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The cost of herbicide resistance measured by a competition experiment

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Summary. The cost of resistance has been measured by a competition experiment over a range of densities, in the absence of herbicide treatment, on two nearly isogenic lines of Foxtail millet, differing in a chloroplastic resistance to herbicide. Three characters have been measured: shoot height, shoot weight, and seed production. Sensitive individuals were better competitors despite a larger decrease in production under within-biotype competition. The cost of resistance was density dependent and increased with density. The cost was higher when measured on seed production and reached 65% at the higher density for resistant individuals. This is compatible with the low frequency or the absence of that gene in natural populations. This work illustrates that the cost is easiest to observe when high levels of constraints are used.

Key words: Herbicide resistance – Cost of resistance – Competition – Density-dependent fitness – Substitution rates

Introduction

In 1956, when no case of herbicide resistance had yet been described, Harper (1956) predicted its appearance on the basis of bacteriological data and population genetics. Since then resistant populations or individuals have been found in numerous species (Ryan 1970; Souza-Machado et al. 1977; Gressel 1979; Mazur and Falco 1989).

In all computer simulations dealing with possible evolution of populations towards resistance, a complete invasion by resistant individuals is observed when there is no cost of resistance: once resistance appears somewhere, it is favored by the selective agent (herbicide, insecticide, etc.) and never selected against afterwards (Gressel and Segel 1978; Maxwel et al. 1990; and for resistance to insecticide: Georghiou and Taylor 1977a, b; Wood and Mani 1981; Tabashnik and Croft 1982). However, in natural and weed populations not subjected to herbicide treatment, it is very rare to find a high frequency of resistant individuals.

Because of its low cost and good efficiency, atrazine has been a much used herbicide for more than 25 years. The most common resistance is due to a point mutation on the chloroplastic *psbA* gene that encodes for a protein in the thylakoid membrane in the chloroplast (Hisberg and McIntosh 1983). Photosynthetic electron transport becomes roughly 1,000-fold less sensitive to atrazine compared to the wild-type chloroplast. A comparison between photosynthetic performance of resistant and suceptible biotypes of *Amaranthus hybridus* has shown that the quantum yield of CO_2 reduction was 23% lower in the resistant biotype (Ort et al. 1983). Ricroch et al. (1987) showed that there is a decrease in the rate of Qa to Qb electron transfer in resistant plants of *Setaria.* We therefore hypothesized a possible pleiotropic effect between cost of resistance and changes in metabolism and resource allocation. A large literature exists on the ecological fitness of biotypes suceptible or resistant to atrazine (Radosevich and Appleby 1973; Conard and Radosevich 1979; Holt and Radosevich 1983; Gressel and Ben Sinai 1985; Holt 1988). The outcome is that resistant individuals always produce less biomass than sensitive individuals, but none of these studies tests the evolution of the cost of resistance on a range of densities. Since resource allocation should vary with density, density can be expected to have a major effect.

The aim of the present research was to investigate whether or not the cost of resistance varies with density, using the competitive interaction between resistant and sensitive individuals in the absence of herbicide at variable densities, thus changing the total available resource per individual. The plant model was foxtail millet (*Setaria italica*), in which closely related sensitive and resistant individuals were obtained.

We used three different forms of analysis to detect the cost of resistance: the de Wit replacement series, the substitution rates, and also size hierarchy. The replacement series' design and mixture experiments have been the subject of several recent review articles (Dekker et al. 1983; Radosevich 1987, 1988; and Connolly 1987). The concepts proposed by de Wit (1960) and de Wit and Van Den Bergh (1965) and the use of this design proposed by Firbank and Watkinson (1985) for determining the respective value of within- and among-type competition provided the basis for the cost of resistance analysis.

Materials and methods

Setaria virdis is an annual grass. Primarily a weed of roadsides, gravel pits, and waste lands, it also occurs as isolated infestations of crops and fields. *Setaria italica* (foxtail millet) is a cultivated cereal used for birdseed or as staple food (China, Japan). It freely hybridizes with *Setaria viridis* despite a selfing rate of more than 98% (Li et al. 1945; Brabant 1982).

