the conduit. Thus, wave transport is a very efficient means of increasing net conduit volume flux. In contrast, a sphere must be significantly larger to rise through the mantle in geological time. The sphere velocity v_s is[1]

$$v_s = \frac{g' r_s^2}{3\nu_0}$$

To give the same velocity as before, we require a radius $r_s =$ 550 km, and therefore a much greater volume of 7.0×10^8 km^3. Spheres are inefficient for other reasons as well. Griffiths[15] has shown that spheres smaller than 200 km are too slow ever to reach the surface.

Thus we envisage a process of mantle flow in which solitary waves trap parcels of material and easily transport them vertically with little dilution. Note that mantle (especially lower mantle) characteristics are poorly constrained, with uncertainties much greater than factors of ten, so the estimates of diffusion velocities are only suggestive. We have also ignored thermal and multicompositional effects, although thermal effects are modelled well by laboratory compositional experiments. But the description presented here avoids problems associated with very wide mantle plumes of uniform viscosity or with very large spheres in the mantle.

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Genetic differentiation between sympatric host races of the apple maggot fly *Rhagoletis pomonella*

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It has been proposed that true fruit flies in the *Rhagoletis pomonella* species group speciate sympatrically (that is, in the absence of geographic isolation) as a consequence of shifts to previously unexploited host plants[1,2]. Because *Rhagoletis* larvae are host-specific fruit parasites and mate selection in these flies is directly coupled to host-plant recognition[3–5], variation for larval survivorship and host preference traits can act as genetically based barriers to gene flow. This reduction in gene flow results in the sympatric divergence of fly populations adapted to alternative hosts. The shift of *R. pomonella* from its native host hawthorn (*Crataegus* spp.) to domestic apples (*Malus pumila*) in eastern North America in the past 200 years[6] provides an opportunity to determine whether host specialization is sufficient to differentiate populations without earlier periods of geographic isolation. We report finding genetic differentiation between co-occurring hawthorn and apple populations of *R. pomonella* at a field site near Grant, Michigan. The result confirms that hawthorn and apple flies represent partially reproductively isolated 'host races' and is consistent with a sympatric mode of divergence for these flies.

Six allozyme loci, aconitase-2 (*Acon-2*), malic enzyme (*Me*), mannose phosphate isomerase (*Mpi*), aspartate amino-transferase (*Aat-2*), NADH-diaphorase-2 (*Dia-2*) and beta-hydroxy acid dehydrogenase (*Had*), showed significant allele frequency differences between flies collected from sympatric hawthorn and apple trees at the Grant, Michigan site (Tables 1 and 2; see Fig. 1 and accompanying legend for a description of the field site, collecting strategy and electrophoretic methods used in the study). Allele frequencies for *Acon-2* and *Me* were significantly different between hawthorn and apple flies across the three years sampled and did not vary significantly among either apple or hawthorn trees within any year (Tables 1 and 2). *Aat-2*, *Dia-2* and *Mpi* also showed host-related differences. But gene frequencies varied among flies from different apple trees for *Aat-2* in 1985 and for *Dia-2* in 1984 and 1985, as well as among hawthorn trees for *Mpi* in 1985 (Tables 1 and 2). Allele frequencies for *Had* differed significantly between hawthorn and apple flies in 1985 but not in 1984 or 1986. *Had* also varied significantly among apple trees in 1984. None of the other seven polymorphic loci resolved in this study showed significant inter- or intra-host frequency differences.

