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Comparison of population growth rates of malathion resistant and susceptible populations of the rice weevil, Sitophilus oryzae (Linnaeus) (Coleoptera:Curculionidae)

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Summary

Population growth parameters of malathion resistant and susceptible populations of the rice weevil *Sitophilus oryzae* (Linnaeus) were compared at temperatures of 20°, 25° and 30°C and a relative humidity of 70%. Five datum populations were used, namely a laboratory reference susceptible culture, a composite field susceptible culture, a field resistant culture, its selected derivative, and a resistant reference culture. The F_1 hybrid offspring of the field susceptible and selected field resistant population was treated as a sixth population.

Resistant populations were not demonstrably different overall from susceptible populations. Although differences were present they were not relatable to resistance and, hence, appeared to be consistent with normal species variation. Observed interactions between temperature and the primary parameters of development, oviposition, and adult longevity, emphasized the importance of using a range of conditions when undertaking an assessment of this nature. The relevance of the parameters, intrinsic rate of natural increase, net reproduction rate and mean generation time to the selection process for resistance is discussed.

1. INTRODUCTION

There is considerable evidence that resistant insects are likely to be less fit or competitive than the susceptible populations from which they were derived (Brown 1967). Where it occurs, this condition could have important implications for the development of resistance and subsequently for the stability of resistance in populations. For populations of grain beetles such as the rice weevil *Sitophilus oryzae* (Linnaeus) the actual growth rate of populations is particularly important. This is because, in the absence of effective control measures, the size of an infestation in a large grain bulk depends on storage time alone, as space and food supply are virtually unlimited. If it is accepted that biological fitness will be reflected in the growth rate of a population, a less fit resistant population would give rise to a smaller infestation than a more fit susceptible population.

In addition to the direct influence of biological fitness on the rate of development of infestations, differential rates of development in mixed populations of resistant, hybrid and susceptible types would influence the composition of eventual populations. For these mixed populations, the more fit type would give rise to bias in the effects of selection or become dominant in the absence of insecticide treatment.

Development of resistance, then, is influenced by biological factors including reproductive competitiveness of the resistant phenotypes and the number of generations on which selection operates (Georghiou and Taylor 1977a). Relevant aspects of the biology of *S. oryzae* were studied in detail by McLagen and Dunn (1935), Birch (1945a,b,c), Richards (1946) and Evans (1977), while the biology of the genus *Sitophilus* was reviewed by Longstaff (1981). The study

reported in this paper was undertaken to compare rates of population growth and related parameters as measures of the biological fitness of malathion resistant and susceptible populations and their inter-population hybrids.

The intrinsic rate of natural increase, r_m, and related parameters (Birch 1948) were utilized as an estimate of overall fitness because they integrated more primary biological parameters than other available methods. They had been shown to be useful for biological comparisons between two or more insect populations by Birch, Dobzhansky, Elliott and Lewontin (1963) and Howe (1963).

2. MATERIALS AND METHODS

Test insects

Six populations of test insects including one hybrid were used.

1. QSOLS2, a lindane susceptible reference culture.
2. QSO188, a representative field susceptible culture.
3. QSO50, a field resistant culture.
4. QSO50 Sel I, a resistant culture from selection of QSO50.
5. CSO231, a reference resistant culture.
6. F_1 hybrids of QSO50 Sel I and QSO188.

Comparative resistance levels of these datum cultures determined by the filter paper method of Champ (1968) are given in Table 1.

Table 1. Response to malathion of datum cultures of susceptible (S) and resistant (R) *Sitophilus oryzae* as LC_{50} and LC_{99} values from probit analyses

Culture	Concentrations (% w/v in non-volatile solvent)			
	LC_{50}	Fiducial limits ($P = 0.05$)	LC_{99}	Fiducial limits ($P = 0.05$)
QSOLS2 (S_1).....	0.28	0.25–0.30	0.65	0.53– 0.85
QSO188 (S_2).....	0.35	0.32–0.39	0.94	0.66– 1.35
CSO231 (R_1).....	3.54	3.10–4.07	45.62	31.76–73.4
QSO50 (R_2).....	1.64	1.39–1.95	4.91	3.55– 9.25
QSO50 Sel I (R_3).....	2.52	2.16–2.99	8.60	7.37–13.74
F_1 Hybrid..... ($S_2R_3 + R_3S_2$)	0.74	0.70–0.78	2.36	2.09– 2.73

Culturing

Stock cultures were maintained at 25° ± 1°C and 70 ± 5% relative humidity (RH). Experimental results in this study were determined using a uniform source of 'Gamut' wheat having a moisture content of 13.8%.

