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SHORT COMMUNICATION

Inter- and intraspecific genetic variation and differentiation in the sibling bean weevils *Zabrotes subfasciatus* and *Z. sylvestris* (Coleoptera: Bruchidae) from Mexico

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Introduction

The Mexican bean weevil, *Zabrotes subfasciatus* (Boheman) (Coleoptera: Bruchidae), is one of the most important pests of stored beans worldwide (Cardona & Posso, 1987; Kapila & Pajni, 1987; Abate & Ampofo, 1996) and the best known member of the bruchid subfamily Amblycerinae. This species probably evolved in Central America and used as original hosts the wild ancestors of the modern cultivated forms of the Lima bean *Phaseolus lunatus*, and the common bean, *P. vulgaris* (Fabaceae). *Zabrotes subfasciatus* became a pest when it established itself as a continuous breeder in stored seeds, and spread to many parts of the tropics and subtropical areas of the world through trade in bean seeds (Southgate, 1978). Although various species and varieties of *Phaseolus* are the preferred hosts, *Z. subfasciatus* has also colonized several other legumes of economic importance (Meik & Dobie, 1986). There are many reports on the interaction of this insect with its host seeds at the biochemical and molecular level, but no attempts have been made to measure the extent of genetic subdivision and gene flow among populations of this species. These data are relevant because restrictions in gene flow between populations play a role in the evolution of local adaptation, including the development of insecticide resistance (Caprio & Tabashnik, 1992) and the establishment of host races (Butlin, 1990).

Recently, some individuals morphologically similar to *Z. subfasciatus* but exhibiting slight differences in behaviour, were found breeding on cultivated *P. vulgaris* seeds from two localities in Mexico. After their taxonomic examination, Romero & Johnson (1999) described these specimens as a new species and named it *Z. sylvestris*, because they hypothesized that it feeds predominantly on wild varieties of *P. lunatus* and *P. vulgaris*. For this reason and because both *Z. subfasciatus* and *Z. sylvestris* are sexually dimorphic and have very similar external morphology this new species has remained unnoticed. However, some features of the morphology and structure of the genitalia of both sexes show slight but consistent differences that can be used as diagnostic characters (Romero & Johnson, 1999).

In this study, allozyme electrophoresis was used to determine the degree of genetic similarity between *Z. subfasciatus* and *Z. sylvestris*, to confirm the status of the second as a new and distinct species, and to provide additional characters that can be used to differentiate between them. Genetic variability was examined in both species, and population genetic structure and gene flow among Mexican populations of *Z. subfasciatus* are also described.

Material and methods

Samples of cultivated seeds of *Phaseolus* showing evidence of damage by bruchids were obtained in markets of small rural towns from five different localities in Mexico: Cuetzalan and Tehuacan, Puebla State (CUE, TEH); Oaxaca, Oaxaca State (OAX); Taxco, Guerrero State (TAX); Tepoztlan, Morelos State (TEP1 and TEP2); and San Luis Potosi, San Luis Potosi State (SLP); and transported to the laboratory in Mexico City. Information provided by the seller confirmed that the beans were cultivated near the town and had been stored before commercialization. Seeds were kept in glass bottles until the adult insects emerged. Thirty bruchids were collected from each seed sample and immediately frozen at

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−80°C. Five *Z. subfasciatus* populations were obtained from seed samples CUE, OAX, TAX, TEP1 and TEP2, and two *Z. sylvestris* populations from seed samples SLP and TEH.

The cellulose acetate gel electrophoresis technique was used (Richardson *et al*., 1986) following the protocol of Herbert & Beaton (1986). Intact whole bruchids were macerated in 30 μl of deionized water inside 1.5-ml microcentrifuge tubes. The homogenate was centrifuged at 6400 rpm for 10 min and the supernatant used. A preliminary survey of 15 enzyme systems revealed six presumptive gene loci that could be reliably scored: IDH-1 and IDH-2 (isocitrate dehydrogenase; E.C. 1.1.1.42), GOT (glutamate oxaloacetate transaminase; E.C. 2.6.1.1), GPDH (glycerol 3-phosphate dehydrogenase; E.C. 1.1.1.8), MDH (malate dehydrogenase; E.C. 1.1.1.37), and PGI (phosphoglucoisomerase, E.C. 5.3.1.9). The following buffers were used: buffer A (citrate phosphate 0.01 M; pH 6.4) for IDH, MDH and PGI; buffer O (Tris-HCl 0.015 M; pH 9.0) for GOT, and buffer TC (Tris-citrate 0.1 M; pH 8.2) for GPDH (Richardson *et al*., 1986).

