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Résumé de l'article

La compétitivité relative de deux biotypes de *Chenopodium album*, un sensible et l'autre résistant aux s-triazines, a été comparée lors de trois expériences menées en serres. En absence de compétition, la production de biomasse sèche n'a pas différé entre les deux biotypes, mais le biotype résistant a alloué moins de matière sèche à la production de semences et a produit moins de semences que le biotype sensible. Les résultats obtenus de séries de remplacement (de Wit) menées à une densité de 400 plants m^{-2} ont indiqué que la proportion relative de la biomasse et du nombre de semences produites par le biotype sensible était toujours plus grande que la proportion de plantes susceptibles présentes dans le mélange. Les effets de la compétition racinaire, de la compétition aérienne, et de la compétition complète (racinaire + aérienne) ont été comparés à des densités de 400, 666, 934, 1200, et 1466 plantules m^{-2} . Les biotypes ont eu l'effet le plus marqué sur toutes les variables mesurées parmi les facteurs étudiés. Les plantules du biotype sensible atteignaient une hauteur plus grande, avaient un indice de surface foliaire (ISF) supérieur, produisaient plus de feuilles, et des rendements foliaire, caulinaire et total plus grands que les plantules résistantes, peu importe la densité de plantules ou le mode de compétition. La compétitivité du biotype sensible à l'égard du biotype résistant s'est exprimée le plus lorsque les deux biotypes rivalisaient entre eux pour la lumière. Les effets de la compétition aérienne sur le rendement, l'ISF, le nombre de feuilles, et la hauteur des plantules étaient aussi importants que la compétition complète. Les effets de la compétition racinaire, bien que significatifs, n'étaient pas aussi importants. Les résultats indiquent que s'il y a arrêt de l'utilisation des s-triazines, la population de *C. album* évoluera naturellement vers la susceptibilité aux s-triazines à cause de la compétitivité supérieure du biotype sensible.

Relative fitness of s-triazine susceptible and resistant biotypes of *Chenopodium album*

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The relative fitness of s-triazine susceptible and resistant biotypes of *Chenopodium album* from Québec were compared in three greenhouse experiments. Under non-competitive conditions, there was no difference in dry matter production between biotypes, but the resistant biotype allocated less dry matter to seed production and produced fewer seeds than the susceptible. Results from de Wit replacement series performed at 400 plants m⁻² indicated that the relative proportion of biomass and seeds produced by the susceptible biotype was always greater than the proportion of susceptible plants present in any given treatment. The effects of root, shoot, and full (root + shoot) competition were compared between and within biotypes at planting densities of 400, 666, 934, 1200, and 1466 seedlings m⁻². Biotype had the most pronounced effect on all variables among the factors studied. The susceptible seedlings were taller, had a greater leaf area index (LAI), more leaves, and greater leaf, stem, and above-ground dry matter yields than the resistant seedlings, regardless of the planting density or the mode of competition. The fitness of the susceptible biotype was greatest when both biotypes were competing for light. The effects of shoot competition for light on yield, LAI, leaf numbers, and seedling height, were as important as those of full competition. The effects of root competition, although significant, were not nearly as important. The data indicate that if s-triazines are no longer used in a field, the *C. album* population will revert naturally to susceptibility because of the superior fitness of the susceptible biotype.

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plantules m⁻². Les biotypes ont eu l'effet le plus marqué sur toutes les variables mesurées parmi les facteurs étudiés. Les plantules du biotype sensible atteignaient une hauteur plus grande, avaient un indice de surface foliaire (ISF) supérieur, produisaient plus de feuilles, et des rendements foliaire, caulinaire et total plus grands que les plantules résistantes, peu importe la densité de plantules ou le mode de compétition. La compétitivité du biotype sensible à l'égard du biotype résistant s'est exprimée le plus lorsque les deux biotypes rivalisaient entre eux pour la lumière. Les effets de la compétition aérienne sur le rendement, l'ISF, le nombre de feuilles, et la hauteur des plantules étaient aussi importants que la compétition complète. Les effets de la compétition racinaire, bien que significatifs, n'étaient pas aussi importants. Les résultats indiquent que s'il y a arrêt de l'utilisation des *s*-triazines, la population de *C. album* évoluera naturellement vers la susceptibilité aux *s*-triazines à cause de la compétitivité supérieure du biotype sensible.