Cytoplasmic resistance to atrazine has been found in populations of *S. viridis major,* a naturally stabilized hybrid between *S. italica* and *S. viridis.* A diallel mating design with a Chinese variety of *S. italica* ("change en viellissant") gave resistant and sensitive F_1 hybrids. These hybrids were then multiplied and backcrossed four times to the crop variety (Darmency and Pernès 1985, 1989). The sensitive and resistant material is largely isogenic for nuclear genes (as the character selected in the backcross has a cytoplasmic inheritance), and we suppose that there is little difference in cytoplasmic genes, except for the one producing herbicide resistance. A residual problem is that the sensitive cytoplasm is then again with its original nuclear environment, whereas the resistant cytoplasm is not. Consequently, possible nuclear/cytoplasmic conflicts and cost of resistance cannot be distinguished.

The competition experiment

Planting arrangement. A basic mixture experiment consisting of sensitive and resistant plants was established in pots in the greenhouse. Each pot of $144 \text{ cm}^2 \times 13$ cm was filled with a 50:50 mixture of silty soil and mold. No fertilizer was added during the experiment. Six different densities were used: 1 (=69.4 plants/m^2), 4, 18, 36, 54, and 72 individuals per pot (=5,000 plants/m^2). For each pot, six seeds were planted in a line, the number of lines giving the total density (except, of course, for one and four plants per pot). The replacement series consisted of only three planting ratios at each density: 100:0, 50:50, and 0:100. The spatial arrangements for the 50:50 mixture were made by alternating sensitive and resistant lines. In instances where a seed did not germinate, a seedling (sowed at the same time in vermiculite) was carefully transplanted as a substitute. During germination, pots were watered daily to ensure uniform seedling emergence and thereafter two or three times per week to prevent wilting.

Each combination of density *ratio was repeated six times. Three replicates were harvested at the first spike emergence of the whole experiment and used to determine growth indices; the three other pots were harvested at seed maturity in order to estimate the fitness value of individuals.

Pots were moved randomly every 3 days to minimize border effects.

Determination of growth indices. The following indices were calculated.
Relative yield (r):
$ra = Xab/Xaa$ (De Wit and Van Den Bergh 1965).
$rb = Xba/Xbb$.
Relative yield total (RYT):
$\text{RYT} = ra + rb$ (De Wit and Van Den Bergh 1965),
where ra = relative yield of genotype a.
Xab = yield of genotype a in mixture with b.
Xaa = yield of genotype a in pure stand.

Growth. All plants were harvested when the first spike of the whole experiment emerged. For each pot, plants were harvested by cutting the shoots at ground level and spatial position was noted. Each plant was weighed and measured. For each pot, the size distribution was analyzed.

Relative fitness. Spike length was measured on all plants. The number of mature seeds was counted for a sample of more than 250 spikes. When there was more than one spike per plant all were harvested.

The data was subjected to analysis of variance. Confidence limits were taken at 95% unless noted otherwise.

Results

In the first experiment, when plants were harvested before flowering, we obtained a log-like relationship between the height of shoots and the weight of shoots. After a log transformation of the weight, the curves became linear except for the small values, which contribute most to the residual variance. Because the correlation coefficients were never lower than 0.94 ($df > 270$), the results will be presented as either a function of the weight or the height of the plants. In the second experiment we used a sample of more than 250 plants to study the correlation between spike length and number of mature seeds per spike. Due to the shape of the resulting curve, a log/log transformation was done. As the correlation coefficient was then greater than 0.88, we used it to transform spike lengths into number of seeds, taking into account the individuals with more than one spike.

The cost of resistance

For the total experiment, resistant plants were significantly lighter (3.89 g compared to 6.13 g for sensitive plants = 36.5% decrease) and had significatively shorter spikes (2.55 cm compared to 3.31 cm for sensitive plants = 23% decrease) ($P < 0.001$).