Allele frequencies were reasonably constant between 1984 and 1985. Of the 13 polymorphic loci, only apple tree number 1 for *Me* ($G = 9.67$, $P \leq 0.01$, 1 d.f.) and hawthorn tree number 1 for *Dia-2* ($G = 4.66$, $P \leq 0.05$, 1 d.f.) had significant frequency differences between 1984 and 1985 (data for *Acon-2*, *Me*, *Mpi*, *Aat-2*, *Dia-2* and *Had* are presented in Table 2). But eight out of a total of 20 tests for *Me*, *Acon-2*, *Mpi*, *Aat-2* and *Dia-2* showed significant differences between 1985 and 1986. Allele frequencies for both apple and hawthorn flies displayed a general trend to become more 'apple-like' in 1986 compared with previous years (Table 1). The shift in 1986 allele frequencies could be explained by selection either in the field or during laboratory rearing, as flies collected as larvae in 1985 and adults in 1986 represent different life-history stages of the same generation. But frequency shifts between 1985 and 1986 were in the same direction and of similar magnitude for both hawthorn and apple flies (Table 1). Therefore, if selection did occur, its effects were uniform across host plants.

Allele frequencies for *Acon-2*, *Me*, *Mpi*, *Aat-2*, *Dia-2* and *Had* may not be evolving independently. Hitch-hiking effects for linked loci and epistatic selection can coordinately change allele frequencies at a number of loci. To examine these possibilities, correlation coefficients were calculated between pairs of non-allelic genes based on Burrows disequilibrium values[7,8]. Significant disequilibrium was found between *Me*/*Acon-2*, *Me*/*Mpi*, *Acon-2*/*Mpi* and *Aat-2*/*Dia-2* (Table 3). These results agree with the known genetic map of *R. pomonella* as *Aat-2* and *Dia-2* are 3.2 centimorgans apart on linkage group I whereas *Acon-2*, *Me* and *Mpi* are very tightly linked on linkage group II (Feder *et al.*, manuscript in preparation). Loci showing genetic differentiation between hawthorn and apple flies therefore map to three different regions of the genome, and hitch-hiking effects are probable among non-allelic genes within at least two of these regions.

Interactions between unlinked loci were not readily apparent from the correlation coefficients. Twenty-one significant tests of gametic disequilibrium were observed in 314 pairwise comparisons between *Mpi*, *Acon-2* or *Me* and either *Aat-2* or *Dia-2* (data not shown). *Had*, which has been mapped to linkage group III (ref. 9), was in gametic equilibrium with either *Acon-2*, *Me*, *Mpi*, *Aat-2* or *Dia-2* in 153 of 160 tests. Although interchromosomal levels of gametic disequilibrium cannot be completely explained by random type I errors, no consistent pattern was observed in either the loci or alleles involved in the significant tests. Allele frequencies for unlinked loci therefore appear to be evolving independently in both hawthorn and apple populations.

Several factors, alone or in combination, could be responsible for the observed allele frequency differences between hawthorn

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Table 1 Allele frequencies for *Me*, *Acon-2*, *Mpi*, *Aat-2*, *Dia-2* and *Had* for flies collected from hawthorn and apple trees at the Hansen site near Grant, Michigan

Year (Stage)	Host	*Me*		*Acon-2*			*Mpi*			*Aat-2*			*Dia-2*		*Had*	
		n	80	*n*	100	95	*n*	100	37	*n*	100	21	*n*	100	*n*	100
1984	Apple-1	99	0.707	99	0.545	0.152	99	0.889	0.056	99	0.279	0.187	96	0.688	99	0.803
(Larvae)	Apple-2	84	0.631	86	0.512	0.221	86	0.884	0.046	86	0.326	0.157	86	0.767	86	0.907
1985	Apple-1	25	0.480	25	0.480	0.240	25	0.900	0.060	25	0.300	0.120	24	0.729	25	0.740
(Larvae)	Apple-2	52	0.587	62	0.484	0.185	65	0.869	0.085	52	0.393	0.183	63	0.802	65	0.838
	Apple-3	51	0.618	50	0.511	0.220	50	0.880	0.060	51	0.294	0.157	50	0.650	51	0.726
1986	Apple-1	46	0.663	46	0.598	0.109	46	0.946	0.000	46	0.272	0.130	46	0.669	46	0.837
(Adults)	Apple-2	39	0.603	39	0.584	0.167	39	0.897	0.000	39	0.269	0.141	39	0.628	39	0.859
1984 (Larvae)	Haw-1	101	0.272	101	0.297	0.490	101	0.703	0.178	101	0.465	0.104	100	0.895	101	0.876
1985	Haw-1	52	0.269	64	0.250	0.500	65	0.785	0.085	51	0.372	0.088	64	0.797	65	0.885
(Larvae)	Haw-2	53	0.274	53	0.273	0.500	53	0.717	0.216	53	0.415	0.066	53	0.877	53	0.877
	Haw-3	51	0.225	52	0.250	0.645	52	0.683	0.183	50	0.410	0.030	52	0.865	52	0.875
1986	Haw-1	61	0.385	61	0.443	0.410	61	0.795	0.148	61	0.402	0.090	61	0.820	61	0.813
(Adults)	Haw-2	63	0.444	63	0.365	0.365	63	0.787	0.131	63	0.460	0.048	63	0.802	63	0.841