INTRODUCTION

Weed resistance to *s*-triazines in Québec was first reported in the late 1970s for bird's rape (*Brassica rapa* L.) by Maltais and Bouchard (1978). During the same period, resistant (R) populations of lamb's-quarters (*Chenopodium album* L.) and Powell amaranth (*Amaranthus powellii* S. Wats.) were reported in Nova Scotia and Ontario, but not in Québec (Bandein *et al.* 1979). A survey conducted in 1988 indicated that *C. album* was the most frequent resistant weed species encountered by corn growers in Québec (Leroux and Piette 1989). Resistance of *C. album* to *s*-triazines results from biochemical modifications of the shielding protein over the Q_B electron acceptor in thylakoid membranes so that the herbicide can no longer inhibit photosynthesis (Purcell *et al.* 1990). In resistant biotype of groundsel (*Senecio vulgaris* L.), the rate of electron transfer in chloroplasts is slower resulting in a reduced efficiency of photochemical reactions (Holt *et al.* 1983). Thus, resistant biotypes are generally less productive and competitive than susceptible (S) biotypes, explaining why susceptible biotypes prevail under competitive conditions, in the absence of *s*-triazines. Studies in Ontario indicated that *s*-triazine susceptible biotypes of *C. album* and *A. powellii* had greater competitive abilities than their respective resistant biotypes (Marriage and Warwick 1980; Weaver and

Warwick 1982), but that there was no difference between biotypes of *Chenopodium strictum* Roth (Warwick and Black 1981).

The relative importance of root and shoot competition between R and S biotypes have not been studied, although it is an important step in understanding the relationships between them. Schreiber (1967) has designed a technique to separate the effects of root and shoot competition. The relative effects of root and shoot competition may be expected to depend on a number of factors, such as: (1) the relative extent to which above-ground factors (i.e., light) and below-ground factors (i.e., water and mineral nutrients) are limiting; (2) the biotypes present; and (3) the relative density of the biotypes. No study has been conducted to compare the relative fitness of susceptible and resistant biotypes of *C. album* from Québec. In addition, most previous studies have not looked at root vs shoot competition during the early growth of biotypes, under intra- and inter-biotype competitive conditions. Thus, three experiments were designed to: 1) compare the productivity of each biotype under non-competitive conditions; 2) compare the competitive ability of biotypes grown in varying proportions at constant density; and 3) determine whether root or shoot competition has more impact on the competitive relationships between biotypes.

MATERIAL AND METHODS

Lamb's-quarters' seeds were collected in the fall of 1985 near Pont-Rouge, Québec (46°45'N, 71°42'W), in a field where corn (*Zea mays* L.) had been grown and treated with atrazine for several years. This population is designated as biotype R. Seeds were collected in the fall of 1985 from the Laval University Experimental Farm, near Saint-Augustin-de-Desmaures, Québec (46°45'N, 71°28'W) in untreated corn plots where atrazine had suppressed lamb's-quarters in this herbicide testing trial. This population is designated as biotype S. Seeds were collected from 50 randomly selected mature plants at each location. Ten seedlings derived from each selected plant were grown and tested against atrazine at rates varying between 1 and 6 kg a.i. ha⁻¹. Atrazine was sprayed postemergence using a compressed air sprayer delivering 200 L ha⁻¹ at 180 kPa pressure. After spraying, plants were placed in a greenhouse with growing conditions as in the non-competitive experiment (see below). The S biotype was susceptible to 1.0 kg a.i. ha⁻¹, but the R biotype was not affected at the highest rate. Bulk samples of each biotype were obtained by combining seed from all selected plants. In order to remove carry-over effects from the field and to increase seed numbers for experimentation, the biotypes were propagated by growing individual plants in pots in separate greenhouses. Seeds from these plants were harvested, tested against atrazine as previously described, and used in the experiments.