Influence of density. Both sensitive and resistant plant weight and spike length, in pure stands as well as in mixtures, decreased significantly as density increased

Table 1. Analysis of variance on shoot size from the total experiment (six densities, three ratios, and three replicates). Model: shoot size = constant + density effect (d) + pure/mixture effect (p/m) + sensitive/resistant effect (s/r) + s/r response to p/m + s/r response to d * p/m + residual

Source	Sum of squares	*df*	Mean square	*F*-ratio	*P*
d	428,872.033	5	85,774.407	185.539	0.000
p/m	281.268	1	281.268	0.608	0.436
s/r	68,194.997	1	68,194.997	147.513	0.000
s/r * p/m	1,409.145	1	1,409.145	3.048	0.081
s/r * d * p/m	6,292.777	5	1,258.555	2.722	0.019
residual	668,484.200	1,446	462.299		

Note: data were untransformed. Log-transformation did not improve normality and gave essentially similar results. As there is no possible mixture with one plant per pot, data for one plant per pot were eliminated in pure/mixture interaction with density

Table 2. Analysis of variance on shoot weight from the total experiment (six densities, three ratios, and three replicates). Model: shoot weight = constant + density effect (d) + pure/mixture effect (p/m) + border effect + sensitive/resistant effect (s/r) + s/r response to d + s/r response to p/m + s/r response to d * p/m + residual

Source	Sum of squares	*df*	Mean square	*F*-ratio	*P*
d	62,623.035	5	12,524.607	665.311	0.000
p/m	132.897	1	132.897	7.060	0.008
border	227.116	8	28.389	1.508	0.149
s/r	2,671.566	1	2,671.566	141.914	0.000
s/r * d	2,742.855	4	685.714	40.726	0.000.
s/r * p/m	180.731	1	180.731	9.600	0.002
s/r * d * p/m	847.751	5	169.550	9.007	0.000
residual	30,948.605	1,644	18.825		

Note: the same footnote as in Table 1 applies

Table 3. Analysis of variance on spike length from the total experiment (six densities, three ratios, and three replicates). Model: spike length = constant + density effect (d) + pure/mixture effect (p/m) + border effect + sensitive/resistant effect (s/r) + s/r response to d + s/r response to p/m + s/r response to d * p/m + residual

Source	Sum of squares	*df*	Mean square	*F*-ratio	*P*
d	366,536.217	4	91,634.054	197.299	0.000
p/m	8.015	1	8.015	0.017	0.896
border	5,938.268	8	742.283	1.598	0.121
s/r	37.184	1	37.184	0.080	0.777
(s/r−d=1	11,006.427	1	11,006.427	24.378	0.000)
s/r * d	9,938.361	4	2,484.590	5.350	0.000
s/r * p/m	2,332.857	1	2,332.857	5.167	0.023
s/r * d * p/m	19,240.937	4	4,810.234	10.357	0.000
residual	613,065.640	1,320	464.444		

Note: the same footnote as in Table 1 applies. Fifty-four and 72 plants/pot densities were pooled

(density in Tables 2 and 3). However, the response was different for resistant and sensitive individuals (s/r and s/r*d in Tables 2 and 3) and depended also on the culture conditions, whether pure stand or mixture (s/r*d*p/m in Tables 2 and 3).

The resistant plants behaved as if they experienced less constraints than sensitive plants when density increased. For example, in pure stands, there was a 51.9% decrease in shoot weight for resistant plants between medium and high densities (36 versus 72 plants/pot), whereas the decrease was more than 60% for the sensitive plants.

Influence of competition. Even at the highest density (5,000 plants/pot) there was no self-thinning. In mixture, sensitive plants always had a significantly higher yield than in pure stand. **Conversely, resistant individuals in mixture experienced a significantly higher decline in shoot yield and seed production compared to the pure stand** (cf p/m, s/r*p/m, and s/r*d*p/m in Tables 2 and 4).

Replacement series

The replacement diagrams between sensitive and resistant plants for the different densities are illustrated in Figs. 1 and 2.