The table is abbreviated and contains the subset of alleles with the highest levels of inter-host differentiation. Alleles were numbered according to their relative mobility to the common allele (100) at the locus. *n*, sample size. Allele *Acon-2*^{95} in this study is the same as *Acon-2*^{91} in McPheron *et al.*[16].

Table 2 *G*-contingency tests for allele frequency differences for *Me*, *Acon-2*, *Mpi*, *Aat-2*, *Dia-2* and *Had* at the Grant, Michigan site

Year (Stage)	Test	*Me*	*Acon-2*	*Mpi*	*Aat-2*	*Dia-2*	*Had*
1986	Among apple trees	0.67 (1)	1.44 (3)	1.39 (2)	5.72 (4)	0.86 (1)	0.16 (1)
(Adults)	Among haw trees	0.90 (1)	6.71 (3)	0.65 (2)	2.34 (4)	0.13 (1)	0.61 (1)
	Between apple-haw	19.90 (1)*	34.60 (3)*	38.10 (2)*	14.79 (4)†	11.32 (1)*	0.44 (1)
1985	Among apple trees	3.07 (2)	3.71 (6)	0.96 (4)	16.45 (8)‡	6.55 (2)‡	4.90 (2)
(Larvae)	Among haw trees	0.78 (2)	10.67 (6)	11.84 (4)‡	10.98 (8)	3.33 (2)	0.06 (2)
	Between apple-haw	60.70 (1)*	44.10 (3)*	—	—	—	10.97 (1)*
	Apples-haw tree 1	—	—	7.10 (2)‡	—	—	—
	Apples-haw tree 2	—	—	15.50 (2)*	—	—	—
	Apples-haw tree 3	—	—	18.50 (2)*	—	—	—
	Apple tree 1-haws	—	—	—	5.43 (4)	3.47 (1)	—
	Apple tree 2-haws	—	—	—	21.22 (4)*	1.11 (1)	—
	Apple tree 3-haws	—	—	—	16.93 (4)†	16.36 (1)*	—
1984	Among apple trees	2.39 (1)	6.32 (3)	1.13 (2)	2.17 (4)	4.14 (1)‡	8.12 (1)†
(Larvae)	Between apple-haw	85.70 (1)*	59.30 (3)*	32.40 (2)*	31.10 (4)*	—	—
	Apple tree 1-haws	—	—	—	—	26.42 (1)*	4.01 (1)‡
	Apple tree 2-haws	—	—	—	—	9.11 (1)†	0.91 (1)
Between	Apple tree 1	5.01 (1)‡	6.30 (3)	6.47 (2)‡	2.93 (4)	0.17 (1)	1.87 (1)
1985/1986	Apple tree 2	0.05 (1)	3.19 (3)	12.60 (2)†	17.98 (4)†	7.30 (1)†	0.16 (1)
(Larvae/	Haw tree 1	3.43 (1)	15.50 (3)†	5.25 (2)	0.88 (4)	0.21 (1)	3.20 (1)
Adults)	Haw tree 2	7.33 (1)†	9.39 (3)‡	3.00 (2)	6.52 (4)	2.45 (1)	0.62 (1)
Between	Apple tree 1	9.67 (1)†	5.60 (3)	0.04 (2)	3.75 (4)	0.62 (1)	0.92 (1)
1984/1985	Apple tree 2	1.45 (1)	2.72 (3)	1.22 (2)	5.52 (4)	0.50 (1)	3.19 (1)
(Larvae)	Haw tree 1	0.16 (1)	4.85 (3)	5.97 (2)	4.12 (4)	4.66 (1)‡	0.05 (1)