Non-competitive experiment

Seeds of each biotype were sown in ten 15-cm diam pots filled with steam-pasteurized potting soil consisting of organic soil, sand, peat moss, vermiculite, and perlite (2:2:2:1:1; v/v/v/v/v). Pots were arranged in a completely randomized design and were spaced apart to prevent any competition. Seedlings with two true leaves were thinned to one per pot soon after emergence, and plants were harvested before seed shedding. The experiment was conducted in a greenhouse (25°C day and 18°C night) with supplemental fluorescent lighting

(400 μmol m⁻² s⁻¹) for 16 h d⁻¹. Plants were irrigated twice daily and fertilized weekly with a solution containing 200 ppm (w/v) each of N, P, and K. The experiment was conducted twice. The above-ground portion of each plant was harvested, divided into reproductive and non-reproductive parts, and dried to a constant weight in a forced air oven set at 70°C. Seeds were separated from other reproductive parts (calyx, pericarp, and rachis) and weighed. Average seed weights, determined from five samples of 200 seeds, were used to calculate seed yield, i.e., total number of seeds per plant. The data were subjected to ANOVA procedures (SAS 1985) and tested for homogeneity of variance using Burr-Foster's test (Anderson and McLean 1974). When significant effects were detected in ANOVA ($P \leq 0.05$), means were compared using unpaired *t*-tests.

Replacement series experiment

The technique used was a conventional replacement series (Bauemer and de Wit 1968). Seeds of each biotype were germinated in Petri dishes at 25°C day and 18°C night with 16 h day⁻¹. Germinated seeds were planted individually in varying proportions on a 4 cm x 4 cm grid in wooden boxes (50 cm long x 40 cm wide x 15 cm deep) filled with potting soil as described above. There were 48 plants per box arranged in eight rows plus 32 plants which constituted a guard row along each edge of the box. This was equivalent to 400 plants m⁻². The biotypes were grown in the following proportions: 100:0, 98:2, 75:25, 50:50, 25:75, 2:98, 0:100. Biotype positions in each box were assigned randomly. Each proportion was replicated four times in a randomized complete block design and the experiment was run twice. The experiment was conducted in a greenhouse with the same conditions as in the non-competitive experiment. Plants were grown for 112 d until most seeds were mature. For each treatment, plants of the same biotype were counted, and divided into dry matter allocated to reproductive and non-reproductive parts. Each seed lot of a given biotype was cleaned and weighed separately. Seed yields of each biotype were determined as above. Both the absolute

and relative biomass and seed yields of each biotype at a given proportion in the mixture were computed. Relative yield for each biotype was calculated as yield at each proportion divided by the mean monoculture yield. The data were subjected to ANOVA procedures (SAS 1985) and tested for homogeneity of variance using Burr-Foster's test (Anderson and McLean 1974).

Modes of competition experiment

Seeds of each biotype were germinated in Petri dishes at 25°C day and 18°C night with 16 h d⁻¹. Caution was taken to visually select seeds of similar size. Germinated seeds were planted individually in competition boxes (Schreiber 1967). Four modes of competition were studied: 1) below-ground inter-biotype competition (hereafter root competition), 2) above-ground inter-biotype competition (hereafter shoot competition), 3) above- and below-ground inter-biotype competition (hereafter full inter-biotype competition), and 4) full intra-biotype competition (hereafter intra-biotype competition). Above-ground partitions (10 cm wide x 15 cm long x 15 cm high) were lined with an aluminized reflective material. The below-ground partitions had the same dimensions (10 cm wide x 15 cm long x 15 cm deep). Each soil partition had drainage holes. The competition boxes were filled with potting soil as above. Seedlings of each biotype (R, S) were planted in rows into each soil partition at five varying densities: 3R + 3S, 5R + 5S, 7R + 7S, 9R + 9S, and 11R + 11S. For studying intra-biotype competition, each biotype was grown in

monoculture at the same overall densities. The total densities used are equivalent to 400, 666, 934, 1200, and 1466 seedlings m⁻², respectively.

