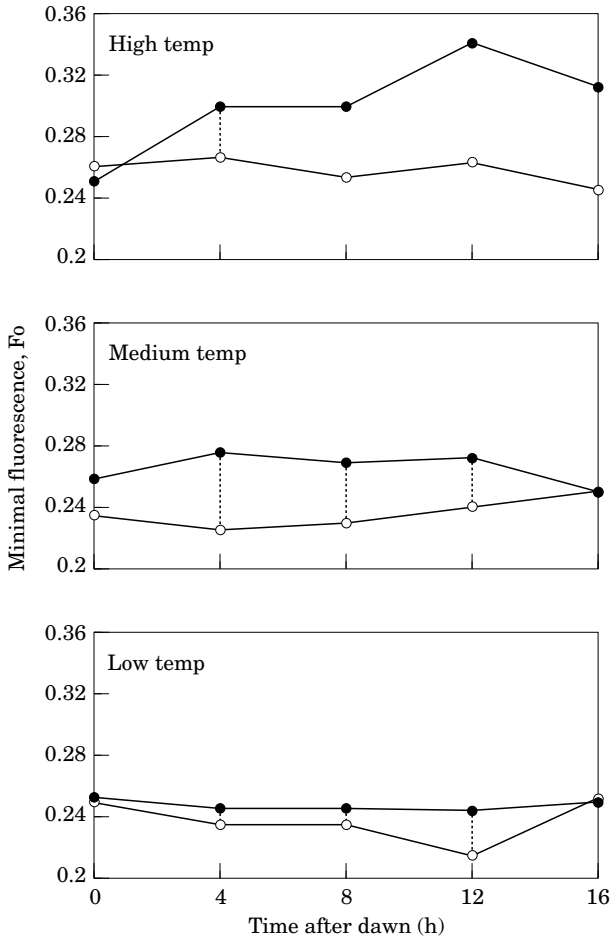

FIG. 3. Minimal fluorescence (Fo) of atrazine R and S biotypes of *Brassica rapa* in high light. Values at each time point were compared by *t*-tests. Those points which were not significantly different at the 5% level are joined by a dotted line. ○, S biotype; ●, R biotype.

DISCUSSION

The results indicate that, when grown in pure stands, triazine-R and -S biotypes of *Brassica rapa* had similar biomass production and responded similarly to changes in light and temperature. However, when grown in competitive mixtures, R and S biotypes responded differently to both light and temperature. The S biotype was a much stronger competitor in all conditions, except high light/low temperature and low light/high temperature regimes when the R biotype had a slight competitive advantage.

Previous experimental reports on the influence of light intensity on the whole plant performance of R and S biotypes differ in their conclusions. For instance, Hobbs (1987) found no differential effect of light on triazine-R and -S biotypes of *Brassica* spp.; R biotypes were less productive at all light levels. In contrast, Ahrens and Stoller (1983) found that at 10% ambient light there was no difference in growth of R and S types of *Amaranthus hybridus*, but R performed less well than S at 40 and 100% ambient light. The present results indicate that the effect of light intensity on the relative biomass of R and S biotypes of *B. rapa* depends on the ambient temperature. At high and medium temperatures the R biotype was adversely affected by high light intensity. However, at low temperatures, high light intensity was more harmful to the S than to the R biotype. These effects on whole plant performance can be explained by the high ΦPSII values of the S biotype at high and medium temperatures and of the R biotype at low temperature.

Photosynthesis in triazine resistant plants of *Senecio vulgaris* (Holt, Stemler and Radosevich, 1981) and *Brassica napus* (Hart and Stemler, 1990*a*, *b*) was reduced compared with S biotypes under high light intensity, but not under low light. These authors concluded firstly, that electron transfer from Qa to Qb, even though this was slower in R plants, was not the rate-limiting step for photosynthesis in low light, and secondly, that the increased susceptibility of R plant PSII to photoinhibitory damage was the cause of their lower photosynthetic rate in high light (Hart and Stemler, 1990*a*, *b*). Presumably, the greater prevalence of the reduced form of Qa when R plants grew in strong light, led to an increased potential for the production of harmful O_2 radical species resulting from its interaction with O_2 (Hart and Stemler, 1990*a*). This hypothesis is supported by the increase of the *B. rapa* R biotype NPQ and Fo′ (both indicating increased potential for photoinhibitory damage) in the high light/high and medium temperature condition.