Degrees of freedom are given in parentheses. Gene frequencies for non-significant intra-host tests were pooled across host trees and these pooled totals were used for inter-host tests (between apple-haw). When significant intra-host heterogeneity was observed for a locus, inter-host tests were conducted on a tree-by-tree basis against the pooled total for the other host (namely apples-haw tree 1).

* $P \leq 0.001$; † $P \leq 0.01$; ‡ $P \leq 0.05$.

and apple flies. Among the possibilities are: (1) post mating reproductive isolation between hawthorn and apple flies; (2) a genetic bottleneck associated with the founding of the apple race; (3) differential larval survivorship associated with the host fruit environment; (4) differential host recognition by adult flies; (5) temporal differences in the timing of adult emergence.

It is very unlikely that post-mating reproductive isolation is involved in differentiating host populations. Hawthorn and apple flies readily mate in the laboratory and produce viable F_1 progeny (R. Prokopy, personal communication). Per cent egg hatch is similar for apple × apple, hawthorn × hawthorn and hawthorn × apple test crosses[10]. Although data from F_2 and backcrosses are needed to completely rule out postmating isolation, the likelihood of reproductive incompatibility between these flies is remote.

A genetic bottleneck during the colonization(s) of apple by *R. pomonella* may have initially caused gene frequency differences between the host races through drift. But for neutral genetic differences to persist requires restricted gene flow between sympatric apple and hawthorn populations. Variation for intrinsic biological factors (that is, differential larval survivorship, host recognition and/or adult emergence) are therefore necessary to account for the continued maintenance of host race differentiation regardless of its original cause.

Although differential selection on larval populations infesting hawthorn and apple fruits could account for genetic divergence, larval selection alone cannot explain the significant frequency differences observed between adults captured directly from hawthorn and apple fruits in 1986 (Tables 1 and 2). Random dispersal of flies between host plants would homogenize adult gene frequencies even if larval selection was intense[11]. Furthermore, adult hawthorn and apple flies show the same pattern and magnitude of host related differentiation as larvae. Gene flow must therefore be restricted between hawthorn and apple popu-

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Table 3 Correlation coefficients (r^{AB}) calculated between pairs of non-allelic genes based on disequilibrium values[7,8]

Year (Stage)	Host	$Me^{100}/Acon^{95}$	Me^{100}/Mpi^{100}	$Mpi^{100}/Acon^{95}$	$Aat\text{-}2^{21}/Dia\text{-}2^{85}$
1984	Apple 1	0.3031*	−0.2823‡	−0.3137*	0.5045*
(Larvae)	Apple 2	0.4242*	−0.1276	−0.1755	0.4752*
	Haw 1	0.2770†	−0.1980‡	−0.3039†	0.6692*
1985	Apple 1	0.2327	−0.3770‡	−0.4354*	0.6991†
(Larvae)	Apple 2	0.3314‡	−0.1997	−0.1782	0.2935‡
	Apple 3	0.5097*	−0.1833	−0.2660	0.6337†
	Haw 1	0.4634†	−0.2780‡	−0.2285	0.5082*
	Haw 2	0.3723†	−0.2731	−0.1681	0.5153*
	Haw 3	0.3951‡	−0.3420‡	−0.2488	0.5357*
1986	Apple 1	0.3311†	−0.1679	−0.3311‡	0.5513*
(Adults)	Apple 2	0.3229†	−0.2724	−0.0362	0.4481*
	Haw 1	0.4551†	−0.3445†	−0.3017‡	0.4990*
	Haw 2	0.5882*	−0.1853	−0.4217*	0.5267*

Significance determined by χ^2 goodness-of-fit tests of Burrows value.
* $P \leq 0.001$; † $P \leq 0.01$; ‡ $P \leq 0.05$.