The treatments were a factorial arrangement of two biotypes, four modes of competition, and five planting densities. Treatments were replicated four times in a randomized complete block design, and the experiment was conducted twice. The experimental conditions (photo- and thermo-periods, irrigation and fertilization) were the same as in the non-competitive experiment. Plants were harvested 25 d after planting when plants started to reach the top of the above-ground partitions. For each treatment, the heights of all plants from the same biotype were measured and averaged. The number of plants of each biotype was recorded at harvest and the above-ground portions of all plants were divided into leaves and stems. The total number of leaves per plant was determined for each biotype. The total leaf area per biotype was measured by placing all the leaves through an automatic planimeter Li-3100 (LiCor Inc., Lincoln, NE). The mean leaf area index was computed for each biotype. All plant parts of a given biotype were weighed fresh and then dried to a constant weight in a forced air oven (70°C). The percentage of dry matter in each biotype was calculated. Total (g m⁻²) dry matter yields of leaf, stem, and above-ground biomass were calculated for each biotype. The data were subjected to factorial analyses of variance (SAS 1985) and submitted to Burr-Foster's test for homogeneity of

Table 1. Above-ground and seed biomass production for susceptible and resistant biotypes of *C. album* grown under non-competitive conditions

Variable	Biotype	
	Susceptible	Resistant
Above-ground dry biomass (g)	30.4 ± 2.8 ^a	25.6 ± 2.8
Above-ground dry biomass allocated to seed (%)	28.2 ± 2.1	21.8 ± 1.7**
Total number of seeds	12468 ± 1494	8567 ± 1382**
Individual seed weight (mg)	0.69 ± 0.01	0.62 ± 0.02**

^a $\bar{X} \pm SE$ based on two experiments each with 10 replicates per biotype.

** Significant at $P \leq 0.001$.

variance (Anderson and McLean 1974). Means were compared using Fisher's protected LSD ($P \leq 0.05$), when treatment effects were significant.

RESULTS AND DISCUSSION

Non-competitive experiment

There was no difference ($P > 0.05$) in above-ground dry matter yield when each biotype was grown in the absence of competition (Table 1). The resistant biotype allocated less dry matter to seed production, produced fewer seeds than the susceptible biotype, and its seeds were lighter. Warwick and Black (1981) found that susceptible plants of *C. album* had greater above-ground and reproductive biomass production than the resistant plants. But Marriage and Warwick (1980) reported no difference in growth and reproductive effort between one resistant

biotype and two susceptible ones. Susceptible biotypes of redroot pigweed (*Amaranthus retroflexus* L.) and common groundsel produced more biomass and seeds than the resistant biotypes under non-competitive conditions (Conard and Radosevich 1979).

Replacement series experiment

In pure stands (100:0 or 0:100) the absolute dry matter yields did not differ ($P > 0.05$) between biotypes (Figure 1). The susceptible biotype of *C. album* outyielded the resistant biotype when they were in equal proportion in the mixture. Biotypes had the same yields when their proportion in the mixture was ca. 24S:76R. When the yields of each biotype were added up at a given proportion, total yields did not differ among proportion treatments (data not shown). In terms of relative dry matter yield, the same results were obtained:

