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A selection response plateau for radiation resistance in the cotton boll weevil

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Summary. Twenty generations of family selection in the cotton boll weevil for 14-day postirradiation survival to 10,000 rads of gamma irradiation has increased survival to nearly 90% as compared with about 35% in the unselected control population. Mean survival time has increased to 21.2 days in the selected population, as compared with 12.8 days in the unselected control. Nearly all of the response to selection occurred in the first 12 generations of selection, with no significant improvement beyond that point. A relaxed selection line was established in generation 12 and has been maintained as a population cage with discrete generations since that time. A comparison in generation 17 between the relaxed selection population and the selected population where both populations were managed in the same way indicated that none of the increase in resistance had been lost due to relaxation of selection (89.2% survival in the relaxed population as compared with 86.0% in the selected population). The rapid increase in response to selection followed by a quick plateau and no decline in the mean following relaxation of selection support the hypothesis that the increased resistance to irradiation resulted from changes in allelic frequencies for a relatively small number of genes. Alleles for increased resistance were either fixed by the selection process or, if still segregating, were not negatively correlated with fitness. Estimates of heritability for other fitness traits indicate selection should be effective for several other traits of importance in the efficiency of a mass rearing program.

Key words: Selection – Radiation resistance – Selection plateau – Cotton boll weevil

Introduction

In recent years the mass release of sterile insects has been an important part of pest management or control programs for several species. While the techniques for producing the sterile insects have varied somewhat, the use of irradiation has been the most common tool for the sterilization process. A major problem, of course, in the use of radiation is its deleterious effects on somatic cells as well as the germ line. As a result irradiated individuals may be rendered relatively ineffective as breeding individuals with a much shortened life expectancy. Our interest in this study was to determine whether there was genetic variability within the cotton boll weevil, *Anthonomous grandis* Boheman, for resistance to irradiation and, if so, whether it was possible to develop a strain with more resistance and a longer life expectancy. A selection experiment was initiated for 14-day postirradiation survival to test for this variation. During the course of the experiment several other fitness traits considered to be important in a mass rearing program also were measured. An earlier paper (Enfield et al. 1981) described the response to selection during the early generations of the experiment and the evidence for considerable genetic variability in the base population for radiation resistance. This paper will concentrate on (1) total response to a plateau for 14-day postirradiation survival, (2) the impact of selection for radiation resistance on other fitness traits, and (3) genetic parameters for other fitness traits of importance in mass rearing and the impact of inbreeding on mean performance of these traits.

Materials and methods

The selection experiment was initiated from a broad base laboratory strain that originated from crossing samples of six wild populations obtained from the cotton growing areas of the United States. A laboratory strain containing the homozygous Ebony mutant was also introduced into the original synthetic to provide a marker for future field testing studies.

The trait chosen for the selection criterion was 14-day postirradiation survival. The selected population was initiated by sampling 30 males and 60 females from the synthetic population which had undergone four generations of random mating before the start of the experiment. The synthetic population was maintained as a large random breeding control population (with discrete generations) which was sampled every four generations to measure the effects of selection. Both the selected and control populations were maintained on a 49-day generation cycle. In generation 12 a sample of the selected population was taken and handled as a random breeding, random selected population until generation 17. At that time a comparison was made between the selected and relaxed-selection line to determine the effects, if any, relaxing selection pressure was having on the population.

In the selected population, 35 males were each mated to 2 females each generation which under perfect conditions with no sterility would provide data on 70 full-sib and 35 half-sib families. Each female was allowed to oviposit for ten days, and eggs were collected daily. On a 49-day generation schedule, females were approximately sixteen days old when egg collections began. Eggs were placed on larval diet daily. Records were kept on egg production, number of larvae and pupae, and adult emergence. In generations where comparisons with the control populations were made these experimental procedures were used in the control as well.