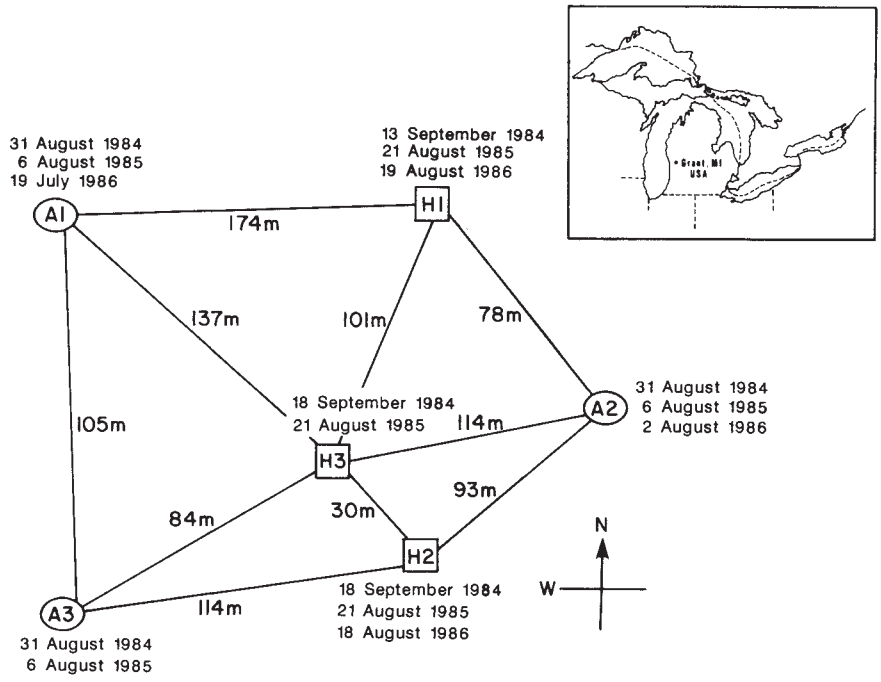

Fig. 1 Scale diagram of study site located near Grant, Michigan, United States. The site is an old field which has remained fallow since at least 1922 (E. Hansen, personal communication). Host tree designations (A, apple; H, hawthorn) are given with collecting dates and inter-tree distances (in metres). In 1984 and 1985 flies were sampled as larvae from infested fruit and reared to adulthood in the laboratory. In contrast, adults were captured directly from host fruits by sweep net in 1986. Standard horizontal starch gel electrophoretic techniques were used[17] and a total of 29 different allozyme systems were resolved (a list of resolved systems is available on request). Isozyme systems that migrated to nearest the cathode were designated 1, the second nearest 2, and so on. Thirteen loci were polymorphic (frequency of the common allele <0.95) and, excluding *Aat-1* which is sex linked, only 15 significant deviations from Hardy-Weinberg equilibrium were observed for these loci in 290 tests. The significant deviations displayed no regular pattern and their number does not differ from random expectation because of type I error.

lations, indicating that the host races are not mating randomly in nature.

