controls, may foster overzealous myelopoiesis in the face of unopposing stimulation. Thus, certain of the myeloproliferative disorders may represent a defect in macrophage-mediated feedback mechanisms.

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European Corn Borer: Pheromone Polymorphism or Sibling Species?

Abstract. *Electrophoretic analyses of the* (Z) *and* (E) *pheromone-attracted males of* Ostrinia nubilalis *(Hübner), the European corn borer, in an area of coexistence indicate that these strains are not freely interbreeding. Although the populations are morphologically indistinguishable, studies of allozyme, pheromone, and hybridization suggest that the* (Z) *and* (E) *entities are genetically differentiated, perhaps to the status of semi- or sibling species.*

Pheromone investigations of the European corn borer, *Ostrinia nubilalis* (Hübner) (*1*), have shown two distinct population types: the (*Z*) strain, producing and attracted to a 97:3 mix of (*Z*)-11- and (*E*)-11-tetradecenyl acetate, and the (*E*) strain, producing and attracted to a 4 : 96 blend of the same compounds (*2, 3*). The (*Z*) strain is widely distributed, representing nearly all the populations surveyed to date in Europe as well as those in North America (*4*), where this important agricultural pest was established by at least two separate introductions in the early 1900's (*5*). The (*E*) strain occurs allopatrically in Italy and New York (*3, 4*). The two strains occur sympatrically and synchronically in central Pennsylvania (*6*), stimulating speculation on the status of *O. nubilalis* as a monotypic species, the possibility of pheromone polymorphism, and the origin and ultimate fate of the strains in sympatry.

Allozyme data suggests genetic divergence between the (*Z*) and (*E*) strains. In Amity Hall, Pennsylvania, males were lured to synthetic blends, ensnared in sticky traps, removed live, and frozen until electrophoretic analyses (*7*). For this group of males attracted to either (*Z*) or (*E*) blends, allozyme frequencies at ten loci (Table 1) show that malate dehydrogenase (MDH-1), isocitrate dehydrogenase (IDH-1), α-glycerophosphate dehydrogenase (α-GPD), and 6-phosphogluconate dehydrogenase (6-PGD) were either monomorphic or had a second allele at a very low frequency. Of the polymorphic loci, glutamate oxaloacetate transaminase (GOT-1 and GOT-2), phosphohexose isomerase (PHI), and phosphoglucomutase (PGM) showed significant differences between strains ($P < .05$), whereas IDH-2 and MDH-2 were not statistically different. When these electrophoretic data are compared with the use of Nei's (*8*) index of genetic identity (*I*), the similarity between strains is 0.997. Values of *I* for sibling species generally range from 0.98 to less than 0.70 (*9*) with only a weak correlation with the degree of morphological identity (*10*). Genetic identity may be especially inadequate to separate species that have recently diverged, because only a few genes may be involved in the initial phase of speciation (*11*). Our data do not rule out the possibility of interbreeding, although if introgression is occurring, it should be of recent origin or of low magnitude.

Natural hybrids of the (*Z*) and (*E*) strains may not be at a survival disadvantage, because laboratory F_1, F_2, and backcross progeny exhibit heterosis. However, in laboratory mating choice tests under confined conditions (in which the necessity for long-distance mate location by pheromone was eliminated), the frequencies of successful interstrain crosses were 6 and 10 percent [for the ♂ (*Z*) × ♀ (*E*) and ♂ (*E*) × ♀ (*Z*) matings, respectively], whereas the frequencies of successful intrastrain control crosses were 80 and 76 percent for the (*Z*) and (*E*) classes. The average daily time of mating in the laboratory within a 24-hour cycle differed by 1.7 hours with considerable overlap, so that exclusive mating cycles alone would not seem to effectively isolate these strains (*12*).

In the field (Table 2), attraction to the various blends indicates yearly shifts in the relative proportions of the strains. In 1973 the two strains appeared to occur in similar numbers, while from 1974 to 1977

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Table 1. Allozyme analyses of *Ostrinia nubilalis* attracted to (*Z*)-11- and (*E*)-11-tetradecenyl acetates (97 : 3 is the (*Z*) strain and 4 : 96 is the (*E*) strain). The samples were collected from 2 to 4 June and 14 to 16 June 1974 at Amity Hall, Pennsylvania.