Analysis of the diagrams. For more than four plants per pot, the curve of weight as a function of ratio for sensitive individuals is convex, while for resistant plants it is concave, indicating the existence of a competitive relationship between these different cytoplasmic genotypes (Harper 1977), i.e., susceptible biotype is a better competitor than resistant biotype. The effects were more pronounced as density increased.

The relative yield and relative yield total indices measured are summarized in Table 5. At low densities, the 50:50 mixture gave an intermediate yield. Consequently, the RYT (ratio between yield of mixture pots and mean yield of the two pure stand pots) did not differ significantly from 1, i.e., there was no evidence of increased performance when the two genotypes were grown in mixture. At medium and high densities (from 36 to 72 plants per pot), mixtures were always significantly out-yielding and the RYT was greater than unity (p/m in Table 2). On the whole, the mixture gave a better result than pure stands.

Different results were obtained when examining the size of shoots or seed production: the mixture was always intermediate between the pure stands and the RYT did not differ significantly from 1, i.e., p/m in Tables 1 and 4. Seed production seems to be inferior at high densities but the high variance masks any significant effect.

Table 4. Analysis of variance on number of seeds from the total experiment (six densities, three ratios, and three replicates). Model: number of seeds = constant + density effect (d) + pure/mixture effect (p/m) + sensitive/resistant effect (s/r) + s/r response to d + s/r response to p/m + s/r response to d * p/m + residual

Source	Sum of squares	*df*	Mean square	*F*-ratio	*P*
d	0.166781E+09	4	0.416953E+08	579.814	0.000
p/m	100,513.263	1	100,513.263	1.398	0.237
s/r	242,161.975	1	242,161.975	3.367	0.067
(s/r−d=1	571,091.201	1	571,091.201	12.321	0.000)
s/r * d	1,670,133.419	4	417,533.355	5.806	0.000
s/r * p/m	231,800.773	1	231,800.773	5.001	0.025
s/r * d * p/m	1,598,965.043	4	399,741.261	5.559	0.000
residual	0.949232E+08	1,320	71,911.539		

Note: the same footnote as in Table 1 applies. Fifty-four and 72 plants/pot densities were pooled

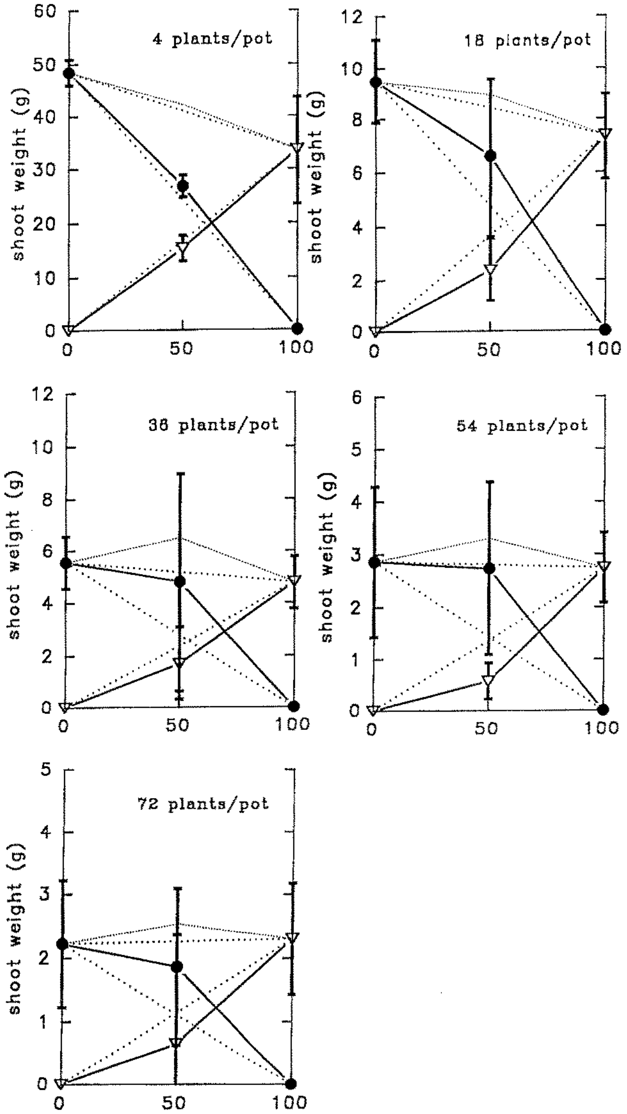

Fig. 1. Mean shoot weight (g) of sensitive (●) or resistant (▿) *Setaria italica* in de Wit (1960) replacement series. The 95% confidence limits are shown as vertical lines. ———: total yield of the mixture; ······: theoretical yield of the two biotypes if among-biotype competition is identical