In the selected population four males and four females were saved from each full-sib family, for potential breeding for the next generation. In a limited number of cases this number was reduced to insure radiation data on at least three individuals per sex per family. All other individuals were irradiated at two days postemergence with 10 krads of ^{60}Co gamma rays at an average dose rate of 6,130 rads/min. The average percent survival at fourteen days postirradiation was determined for each family. The criterion for chosing parents for the next generation was the mean survival for the half-sib family. The unirradiated individuals whose irradiated half-sibs had the best survival were chosen as parents for the next generation. In generation 19 when it had become apparent that the population had plateaued, the selection criterion was changed to 21-day postirradiation survival. This will be continued for several generations to determine whether there is additional genetic variability that can still be utilized to further increase longevity. Complete pedigree data were maintained on all selected population individuals and coefficients of inbreeding were calculated for all selected families each generation. This enabled us to evaluate the effects of inbreeding of the dam or her progeny on various fitness traits of importance in a mass rearing program. Since level of inbreeding is confounded with generations of selection, all analyses involving inbreeding effects were done on a within generation basis.

Results and discussion

The pattern of response to selection for postirradiation survival is shown graphically in Fig. 1. Data are plotted for each generation in the selected population and every fourth generation in the control. By the eleventh generation mean survival had reached nearly 90% where it was to remain at a plateau for the next nine generations with very little fluctuation around that point. The accumulated response of approximately 65% was accomplished with a cumulative selection differential of 132 in the first eleven generations. This represents a realized heritability for half-sib family means of approximately 0.4 for this period.

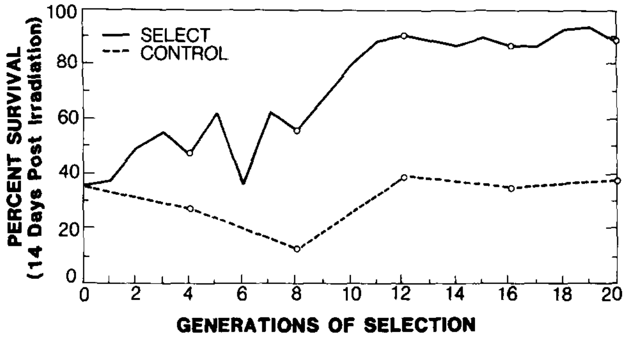

Fig. 1. Response to 20 generations of selection for 14-day postirradiation survival

There is the question at the plateau of whether additive genetic variance had been exhausted or whether the selection differential had been sufficiently reduced to render selection ineffective. Two pieces of data bear on this point. First, accumulated selection differential for generations 12 through 19 was 56 (seven per generation), which should have enabled further advance if additive genetic variance remained and there was no negative correlation with fitness. Data will be presented later to argue that the latter was not an issue. Second, estimates of heritability obtained from dam-daughter regression analyses strongly suggest that selection had been effective in exhausting additive genetic variance. These estimates pooled for the first ten generations and the last ten are given in Table 5 along with heritability estimates for other traits. Even though sampling errors for these estimates are large, the best statistical estimate of heritability for the last ten generations is zero.

The rapid response to selection followed by an early plateau is consistent for traits with a relatively small number of genes with large effects. Using the methodology for the nonepistatic model described by Comstock and Enfield (1981), the number of genes affecting the trait can be approximated from the information on the total response to selection and the initial additive genetic variance. Using values of 55 and 465 for these two parameters, the best estimate of number of segregating genes in the base population would be three. The estimate of additive genetic variance was obtained from the realized heritability estimate of half-sib family means, which has as its expected value: 1/4 additive genetic variance/phenotypic variance of half-sib family means.

Figure 2 provides a comparison of the 28-day mortality curves for the selected and control populations in generation 20. The curves for the two populations in generations 12 and 16 are nearly identical to this. These data can be summarized in several ways. Fourteen-day postirradiation mortality has been reduced to 12% in the selected population as compared with 63% in the controls. The half-life (number of days postirradiation for 50% mortality) was increased by 8.4 days from 12.8 in the controls to 21.2 in the selected population. It was thought initially that an increase in life expectancy of one week should have a dramatic impact on the utility of the strain as a sterile release stock if the laboratory results carried into the field. Finally, a maximum difference in mortality occurs at the sixteenth day postirradiation where the two strains differ by 59% in mortality.