The BIOSYS-1 program (Swofford & Selander, 1981) was used to estimate allelic frequencies at each locus, mean number of alleles per locus and the percentage of polymorphic loci (95% criterion) for each population. The expected average heterozygosity was calculated using Levene's (1949) formula, which gives an unbiased estimate. Agreement of genotypic frequencies with expectations under Hardy-Weinberg equilibrium was tested with a goodness-of-fit chi-square after the genotypes were pooled into three classes: homozygotes for the most common allele, heterozygotes between the most common allele and another allele, and any other combination.

Population genetic structure was analysed using the procedure of Weir & Cockerham (1984) to calculate *F*-statistics (Wright, 1951). At each locus, mean and variance of F_{IS}, F_{ST} and F_{IT} were estimated by jackknifing over populations, and a summary value for each *F*-statistic was calculated by jackknifing over loci. To test whether the jackknifed means of F_{IS}, F_{ST} and F_{IT} at each locus were significantly different from zero, simple *t*-tests were used. The 95% confidence intervals (CI) for the summary values were obtained by bootstrapping with 1000 resamples (Weir, 1990). Gene flow among populations was calculated from the summary value of F_{ST}, using Wright's formula $Nm = (1 - F_{ST}) / 4F_{ST}$ (Wright, 1951).

The degree of genetic similarity among populations was estimated using Nei's unbiased genetic distance (Nei, 1978) and a dendrogram based on these data was constructed with the unweighted pair-group method with an arithmetic average (UPGMA) algorithm (Sneath & Sokal, 1973).

Results

Allelic frequencies at each locus for *Z. subfasciatus* and *Z. sylvestris* populations are shown in table 1. MDH and GPDH were completely monomorphic. Two distinct alleles alternatively fixed in each of the species were found at the PGI locus. The slowly migrating electromorph 'A' characterized *Z. sylvestris* populations, while the fast electromorph 'B' was found in all *Z. subfasciatus* populations. The other three polymorphic loci showed variable levels of interspecific differentiation. At the GOT locus, electromorph 'A' was absent in *Z. sylvestris*, but present in all *Z. subfasciatus* populations, while electromorph 'C' was found at high frequency in *Z. sylvestris*, but present in only one *Z. subfasciatus* population. Allele 'A' at the IDH-1 loci was fixed in both populations of *Z. sylvestris* and present at an intermediate frequency only in population TAX of *Z. subfasciatus*. In contrast, allele 'A' at the IDH-2 locus was present at similar frequencies in all populations of both species.

At the species level, *Z. subfasciatus* showed polymorphism at three of the six loci studied (50%), while *Z. sylvestris* was polymorphic at only one locus (16.7%). Mean number of alleles per locus was 2.3 in *Z. subfasciatus* and 1.2 in *Z. sylvestris*. Genetic variability estimators calculated at the population level are presented in table 2. Mean number of alleles per locus ranged from 1.5 to 1.8 in *Z. subfasciatus* populations and from 1.0 to 1.2 in *Z. sylvestris*. The percentage of polymorphic loci ranged from 33.3 to 50.0 and from 0.0 to 16.7, respectively, for the two species. Expected average heterozygosity ranged from 0.12 to 0.21 in *Z. subfasciatus* and from 0.0 to 0.06 in *Z. sylvestris*. A significant deficiency of heterozygotes was detected at the GOT locus in population TEP2 ($\chi^2 = 4.261$; $P = 0.039$). No other deviations from Hardy-Weinberg equilibrium were found.

Values of Nei's unbiased genetic distance between pairs of interspecific populations were between 0.421 and 0.643, with an average distance of 0.572 separating both species. The unweighted pair-group method with an arithmetic average dendrogram constructed on the basis of these distances is presented in fig. 1.

Intraspecific *F*-statistics and gene flow values calculated for *Z. subfasciatus* are shown in table 3. F_{IS} values were significant and positive at the IDH-1 and IDH-2 loci, indicating a deficiency of heterozygotes, but the overall value was not significant. F_{ST} values for the three intraspecifically polymorphic loci and the overall value ($F_{ST} = 0.305 \pm 0.039$) were significant. This F_{ST} value means that on average 31% of the total variance of allele frequencies is caused by genetic differences among populations. As expected from this considerable interpopulation differentiation, the gene flow estimate was very low ($Nm = 0.570$). Intraspecific Nei's genetic distances ranged from 0.014 to 0.169 (fig. 1). The genetic distance between pairs of populations did not correspond to geographic proximity. For example, populations TEP1 and TEP2, which were obtained from *P. vulgaris* beans bought in the same market and probably cultivated within the same area, were separated by a genetic distance of 0.065, which is larger than the value of 0.014 that separated populations OAX and TEP1 (fig. 1), that are several hundred kilometres apart.