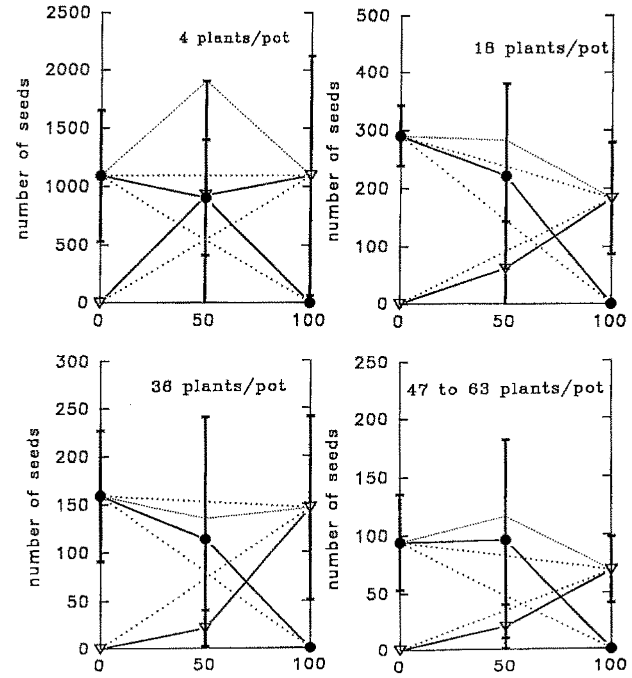

Fig. 2. Number of seeds of sensitive (●) or resistant (▿) *Setaria italica* in de Wit (1960) replacement series. The 95% confidence limits are shown as vertical lines. ———: total yield of the mixture; ······: theoretical yield of the two biotypes if among-biotype competition is identical

Substitution rates (Connolly 1987). The substitution rates calculated for each type (genotype, cultivar, variety, species, etc.) in a particular mixture are used to assess how the individuals of one type compensate for individuals of the other type. For example, a substitution rate of 2 for one taxon in a two-taxa mixture means that a substitution of one individual of the second taxon for two individuals of the first taxon leaves the yield of individuals of the first taxon unchanged (Note that there are slight differences between the definitions given by Connolly and Nolan 1976; Nunney 1980; Suehiro and Ogawa 1980; Spitters 1983; Firbank and Watkinson 1985.)

Table 5. Growth indices for shoot weight, shoot height and seed production measured from the total experiment (six densities, three ratios, and three replicates)

Density	*ra*	*rb*	RYT = *ra* + *rb*
Shoot weight			
4	0.554	0.459	1.013
18	0.694	0.323	1.017
36	0.865	0.481	1.346
54	0.952	0.240	1.192
72	0.843	0.290	1.133
Shoot height			
4	0.528	0.546	1.074
18	0.561	0.435	0.996
36	0.574	0.462	1.056
54	0.594	0.396	0.990
72	0.603	0.402	1.005
Seed production			
4	0.830	0.851	1.681
18	0.759	0.336	1.095
36	0.717	0.217	0.934
43	0.682	0.241	0.923
51	0.636	0.250	0.886
58	0.665	0.208	0.873

Table 6. Substitution rates measured on shoot height

Cost of a sensitive individual for a resistant plant

Mixture dens.		Equivalent resist. dens.	Substit. rate
9*s* + 9*r*	=	29*r*	2.22
12*s* + 12*r*	=	39*r*	2.25
15*s* + 15*r*	=	49*r*	2.27
18*s* + 18*r*	=	59.5*r*	2.30
20*s* + 20*r*	=	66.5*r*	2.33
21.5*s* + 21.5*r*	=	72*r*	2.35