A very important practical question is whether the gain in survival will be maintained under mass rearing, random mating conditions or whether natural selection will decrease mean survival. Table 1 provides a comparison in generation 17 between the selected population and the relaxed selection population that had been random mated in a population cage since generation 12 when the plateau had apparently already been reached. There is no indication that artificial selection was required to maintain the high level of survival. This comparison provides further evidence that the limited number of genes affecting 14-day postirradiation survival had indeed been fixed by generation 12. No significant differences were observed for other fitness parameters between the two populations although there is some suggestion of less sterility in the population where selection had been continued.

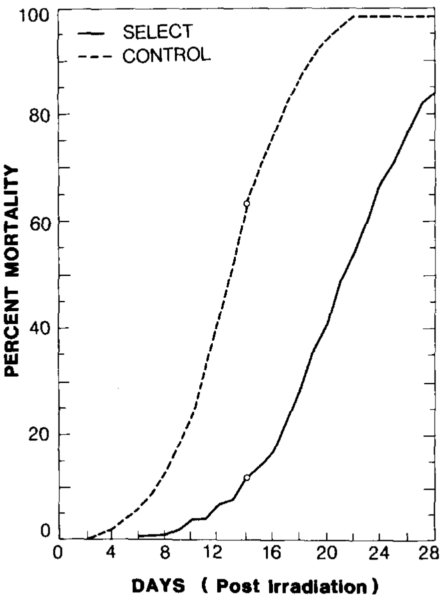

Fig. 2. Generation 20 mortality curves for the selected and control populations

Table 1. Generation 17 comparisons between the selected and relaxed populations

	Selected population	Relaxed population	Difference (S–R)
Irradiation survival	86.0	89.2	−3.2±3.3
Percent sterility	26.0	40.0	14.0±8.0
10-day egg production	43.5	40.9	2.6±4.4
Percent egg-adult survival	46.9	49.9	−3.0±2.6

Table 2. Linear regression coefficients of fitness traits on generations of selection

Trait	b±SE
Percent sterility	−0.41±0.27
10-day egg production	−0.17±0.27
10-day production of adults	−0.16±0.12
Percent egg to adult survival	0.60±0.16

Since longevity is only one of many traits of importance in a mass rearing stock, we have collected considerable data on other fitness parameters to determine their interrelationships and the feasibility of attempting genetic improvement for other traits. The impact of the selection for postirradiation survival on other traits is of interest. Table 2 shows the changes for several fitness traits in the selected population as measured by linear regression coefficients over the twenty generations. It should be emphasized that at least three forces may be operating in these time trends. They are (1) the effects of selection, (2) accumulative effects of inbreeding over time, and (3) adaptation to an artificial diet and laboratory conditions. These effects can be sorted out somewhat better by the additional data in Table 3 comparing the selected population and control population means in generation 20 along with the original base population mean for each trait. The control population differs from the selected population not only by the effects of selection, but also by level of inbreeding. Because of finite population size ($N_e \cong 33$) the inbreeding level had reached nearly 30% in the selected population by generation 20. Inbreeding effects in the control would be trivial because of the large populations maintained. Both populations would have undergone the same number of generations of laboratory adaption with a greater opportunity for natural selection in the control population.

Taking the data in total, it appears that selection for postirradiation survival has a positive effect on fertility.

Table 3. Generation 20 comparisons between the selected and control populations

	Generation 0	Generation 20		
	Base population	Select	Control	S–C
14-day postirradiation survival	34.9	87.9	37.2	50.7±2.9
Percent sterile matings	33.0	26.0	46.0	-20.0±7.0
10-day egg production	41.5	43.5	68.2	-24.7±6.6
10-day adult production	23.0	22.2	35.9	-13.7±3.4
Percent egg-adult survival	37.6	52.6	56.5	-3.9±2.8

Inbreeding per se would be expected to have a negative effect on this and other fitness traits. The correlated response was apparently strong enough to overcome this effect.