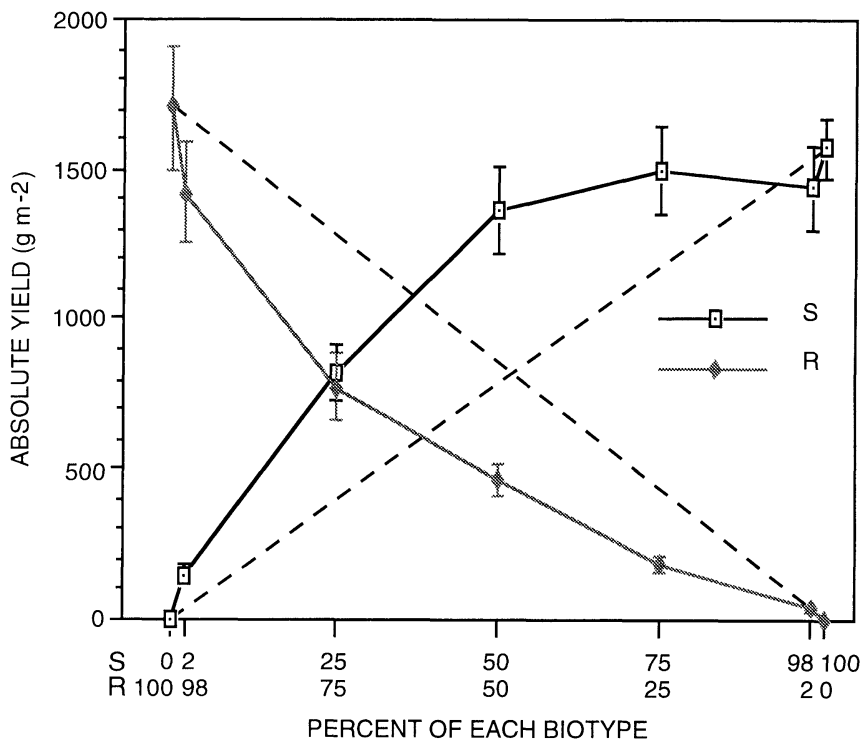


Figure 1. Absolute dry matter yield of resistant (R) and susceptible (S) biotypes of *C. album* grown in varying proportions at constant density. The vertical bars are 95% confidence limits based on two experiments each with four replicates. The no competition lines (---) for each biotype are shown. Proportion is expressed as percent of the total biotype mixture.

the susceptible biotype was more fit than the resistant biotype when it made up ca. 25% or more of the mixture. The mean percentages of dry biomass allocated to reproductive parts were $41.3 \pm 3.4\%$ and $32.2 \pm 4.9\%$, for the susceptible and resistant biotypes, respectively. The proportions in the mixture did not influence the pattern of allocation. Our data support the finding of Warwick and Black (1981) who reported that the relative proportion of biomass produced by the susceptible biotype was constantly greater than the proportion of susceptible *C. album* plants present in any given treatment.

Absolute seed yields of the biotypes did not differ when they were grown in pure stands (data not shown). Seed yields of each biotype were similar when biotypes were grown in the proportion

25S:75R. Total seed yields did not differ among proportion treatments when seed yields of each biotype were summed (data not shown). Relative seed yields of the susceptible biotype were greater than that of the resistant biotype at all proportions in the mixture (Figure 2). Seed weights of the susceptible and resistant biotypes were 0.65 ± 0.01 mg and 0.60 ± 0.02 mg, respectively, and were not influenced by proportions in the mixture. Weaver and Warwick (1982) and Conard and Radosevich (1979) have reported similar results for *s*-triazine resistant and susceptible biotypes of *Amaranthus* spp. and *Senecio vulgaris*.

Modes of competition experiment

Biotypes, planting densities and modes of competition had highly significant ($P \leq 0.001$) effects on dry matter yields of