Correl. coeff. = 0.992, $\alpha = 0.0001$

Cost of a resistant individual for a sensitive plant

Mixture dens.		Equivalent sens. dens.	Substit. rate
14*s* + 14*r*	=	18*s*	0.29
18*s* + 18*r*	=	23*s*	0.28
22*s* + 22*r*	=	28*s*	0.27
25*s* + 25*r*	=	32*s*	0.28
26*s* + 26*r*	=	33*s*	0.27
30*s* + 30*r*	=	38*s*	0.27
33*s* + 33*r*	=	42*s*	0.27
36*s* + 36*r*	=	46*s*	0.28

Correl. coeff. = 0.5137, $\alpha = 0.19$

Table 7. Substitution rates measured on seed production

Cost of a sensitive individual for a resistant plant

Mixture dens.		Equivalent resist. dens.	Substit. rate
9*s* + 9*r*	=	29*r*	2.22
12*s* + 12*r*	=	44*r*	2.67
15*s* + 15*r*	=	59*r*	2.93
17.5*s* + 17.5*r*	=	71*r*	3.06

Correl. coeff. = 0.9561, $\alpha = 0.0439$

Cost of a resistant individual for a sensitive plant

Mixture dens.		Equivalent sens. dens.	Substit. rate
15*s* + 15*r*	=	18.5*s*	0.23
19*s* + 19*r*	=	26*s*	0.27
23*s* + 23*r*	=	34*s*	0.48
28*s* + 28*r*	=	44*s*	0.57
33*s* + 33*r*	=	55*s*	0.67
36*s* + 36*r*	=	61.5*s*	0.71

Correl. coeff. = 0.9266, $\alpha = 0.0079$

Therefore, the substitution rate for a given genotype in a sensitive/resistant mixture measures the value of an individual of the other genotype in terms of its own individuals. After fitting the log-linear model to the data over a range of densities from 18 to 72 plants per pot, we were able to calculate the substitution rates. For example, resistant individuals in a mixture of 15 resistant and 15 sensitive plants were on average the same size as 49 resistant plants in the pure stand. Thus, the 15 sensitive plants could be substituted for by 34 resistant plants; the substitution rate in this case would be 0.44, signifying that one resistant individual equals 0.44 sensitive individual.

The results are given in Tables 6 and 7. The correlation coefficients indicate that substitution rates are dependent on density when seed production is used, but not when height is used (Tables 6 and 7). In all cases, for a resistant plant the sensitive plant is worth more than one resistant plant, but the relation is not symmetrical: i.e., a resistant plant is more constrained than the inverse constraint sustained by a sensitive plant.

Discussion

If greenhouse experiments are reliable models of natural situations, the lower fitness of the resistant type in the absence of herbicide treatment could partly explain the rare occurrence of atrazine resistance in natural populations as the advantage of resistance is balanced by a cost in growth and seed production.

At low density, there may be no detectable cost of herbicide resistance even on seed production. Stowe and Holt (1988), when looking for a possible cost of atrazine resistance in *Senecio vulgaris* at a single density (one plant/pot) after 6, 8, and 10 weeks of growth, found that the cost of 60% at 6 weeks was only 30% after 8 weeks, and was less than 2% after 10 weeks (measured on root + shoot + leaf dry weight). Therefore, it seems that resistant individuals are able to compensate for the cost over the growing season. Such a result could explain why we found no cost at low densities on seed production (i.e., after the compensation of cost over time) and a cost on height and weight of shoot parts measured before the flowering season (i.e., before the compensation of cost over time).

The De Wit replacement series give rapid qualitative results. However, without a range of increasing densities, there is no way to measure or even separate within- and among-biotype competition in mixture, because the perceived density by plants is different from planting density and from the ratio of the two biotypes. The perceived density can be approached by measuring substitution rates.