There appears to be little change in either egg production or total adult production over time in the selected population. An increase in both in the control population can most easily be explained by adaptation to laboratory conditions. The improvement in egg to adult survival in both populations probably represents natural selection for survival on an artificial diet.

The effects of inbreeding on the various parameters are given in Table 4. These data were calculated on a within generation basis to remove the confounding effects of selection. Individual generation estimates were then pooled by weighting each generation inversely to the variance of the estimate. Since the variation in level of inbreeding within a generation is low, standard errors are large. All estimates are in the direction expected however, with the greatest effect of inbreeding being on egg to adult survival.

Finally, estimates of heritability were obtained for those traits of importance in the efficiency of mass rearing. These are presented in Table 5. Heritability of egg production is low as is commonly the case. The heritability of both adult production and egg to adult survival would indicate improvement in both through selection should be possible. The former is probably largely a function of egg to adult survival since egg production itself is lowly heritable.

Table 4. Summary of regression of fitness parameters on level of inbreeding within generations

Trait	b±SE
Egg to adult survival-progeny inbreeding	-0.46±0.26
Irradiation survival-progeny inbreeding	-0.24±0.26
10-day egg production-dams inbreeding	-0.04±0.27

Table 5. Estimates of heritability for fitness traits from dam-daughter regression analyses

10-day egg production	0.14±0.08
10-day adult production	0.32±0.08
Percent egg-adult survival in family	0.26±0.08
Family irradiation survival	
Generations 1–10	0.22±0.14
Generations 11–20	0.00±0.18

Prior to this work experiments with other insect populations had suggested the possibility of genetic variation for radiation resistance. The work of Stahler (1971) and Terzian and Stahler (1966) indicated that selection for radiation resistance was effective in the mosquito. Brower et al. (1973) however, were not able to demonstrate that selection was effective in increasing radiation resistance in the flour beetle. The nature of genetic variation for radiation resistance in *Drosophila melanogaster* was shown by Westerman and Parsons (1972, 1973) to be a function of radiation level; the higher the radiation level the more additive the effects appeared to be. Eiche (1973) used chromosome substitution techniques in *Drosophila* to demonstrate that genes for radiation resistance were scattered on several chromosomes making the trait polygenic in nature. This supported the earlier work of Parsons et al. (1969) who showed that polymorphic genes with additive effects were associated with both the second and third chromosomes in *Drosophila.* The analyses of Ogaki and Nakashima-Tanaka (1966) supported the hypothesis of a very limited number of genes for radiation resistance located at the far end of chromosome III. Their reciprocal cross data also suggested the alleles for resistance were dominant rather than additive.

Robertson (1967) suggested that most quantitative genetic variation can be attributed to a small number of genes with large effects. Falconer (1960) in summarizing results from many of the early selection experiments indicated that progress from selection usually will cease by 25 generations. This experiment is consistent with both of those views.

On the other hand, more recent experiments of Enfield (1977), Yoo (1980), and Dudley (1977) have shown that progress from selection may continue for 50 to 100 generations and that very large numbers of genes are responsible for the continuing response. Hill (1982) argues that the larger effective population sizes of these experiments had permitted recurrent mutation to be an ongoing source of new variation for further progress from selection. Enfield (1981) pointed out that a very large number of factors are involved in the limits to response and that no single selection experiment has or can evaluate the relative importance of all of these factors.

An overview of all of the selection experiments suggests that there is no reason to expect quantitative traits as a class to respond to selection in the same way; i.e., trait specificity is likely to be highly important. Radiation resistance in this and most other experiments appears to best fit that class of quantitative traits affected by a relatively small number of genes with large effects.

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