Discussion

Romero & Johnson (1999) were initially hesitant to consider *Z. sylvestris* as a new and distinct species from *Z. subfasciatus*, because other species of bruchids of economic importance have shown various biotypes and behavioural and morphological variation when studied intensively (e.g. Messina & Renwick, 1985). In this study, alternative alleles fixed at the PGI locus were found, which may be used as diagnostic characters, in addition to the morphological differences already described by Romero & Johnson (1999). The absence of heterozygous individuals at this locus indicates that gene flow between *Z. subfasciatus* and *Z. sylvestris*, if it occurs, must be extremely low. Experimental attempts to cross them in the laboratory resulted in infrequent oviposition by the females of both species, and

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Table 1. Sample size (*n*) and allelic frequencies for *Zabrotes subfasciatus* and *Z. sylvestris* populations.

Locus	Populations						
	Cuetzalan	Oaxaca	Taxco	Tepoztlan 1	Tepoztlan 2	San Luis Potosi	Tehuacan
PGI							
(*n*)	30	30	30	30	30	30	30
A	0.000	0.000	0.000	0.000	0.000	1.000	1.000
B	1.000	1.000	1.000	1.000	1.000	0.000	0.000
GOT							
(*n*)	27	25	28	29	28	30	30
A	0.056	0.640	0.875	0.707	0.286	0.000	0.000
B	0.296	0.360	0.125	0.293	0.179	0.000	0.217
C	0.019	0.000	0.000	0.000	0.000	1.000	0.783
D	0.630	0.000	0.000	0.000	0.536	0.000	0.000
IDH-1							
(*n*)	28	28	28	29	28	30	30
A	0.000	0.000	0.518	0.000	0.000	1.000	1.000
B	0.161	0.071	0.179	0.224	0.054	0.000	0.000
C	0.821	0.929	0.304	0.638	0.946	0.000	0.000
D	0.018	0.000	0.000	0.138	0.000	0.000	0.000
IDH-2							
(*n*)	30	27	27	29	30	30	30
A	1.000	0.981	1.000	0.828	1.000	1.000	1.000
B	0.000	0.000	0.000	0.172	0.000	0.000	0.000
C	0.000	0.019	0.000	0.000	0.000	0.000	0.000
MDH							
(*n*)	30	30	30	30	30	30	30
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPDH							
(*n*)	30	30	30	30	30	30	30
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Alleles are designated by letters (A–D) according to relative mobility of electromorphs.

Table 2. Mean number of alleles, percentage polymorphism, and observed and expected heterozygosities for *Zabrotes subfasciatus* and *Z. sylvestris*.

Population	Mean number of alleles per locus	% loci polymorphic	Mean heterozygosity	
			Observed	Expected
Z. subfasciatus				
CUE	1.8 (0.5)	33.3	0.128 (0.085)	0.138 (0.092)
OAX	1.5 (0.2)	33.3	0.110 (0.077)	0.107 (0.076)
TAX	1.5 (0.3)	33.3	0.143 (0.101)	0.140 (0.102)
TEP1	1.7 (0.3)	50.0	0.213 (0.101)	0.208 (0.098)
TEP2	1.5 (0.3)	33.3	0.077 (0.070)	0.119 (0.100)
Z. sylvestris				
SLP	1.0 (0.0)	0.0	0.000 (0.000)	0.000 (0.000)
TEH	1.2 (0.2)	16.7	0.050 (0.050)	0.058 (0.058)

Standard errors are included in parentheses. A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95. Expected heterozygosity was calculated according to Levene's (1949) unbiased method.

none of these eggs developed into adult hybrids (A. Callejas, unpublished data). All this evidence suggests that *Z. subfasciatus* and *Z. sylvestris* are in fact sibling species, i.e. morphologically almost indistinguishable but fully isolated genetically from each other (e.g. Ayala *et al.*, 1974). The average genetic distance between *Z. subfasciatus* and *Z. sylvestris* ($D = 0.572$) is within the reported range in similar comparisons of pairs of sibling species (Ayala *et al.*, 1974; Menken, 1989). For example, the average genetic distances between pairs of sibling species in the *Drosophila willistoni* (Sturtevant) (Diptera: Drosophilidae) group ranged from 0.413 to 0.665 (Ayala *et al.*, 1974).