We found that the cost of resistance is highly dependent not only on total density, but also on relative density, since substitution rates are different from 1 and therefore the perceived total density for each individual will change at each generation. Thus, if one aims to predict whether resistance will decrease or be maintained in populations not submitted to herbicide treatment, the fitness of resistant and sensitive plants must be estimated in each particular case (each generation, density, mixture, etc.). The cost of resistance also varied according to the character.

The output of measures

Depending on the character, the outcomes and conclusions will be different. A nondestructive measure such as shoot height is enough to determine qualitative competitive interactions between sensitive and resistant biotypes (the sensitive biotype was always a better competitor compared to the resistant type and the measure cost was 12.4% of the mean value but independent of density). A destructive measure (shoot weight) made it possible to detect some "out yielding" effect, but still did not reflect the evolution of fitness with density, as substitution rates did not change much with increasing densities.

The highest cost of resistance was observed on seed production for densities higher than 1,250 plants/m^2. This cost clearly increased with density and reached 65.25% at 4,028 plants/m^2 for seed production. This character is a rough measure of fitness as *Setaria* is highly selfing, although a better approach of fitness would, of course, need to test whether or not germination rates of resistant and sensitive seeds are different depending on growth conditions (density, mixture etc.).

Validity of predictions

The fitness of sensitive and resistant plants at any density or ratio, on the tested range of densities, can be predicted if the response curve to within-biotype competition (response of pure stands to densities) and the substitution rates are known. However, in order to predict the frequency trend for resistant plants in a population (as a stochastic process), the distribution of size or "fitness" of the individuals is as important as the mean value, and moreover the distribution may vary according to density.

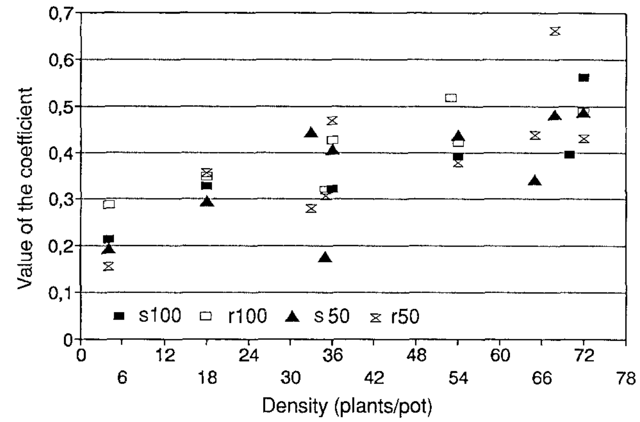

Fig. 3. Gini coefficient measured on shoot weight over the range of densities. At 4 and 18 plants/pot, the three replicates were pooled as one measure. "s100" and "r100" are the measures, respectively, on sensitive and resistant pure stand pots, "s50" and "r50" are the measures, respectively, on sensitive and resistant individuals of mixture pots. The regression slopes are all significant different from 0

As described by Yoda et al. (1963), Obeid et al. (1967), Ford (1975), Knox et al. (1989), and Weiner and Solbrig (1984), the distribution of size in plant populations often reveals an excess of small individuals and a lack of medium ones. Different coefficients may be used to measure the skewness or asymmetry of a distribution. Accoring to Knox et al. (1989), these coefficients provide robust indicators of density effects on growth and size-selective mortality. In our experiment we found that the Gini coefficient measured on shoot size or weight, increased with density, showing an increase of size inequality with density as shown in Fig. 3. The Gini coefficient is determined as $\sum_i \sum_j |x_i - x_j| / 2n(n-1)\,\bar{x}$. The terms x_i and x_j are measures of the character for individuals i and j, n is the number of individuals in the pot, and $\bar{x}$ is the mean value of the character over the whole pot.

Since seed production is correlated with shoot size, an abnormally large proportion of genes in a population may come from a very small number of individuals of the previous generations (Leverich and Levin 1979). Thus, this inequality of distribution will increase the variance and skewness, and therefore may result in a possible longer (or shorter) maintenance than predicted of resistance at higher densities, since some of the large individuals may be resistant. The validity of the predictions based on fitness measures of cost thus decrease when density increases.

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