Pre-adult development and survival

Pre-adult development and survival were determined at 20°, 25° and 30° each ± 0.5°C and 70 ± 5% RH, in a multi-temperature incubator using a saturated solution of a salt for humidity control. Duration of pre-adult stages, the time from oviposition to emergence of an adult, was estimated as a single total period. Grain was firstly exposed to oviposition overnight for 17 h at 25°C and 70% RH then transferred to the datum temperature. Three lots of 200 grains, each with an oviposition plug, were selected without conscious bias and held for insect emergence in plastic vials with wire gauze lids. During the emergence period, grains were sieved

daily to remove emerging adults. After completion of emergence, grains were dissected and numbers of undeveloped eggs and mortality among other stages were recorded.

Longevity and fecundity of adult females

The longevity and fecundity of adult females were estimated at each temperature from 40 individuals each confined with two males in a small vial with a gauzed lid. Ten grains of wheat were supplied for oviposition, and replaced each 7 days. Grains were removed and dissected and egg numbers recorded after wheat had been held for at least 1 day in 0.5% acid fuchsin (in 70% alcohol plus 5% glacial acetic acid) to stain egg plugs (Frankenfeld 1948). Dead females were recorded at each weekly change of wheat and the sex confirmed by dissection. Temperature and humidity were the same as for development times.

The inclusion of more than one male with each female simulated the situation where a female may mate with more than one male and reduced possible anomalies due to infertile males. Since this study sought only to compare adult longevity and fecundity between populations the consequent effects of density were assumed not to have significantly influenced comparative values.

Population increase

Parameters used followed Andrewartha and Birch (1954). Detailed computation followed the method of Bengston (1969) adapted for a single immature stage. Parameters estimated were intrinsic rate of natural increase, r_m; net reproduction rate, R_0; and mean generation time, T.

The intrinsic rate of natural increase, r_m, was calculated from the observed data on pre-adult survival, pre-adult development time, adult female longevity and fecundity. These data were first used to construct life tables with x, the pivotal age, based on the mid-point of the observation periods (1 week) and including a single observation period for all of the immature stages, which are difficult to observe more closely because they are spent within the grain. The other schedules were l_x, the proportion of females alive at the commencement of each age interval, and m_x, the number of female offspring produced per surviving female produced within each age interval.

Under the defined conditions,

$$\int_0^\infty e^{-r_m x} l_x m_x = 1$$

and the value for r_m may be estimated from the approximation

$$\Sigma e^{-r_m x} l_x m_x - 1$$

Net reproduction rate, R_0, the multiplication per generation, was calculated as the sum of the products $l_x m_x$,

$$R_0 = \Sigma\, l_x m_x$$

Mean generation time T, the generation time of a population with a non-overlapping life cycle having the same net reproduction rate and the same intrinsic rate of increase as the datum population, was calculated as

$$T = \frac{\log_e R_0}{r_m}$$

3. RESULTS

Duration of pre-adult development

As anticipated, the time for pre-adult development decreased in all cultures as temperature increased (Figure 1A). The magnitude of the decrease varied substantially between cultures and

the culture × temperature interaction was significant ($P = 0.05$). Males and females were not significantly different ($P = 0.05$), nor were the reciprocal crosses of the F_1 hybrid ($P = 0.01$).

Survival of pre-adult stages

Pre-adult survival did not differ significantly between datum temperatures (Figure 1B). During counts, most mortality was observed to have occurred at the egg or first larval instar stage. This agreed with the findings of Birch (1945b).