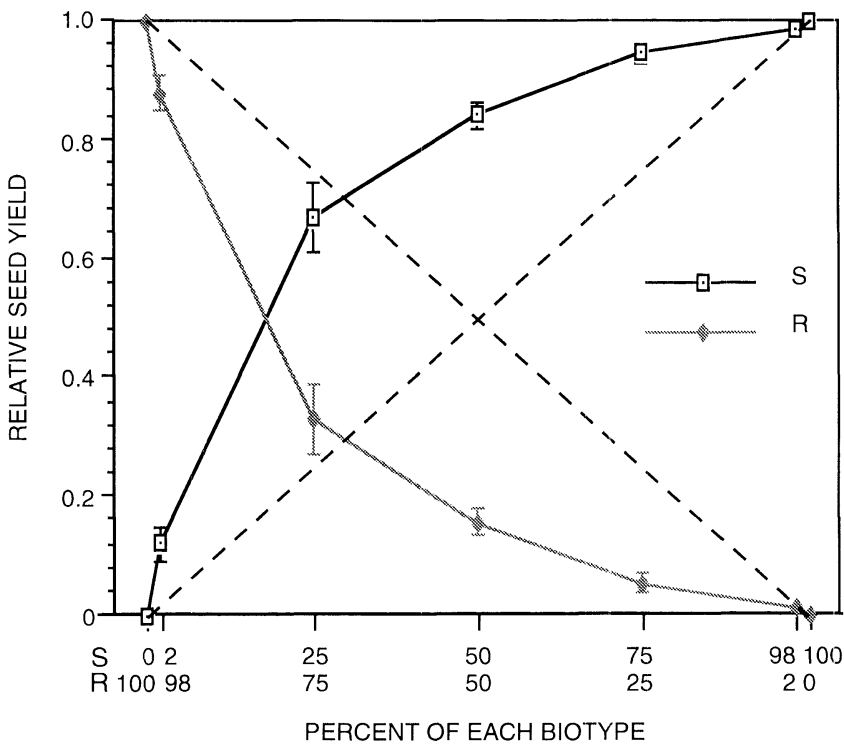


Figure 2. Relative seed yield of resistant (R) and susceptible (S) biotypes of *C. album* grown in varying proportions at constant density. The vertical bars are 95% confidence limits based on two experiments each with four replicates. The no competition lines (---) for each biotype are shown. Proportion is expressed as percent of the total biotype mixture.

leaf, stem, and total above-ground biomass. The biotype effect was the most pronounced of the factors studied for any variables. Thus, the data was averaged over all planting densities. The susceptible biotype of *C. album* consistently outyielded the resistant biotype, regardless of the mode of

competition or the planting density used (Figure 3). The greatest difference in yield between the two biotypes was found when plants were competing for light, rather than for soil resources. The effect of shoot competition was as important as that of full (root + shoot) competition, regardless of the plant