Several studies on the effects of temperature on the relative productivity of R and S weed biotypes have shown little, if any, apparent disadvantage for R biotypes at lower temperatures, e.g. *Polygonum lapathifolium* (Gasquez, Darmency and Compoint, 1981) and *Setaria italica* (Darmency and Pernès, 1989). In some cases R was more productive than S at low temperatures (e.g. *Phalaris paradoxa*; Schönfeld *et al.*, 1987), even though the S biotype was more productive at higher temperatures. In contrast, for *Solanum nigrum* (Jacobs *et al.*, 1988) and *Chenopodium album* (Vencill, Foy and Orcutt, 1987) there appeared to be no differential effect of temperature on R and S biotypes. However, none of these examples used formalized competition experiments.

The present results indicate that the effects of temperature on R and S biotypes of *B. rapa* can depend on the light intensity at which the plants are grown. At high light the dry flower weight of the R biotype is adversely affected by increasing temperatures, especially in competition; however, at low light the competitiveness of the R biotype is enhanced by increasing temperature.

Evidence from fluorescence and electron transfer studies indicates that R biotypes are more inhibited at higher temperatures than S biotypes. It is well documented in several species that triazine resistant PSII reaction centres are much more sensitive to temperatures above 35 °C (Ducruet and Lemoine, 1985; Ducruet and Ort, 1988; Havaux, 1989; Fuks *et al.*, 1992). A further slowing of Qa to Qb electron flow leads to yet higher levels of reduced Qa and thus greater potential for photoinhibitory damage. This is possibly because the mutated electron binding site in the R PSII complex may be more sensitive to deformation by high temperature (Ducruet and Ort, 1988). Less is known about temperature sensitivity of resistant chloroplasts at temperatures below 35 °C. For *Polygonum lapathifolium* R

biotypes had a lower photosynthetic rate than S at 20–25 °C, but a higher rate at 10–15 °C (Darmency and Gasquez, 1982). In the present study, the reduced competitiveness of the R biotype at higher temperatures under high light can be explained by such differences in PSII function (see above). However, the enhanced performance of the R biotype in high temperature under low light appears to be due to factors other than PSII function as no difference in fluorescence parameters were found between the R and S biotypes in these conditions.

The data presented here appear to concur with previous findings in many respects, but some of the results are surprising. Predictably, in high light and high temperatures R plants were less competitive than S due to reduced PSII efficiency, apparently because of an increased susceptibility to photoinhibition. However, surprisingly, at low temperature but still in high light the R biotype had a higher PSII efficiency and was the better competitor. This suggests that a low temperature response, similar to that found by Darmency and Gasquez (1982), was adequate to compensate for the damage caused by high light, although the mechanism by which this could occur remains unclear. In *B. napus*, Hart and Stemler (1990*a*) observed that R plants had a faster recovery time than S after exposure to photoinhibitory conditions, possibly due to a greater capacity for damage repair. Such an effect could explain why R plants were more competitive than S in high light/low temperature conditions.

The other surprising result was the greater competitive ability of R plants in low light and high temperature, particularly as previous work suggested that R plants were better adapted to lower temperatures (Darmency and Gasquez, 1982). At these low light levels neither S nor R biotypes would have been affected by photoinhibition and there were no differences in their fluorescence characteristics. The differential effect of temperature under low light, even though not at great as under high light, is therefore puzzling. R plants often have other alterations to the chloroplast not directly connected with D1 electron binding. For instance, it is commonly observed that R and S chloroplasts differ in lipid and fatty acid composition (Vencill *et al.*, 1987). It seems likely that associated alterations such as these could be responsible for the surprising low light effects found here.

Poor competitiveness, in the absence of herbicide, of R weed biotypes, both with S biotypes and with the crop, has been shown to be a major factor in hastening the reversion of resistant weed populations to susceptible after herbicide application has ceased (Maxwell *et al.*, 1990). Our results indicate that relatively small variations in both light and temperature, well within the range encountered during British summer time, can have large effects on the relative competitiveness of triazine R and S biotypes in this species. Such effects have important implications for the management of herbicide resistance in agricultural communities, and for the dissemination of resistance genes through semi-natural communities. In the light of predicted climate changes, interactions between climate and resistance should be studied across a wider range of herbicide types and weed species.

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