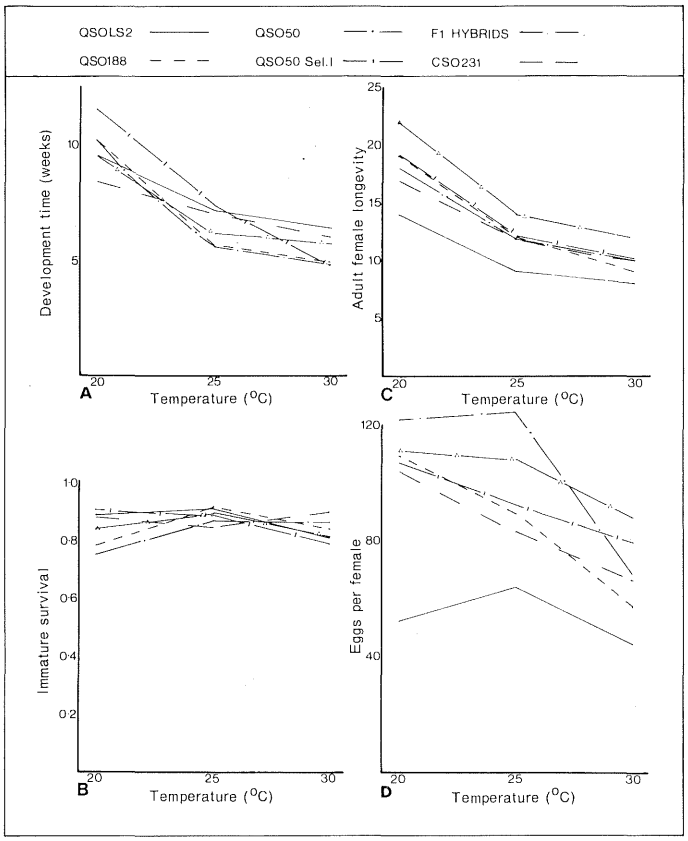

Figure 1. A. Development time; B. Immature survival; C. Adult longevity; D. Eggs per female (total fecundity), for six populations of rice weevil at three temperatures.

Adult longevity

Longevity generally decreased with temperature (Figure 1C) but, as with development, cultures differed relative to each other at each temperature resulting in significant interaction ($P = 0.05$).

Fecundity

Fecundity generally, though not always, decreased with temperature (Figure 1D), but again the interaction between cultures was highly significant ($P = 0.01$). Observations indicated that the reliability of plugs as an indicator of eggs approximated 0.9 at each temperature.

Intrinsic rate of natural increase

Values for intrinsic rates of natural increase, r_m, are shown in Table 2. These values integrate the effects of development time, immature survival, adult longevity and fecundity. They do not indicate any influence of resistance. Although atypical trends were exhibited by cultures with high resistance values, namely CSO231 and QSO50 Sel I, neither was consistently better or worse than other cultures. Values for r_m related most closely to the duration of pre-adult development. This parameter was a major source of difference between the r_m calculated by Birch (1948) for *S. oryzae* at 30°C and 70% RH and the corresponding values calculated in this study.

Table 2. Intrinsic rate of natural increase (r_m) per week for malathion resistant (R) and susceptible (S) *Sitophilus oryzae* at 70% RH and three temperatures

Culture	Temperature °C		
	20	25	30
QSOLS2 (S_1)	0.196 00	0.322 21	0.289 08
QSO188 (S_2)	0.232 54	0.384 22	0.406 60
CSO231 (R_1)	0.272 96	0.314 11	0.369 82
QSO50 (R_2)	0.226 59	0.431 66	0.400 50
QSO50 Sel I (R_3)	0.219 24	0.332 61	0.454 30
F_1 Hybrid ($S_2R_3 + R_3S_2$)	0.247 90	0.364 98	0.371 92

Net reproduction rate

Values for net reproduction rate, R_0, are shown in Table 3. Variation with temperature was evident for all cultures, reflecting differences in total fecundity, but there were no trends consistently related to resistance levels.

Table 3. Net reproduction rate (R_0) for malathion resistant (R) and susceptible (S) *Sitophilus oryzae* at 70% RH and three temperatures

Culture	Temperature °C		
	20	25	30
QSOLS2 (S_1)	21.71	29.81	17.85
QSO188 (S_2)	42.73	38.79	23.91
CSO231 (R_1)	45.85	35.12	29.67
QSO50 (R_2)	46.21	54.36	28.38
QSO50 Sel I (R_3)	48.88	39.66	35.55
F_1 Hybrid ($S_2R_3 + R_3S_2$)	46.78	47.89	36.25

Mean generation time

Values for mean generation time, T, are shown in Table 4. Cultures again varied relative to each other from temperature to temperature. In the consideration of the effects of selection for insecticide resistance, the number of generations on which selection operates during a storage term is an important factor.