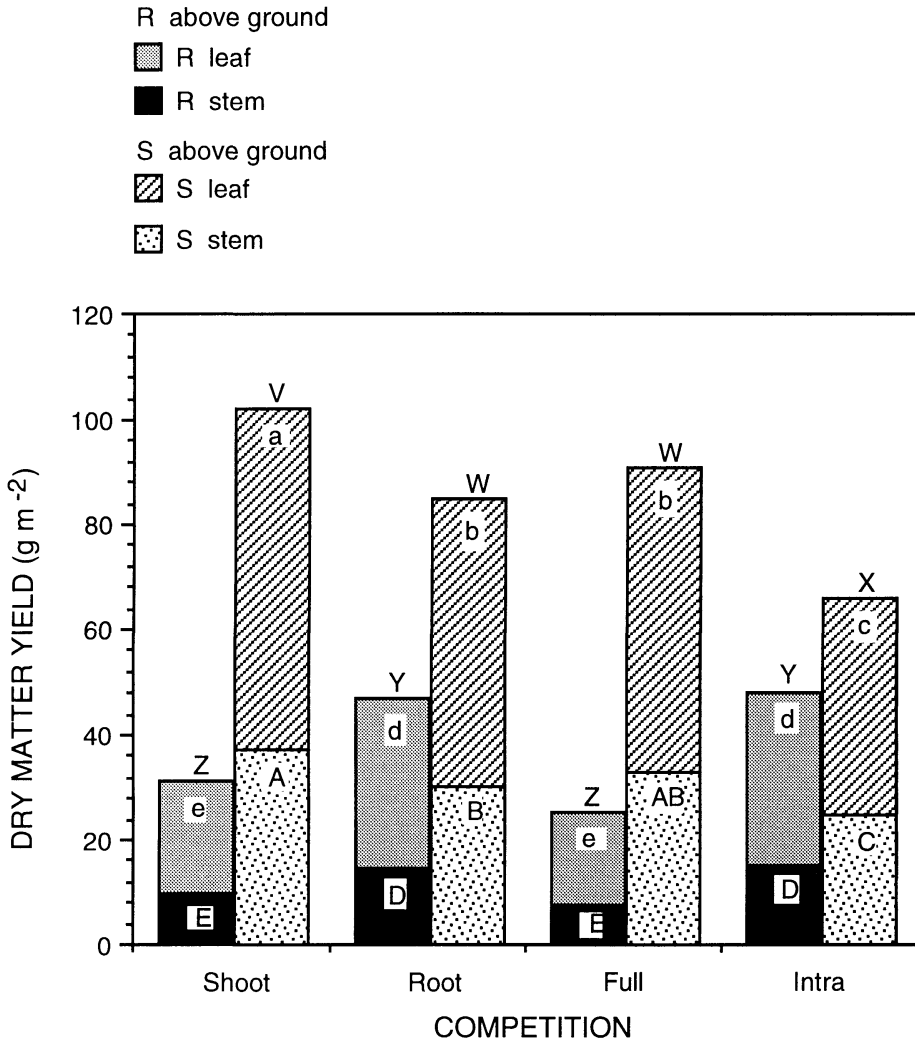


Figure 3. Dry matter yields of leaf, stem, and total above-ground biomass for resistant (R) and susceptible (S) biotypes of *C. album* grown under four modes of competition. Within a plant component (same group of letters, i.e., A-E, a-e, V-Z), bars with the same letter do not differ significantly at $P = 0.05$. Means are based on two experiments each with five planting densities and four replicates.

parts. When biotypes were grown in monoculture, under conditions of full competition, the susceptible biotype had a greater yield ($P \leq 0.05$) than the resistant one (Figure 3). But under these conditions, there was much less

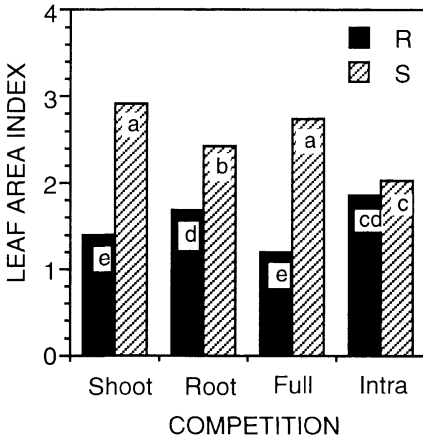


Figure 4. Leaf area index for resistant (R) and susceptible (S) biotypes of *C. album* grown under four modes of competition. Bars with the same letter do not differ significantly at $P = 0.05$. Means are based on two experiments each with five planting densities and four replicates.

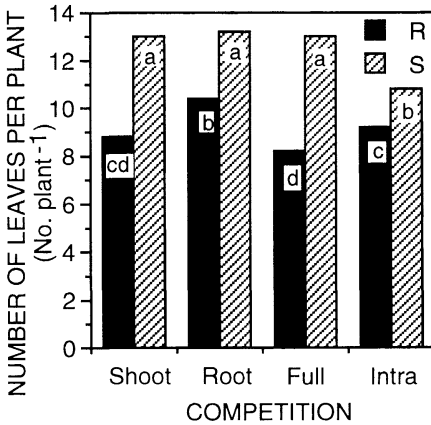


Figure 5. Mean number of leaves per plant for resistant (R) and susceptible (S) biotypes of *C. album* grown under four modes of competition. Bars with the same letter do not differ significantly at $P = 0.05$. Means are based on two experiments each with five planting densities and four replicates.

difference in yield between biotypes, indicating that intra-biotype competition is more severe among susceptible plants, and less among resistant plants. When averaged over all modes of competition, the resistant biotype at the highest planting density had yield equivalent to the susceptible biotype at the lowest density, thus causing a significant ($P \leq 0.05$) biotype by planting density interaction (data not shown). The planting densities did not influence the response of biotypes to the modes of competition.