Locus*	Alleles	(*Z*)-attracted	(*E*)-attracted	Statistical data
GOT-1	a	0.016	0.059	$G = 7.805$†
	b	0.913	0.860	$P < .025$ (d.f. = 2)
	c	0.070	0.081	
		(n = 426)	(n = 186)	
GOT-2	a	0.011	0.020	$G = 7.965$
	b	0.987	0.939	$P < .005$ (d.f. = 1)
	c	0.003	0.041	(rare alleles lumped)
		(n = 372)	(n = 148)	
PHI	a	0.223	0.122	$G = 16.366$
	b	0.700	0.713	$P < .005$ (d.f. = 2)
	c	0.077	0.165	
		(n = 426)	(n = 188)	
PGM	a	0.019	0.061	$G = 10.366$
	b	0.977	0.917	$P < .005$ (d.f. = 1)
	c	0.005	0.022	(rare alleles lumped)
		(n = 428)	(n = 180)	
IDH-2	a	0.313	0.265	$G = 0.859$
	b	0.687	0.735	$.1 < P < .5$ (d.f. = 1)
		(n = 284)	(n = 102)	
MDH-2	a	0.039	0.050	$G = 0.285$
	b	0.961	0.950	$.5 < P < .9$ (d.f. = 1)
		(n = 284)	(n = 140)	

*MDH-1, IDH-1, α-GPD, and 6-PGD were either monomorphic or had a second allele at very low frequency. Abbreviations: GOT, glutamate oxaloacetate transaminase; PHI, phosphohexose isomerase; PGM, phosphoglucomutase; IDH, isocitrate dehydrogenase; MDH, malate dehydrogenase; α-GPD, α-glycerophosphate dehydrogenase; 6-PGD, 6-phosphogluconate dehydrogenase. The number of alleles sampled is n. †G is the test of independence.

the population of the (*E*) strain was reduced. Such a shift could be expected in reproductively isolated strains because of competition for the same food resource or differential response to physical environmental factors. Males attracted to a 50 : 50 mix of (*Z*) : (*E*) may represent hybrids or a mixture of individuals responding to (*Z*) and (*E*), respectively. Allozyme data on these individuals do not permit us to distinguish between these two possibilities. It should be emphasized that relative trap catch cannot be used to infer behavioral classes. Individuals captured at a 50 : 50 blend actually may be optimally attracted to a 97 : 3 or 4 : 96 blend of (*Z*) or (*E*), respectively. Since the searching process is terminated when a male is ensnared in a trap, a trapping technique may limit opportunities for the individual to seek the blend with the lowest behavioral threshold, as has been demonstrated in the attraction of oriental fruit moth males [*Grapholitha molesta* (Busck)] to alterations of its attractant blend (*13*).

In the study of Lepidoptera, genital morphology has, in the past, been paramount in delineating species taxa. Nevertheless, genitalia are not routinely useful in separation of sibling species (*14*). The genitalia, the maculation, and the color of the wings of *O. nubilalis* are polymorphic (*15*); and no qualitative characters distinguish the (*Z*) and (*E*) strains (*16*).

Although both the (*Z*) and (*E*) strains occur in Europe, on the basis of the trapping conducted to date at 20 localities there is no obvious distributional overlap (*4*). Since introductions of *O. nubilalis* into North America from both central Europe and Italy were likely, and since the (*Z*) and (*E*) strains have been found in these areas, the presence of both strains in North America is not unexpected. In Europe the strains could be semispecies (allopatric populations that have partially completed the process of speciation) or sibling species. In the absence of a study on an area of sympatry, sibling species status will be difficult to establish.

The area of secondary contact in central Pennsylvania may be of recent origin. It is clear that a simple pheromone polymorphism explanation (*4*) is not in agreement with the degree of genetic differentiation (*7, 10*). Hybridization and introgression cannot be ruled out, particularly since hybrids may exhibit increased viability. But the differences in attractant pheromone, mating periodicity, and close range mating behavior suggest that hybrid crosses of the (*Z*) and (*E*) entities will be less frequent than intrastrain matings. Determination of the ultimate fate of these morphologically indistinguishable populations in sympatry will necessitate continued pheromone and allozyme monitoring.

Table 2. Attraction of males to (*Z*)- and (*E*)-11-tetradecenyl acetate blends in Amity Hall, Pennsylvania, during the first adult flight period.

Year	Total male catch		
	97 : 3	50 : 50	4 : 96
1973*	111	6	66
1974†	663	90	125
1975‡	98	15	18
1976§	102	25	20
1977‖	35	6	3

*In 1973 a spectrum of 12 blends from pure (*Z*) to pure (*E*) was tested (*6*). The 97 : 3 mix includes catches from 99 : 1 to 95 : 5; the 50 : 50 mix from 70 : 30 to 20 : 80; the 4 : 96 mix from 6 : 94 to 2 : 98. Test conducted from 10 June to 3 July. †Test conducted from 2 to 4 June and 14 to 16 June. ‡Test conducted from 11 to 14 June. §Test conducted from 9 to 25 June. ‖Test conducted from 27 May to 17 June.

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