Table 4. Mean generation time (*T*) in weeks for malathion resistant (R) and susceptible (S) *Sitophilus oryzae* at 70% RH and three temperatures

Culture	Temperature °C		
	20	25	30
QSOLS2 (S_1)	15.70	10.54	9.97
QSO188 (S_2)	16.15	9.52	7.81
CSO231 (R_1)	14.01	11.33	9.17
QSO50 (R_2)	16.92	9.62	8.35
QSO50 Sel I (R_3)	17.74	11.06	7.86
F_1 Hybrid ($S_2R_3 + R_3S_2$)	15.51	10.60	9.65

4. DISCUSSION

The importance of population growth parameters in the consideration of insecticide resistance lies in the influence of these factors on the selection process. Development of resistance is influenced by genetic factors, including the level of resistance conferred by the resistance allele(s) and dominance of the character, biological factors, including the fitness of the heterozygous and homozygous resistant phenotypes, and operational influences, including previous selection with other insecticides (Georghiou and Taylor 1977a,b). If resistant phenotypes (present when resistance is in the incipient stage) were biologically less fit than the wild susceptible phenotypes, selection would be slowed. In this study, populations with high levels of resistance (Table 1) were not demonstrably less fit overall than susceptible populations; nor were the inter-population hybrids.

Relative levels of fitness, estimated as the r_m, differed between populations from one condition to another, but overall they presented a pattern concluded to be consistent with normal species variation. This implied that the proportion of resistant types in the population would remain stable after relaxation of selection pressure without substantial change, other than by genetic drift, until the onset of some opposing selection pressure. However, diminution of resistance levels could be expected from the work of Keiding (1967) for houseflies, due to loss of unstable favourable combinations of enhancement genes. Unpublished data (Queensland Department of Primary Industries) show that, for DDT and lindane, an initial reduction in resistance levels occurred early after relaxation of selection pressure, but that low level resistance was still present in populations of *S. oryzae* after a decade.

The characteristics of the resistant heterozygote are specially important during the incipient stages of resistance when the resistant phenotypes can be expected to be almost exclusively heterozygous for the character, or when resistant and susceptible populations interact, such as by migration or mixing of infested grain bulks. These were both represented in this study by the F_1 hybrid offspring of resistant and susceptible parents (Table 1) although these were possibly more appropriate to the second situation than the first. The competitive fitness of this type is most important when the character is substantially recessive, as is known to occur in *S. oryzae* (Heather 1979), and selection levels are low. In these circumstances the slightly more resistant heterozygote must compete with the more tolerant wild type susceptible.

The observed statistical interaction between temperature and culture on pre-adult development, adult longevity and fecundity (Figure 1B) has important implications for experimental methodology. They emphasize that, strictly, observations at a single temperature can be applied only to that temperature. The extent of differences in results between temperatures was nevertheless surprising. For example, total fecundity for QSO50 was 125 at 25°C compared to approximately 93 for its selected derivative culture QSO50 Sel I, whereas at 30°C the value

for QSO50 was 66 compared to 80 for QSO50 Sel I. Therefore, what could have been construed as evidence that increased resistance was associated with decreased fecundity on the basis of the data at 25°C is seen to be an artefact when additional temperatures are considered. While these differences may reflect, at least in part, the influence of selection associated with many generations of laboratory breeding, and hence not be typical of field populations, the desirability of using a range of experimental conditions for assessments of this nature will be apparent.

The findings of these experiments indicated that, by the time malathion resistance in *S. oryzae* became apparent, the resistant phenotypes were not biologically disadvantaged compared to susceptible phenotypes. This situation is at variance with the general trends reported for most other pests, but the study was undertaken in greater detail and was a more comprehensive assessment than most others reported in literature. Therefore, some of the differences reported from individual parameters for other resistant populations could well prove to be fortuitous correlations, as suggested by Champ and Dyte (1976). Malathion resistance can, therefore, be expected to persist in field populations of the rice weevil, although the actual levels of resistance could be expected to decrease.

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