At harvest, the susceptible plants averaged 5 cm taller ($P \leq 0.001$) than the resistant plants when grown under inter-biotype competition, regardless of modes of competition or planting densities. The resistant biotype had a greater height under intra-biotype than inter-biotype competitions, whereas the opposite was true for the susceptible biotype.

The leaf area index (LAI) of the susceptible biotype was consistently greater than that of the resistant biotype, for all modes of inter-biotype competition (Figure 4). The greatest difference in LAI existed when biotypes competed for light or for both light and soil resources (full competition). The resistant biotype was less affected by the susceptible when competing for soil resources. In monoculture, the LAI did not differ ($P > 0.05$) between the two biotypes. As compared to full inter-biotype competition, the LAI of the susceptible biotype was much reduced by full intra-biotype competition, indicating that it is a greater competitor than the resistant biotype. At the highest planting density, the LAI of the resistant biotype was equivalent to that of the susceptible biotype at low planting densities, the biotype by planting density interaction being highly significant ($P \leq 0.001$). There was no planting density by mode of competition interaction.

The susceptible biotype had more leaves per plant ($P \leq 0.001$) than the resistant biotype, under all modes of inter-biotype competition (Figure 5). The susceptible biotype produced fewer leaves under intra- than inter-biotype competition. The smallest difference in

leaf number between the two biotypes existed for root competition while the highest was for shoot competition. The effect of shoot competition was similar to full competition. The plants produced fewer leaves as planting densities increased. At the highest density the susceptible biotype had a number of leaves similar to that of the resistant biotype at the lowest densities, thus causing a significant ($P \leq 0.05$) biotype by planting density interaction. There was no planting density by mode of competition interaction.

Both root and shoot competition between the two biotypes affected the growth of the resistant biotype proportionately more than that of the susceptible biotype. The relative severity of root and shoot competition will depend on the relative supply of the various limiting resources. In this study, root competition occurred despite the fact that soil was fertilized and kept close to field capacity. Water and nutrients should not have been the most limiting factors. The effect of competition for light amounted to that of full competition, whereas root competition had much less effect. This indicates that the susceptible biotype is a greater competitor for light than the resistant biotype. Such a result is not surprising because resistance to *s*-triazines is accompanied by a reduction in photosynthetic efficiency (Holt *et al.* 1983). Therefore, the susceptible biotype has a more efficient photosynthetic activity when biotypes are grown under the same environment. With time, the susceptible biotype accumulates more dry matter to develop a dense canopy over the less productive resistant biotype.

Marriage and Warwick (1980) have reported that *s*-triazine resistant seedlings of *C. album* had a slower growth rate than the susceptible seedlings up to 23 d after emergence. Thus the susceptible biotype starts with a marked competitive advantage over the resistant one during the initial stage of growth. According to the replacement series, this advantage is maintained during all stages of growth, resulting in greater growth and seed prolificity. Fitness is the evolutionary success of a biotype based on its survival and reproductive capacity (Crow 1986).

Fitness plays an important role in herbicide resistance models (Maxwell *et al.* 1990). In the presence of *s*-triazines, the resistant biotype is more fit than the susceptible because of its capacity to survive and reproduce. But in the absence of *s*-triazines, our data indicate that the susceptible biotype has a greater fitness. Resistance to *s*-triazines was consistently accompanied by reduced fitness when the herbicide was not used (Conard and Radosevich 1979; Holt *et al.* 1983; Marriage and Warwick 1980; Warwick and Black 1981; Weaver and Warwick 1982). If *s*-triazines herbicides are no longer used in a field, the weed population will revert naturally to susceptibility because of the greater fitness of the susceptible biotype. This information may be useful in implementing weed management strategies to combat resistance to *s*-triazines.

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