The existence of sibling species is very frequent in insects (e.g. Futuyma, 1991; Payne & Berlocher, 1995). Despite their similar appearance, they may differ significantly in physiological and ecological traits. Adequate tools to distinguish sibling species are particularly relevant when there are also differences in economic importance. For

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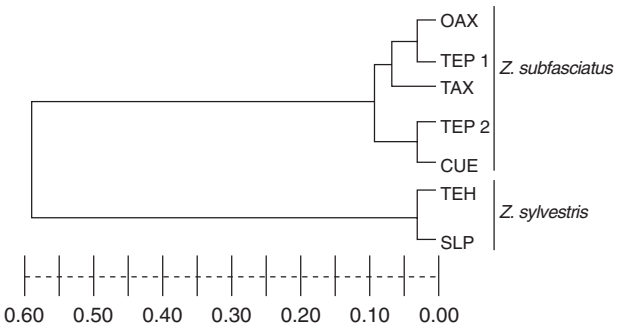

Fig. 1. Unweighted pair-group method with arithmetic average dendrogram based on Nei's unbiased genetic distances for *Zabrotes subfasciatus* and *Z. sylvestris*. See text for population abbreviations.

example, the discovery that the European mosquito *Anopheles maculipennis* Meigen (Diptera: Culicidae) is actually a cluster of sibling species was of great practical interest because some transmit human malaria and others do not (Korvenkontio *et al*., 1979). *Zabrotes sylvestris* is only known from the individuals collected in Tehuacan and San Luis Potosi during this study, and from some old specimens from Berkeley, California (Romero & Johnson, 1999). The geographical distribution of this insect and the frequency with which it feeds on cultivated beans remain to be determined, considering that it has probably been often confused with *Z. subfasciatus*. This information is necessary to establish the actual and potential importance of *Z. sylvestris* as a pest. The allozyme markers described in this work may be useful for these purposes.

The situation represented by *Z. subfasciatus* and *Z. sylvestris* may constitute a case analogous to that of another pair of bruchid sibling species of Mesoamerican origin, *Acanthoscelides obtectus* (Say) and *A. obvelatus* (Bridwell) (Coleoptera: Bruchidae). The first is cosmopolitan and it is considered the most important pest of stored beans in many countries, while *A. obvelatus* has retained its ancestral distribution restricted to Mexico and Central America (Johnson, 1983; Cardona & Posso, 1987). The worldwide spread of *A. obtectus* and its success as a pest has been explained as a result of its ability to continuously reproduce throughout the year, whereas *A. obvelatus* is univoltine (Delgado *et al*., 1988). A recent study of these two species using allozymes showed that levels of genetic variation are significantly higher in *A. obtectus* than in *A. obvelatus* (González-Rodríguez *et al*., 2000). *Zabrotes subfasciatus* is also a continuous breeder and from the data presented above it seems that this species has more alleles per locus, and higher heterozygosity and percentage of polymorphic loci, at the species and population levels, than *Z. sylvestris*. However, the statistical significance of these differences was not determined, since data from a larger number of populations are needed to apply a statistical test. It should also be recognized that the small number of polymorphic loci used in this study might cast some doubt on the reliability of the genetic variation measures obtained. Further research based on a more detailed sampling of populations and more precise molecular markers would be desirable, because it is probable that differences in levels of genetic variation and key life history traits may explain, at least to some extent, why some insects rapidly develop as pests, while other closely related species do not.

Intraspecifically, there was a high degree of genetic subdivision among the five *Z. subfasciatus* populations surveyed. Previously, it has been reported that populations of this species from Colombia, Uganda, Zimbabwe and Mexico differed significantly in fecundity, patterns of egg distribution, times of development, adult sizes and response to different cultivars of host seed (Credland & Dendy, 1992). Our data show that there is also considerable heterogeneity in the frequency of presumably neutral markers and low gene flow among populations collected at a smaller geographical scale. A lack of correspondence between genetic and geographical distances was also observed. However, these results may not reflect the true population genetic structure of *Z. subfasciatus* for two reasons. The first one is that in spite of what was claimed by market traders, some bean seeds may not have been produced locally. The second reason is again the limited number of polymorphic loci employed in the analyses, possibly leading to biased estimates. Corroboration of the results reported in this study must await further detailed research, but if the same kinds of pattern are found using better molecular and sampling techniques, the question immediately would arise of what factors could be causing such a strong genetic structuring among populations of this insect.

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Table 3. Intraspecific *F*-statistics (means ± SE) and estimated gene flow (*N*m) for *Zabrotes subfasciatus*.

Locus	F_{IS}	F_{IT}	F_{ST}
GOT	0.050±0.112 NS	0.367±0.114**	0.334±0.097**
IDH-1	0.077±0.048*	0.368±0.141**	0.322±0.180*
IDH-2	0.079±0.039*	0.306±0.147*	0.238±0.114*
Overall values	0.055±0.025 NS	0.343±0.022**	0.305±0.039*
95% CI	0.040–0.086	0.178–0.351	0.139–0.324
*N*m			0.570

Single locus values were obtained by jackknifing over populations and overall values by jackknifing over loci. Significance levels were determined by t-tests. Confidence intervals for the overall value were calculated by bootstrapping.
*$P < 0.05$; ** $P < 0.005$; NS, not significant.

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Insect Movement: Mechanisms and Consequences

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