Traits involved in host recognition and the timing of adult eclosion are the most likely candidates responsible for reducing gene flow between hawthorn and apple races. Host acceptance behaviours do differ between hawthorn and apple flies[12] and former adult experience can affect host preference in *R. pomonella*[13]. Field studies have shown that hawthorn and apple flies differ in their mean adult emergence times by about a week and a half in the field[14] and by even more under laboratory conditions[15]. Also, the distribution of adults at the Grant site closely follows the fruiting phenology of their host plants, because early in the summer flies are abundant on ripe apples but scarce on immature hawthorns, whereas the reverse is true three to four weeks later in the season when hawthorns ripen (see Fig. 1 for adult collecting dates). Differences in diapause termination and host preference, together with adult conditioning, could all contribute to the establishment of an assortative mating system, with early emerging adults tending to reproduce on apples and later emerging flies on hawthorns.

The existence of genetic differentiation between sympatric hawthorn and apple populations of *R. pomonella* at the Grant, Michigan site confirms the status of these flies as non-randomly mating host races. The recent formation of the apple race indicates that these flies are diverging sympatrically in the absence of geographic isolation. More research is needed, however, to clarify which biological factors are most significant in creating and maintaining host related frequency differences at the Grant, Michigan site.

The geographic pattern of genetic differentiation between apple and hawthorn populations of *R. pomonella* appears to be complex. In an accompanying letter, McPheron *et al.*[16] also document significant frequency differences at a sympatric site in Urbana, Illinois. Their results differ slightly from ours, however, in the pattern of loci and frequencies of alleles displaying inter-host differentiation. In addition, a recently completed analysis of geographic variation across the eastern United States (Feder *et al.*, manuscript in preparation) indicates that north–south allele frequency clines exist for both apple and hawthorn flies across their ranges for five of the six loci showing host-associated heterogeneity. Inter-host differences are therefore superimposed on latitudinal patterns of variation within the hawthorn and apple races and these clines help to explain the genetic differences between sites in Michigan and Illinois. The

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results from the geographical survey raise the question of whether sympatric mechanisms alone account for the development of complete reproductive isolation between *R. pomonella* populations. We consequently believe that it is inappropriate to state definitively that hawthorn and apple races represent 'incipient' species. But the *R. pomonella* complex contains a number of sympatrically distributed sibling species specializing on different host plants which are inter-fertile in laboratory crosses, yet remain distinct in nature[1,17].

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Genetic differences between host races of *Rhagoletis pomonella*

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Sympatric speciation by the formation of host races (parasite populations associated with different plant or animal hosts) has been the subject of great controversy. It has been difficult to demonstrate the existence of host races[1,2], much less to prove that host races are evolving toward species status. Genetic polymorphism attributable to association with different resources does occur[3], but the phenomenon is far from ubiquitous in parasite populations. The apple maggot fly *Rhagoletis pomonella* uses a variety of host plants, and Bush[4,5] has argued that it is a likely candidate for speciation by a sympatric mode. So far however there has been no direct evidence of any genetic differentiation between host-associated fly populations. We report significant differences in allele frequencies between fly populations reared from sympatric apple (*Malus pumila*) and hawthorn (*Crataegus mollis*) trees at a field site in Urbana, Illinois, in the United States.

Genetic heterogeneity was evident both in the five paired apple–hawthorn comparisons and in comparisons within a single host species over the five sites (Table 1; see Fig. 1 for the spatial arrangement of trees and the methods used). Allele frequencies at the enzymes cytosolic aconitase (*Acon-2*) and β-hydroxyacid dehydrogenase (*Had*) were consistently different between apple and hawthorn fly populations (Table 2). In each of the five paired apple–hawthorn comparisons, the frequency of $Acon\text{-}2^{100}$ was lower in the apple sample than in the corresponding hawthorn sample (Table 2). Conversely, frequencies of both $Acon\text{-}2^{75}$ and $Acon\text{-}2^{109}$ were higher in every apple sample than in the corresponding paired hawthorn samples. *Had* allele frequencies displayed a similar consistency between the paired apple and hawthorn samples. The frequency of Had^{100} was always greater in the apple sample than in the respective hawthorn sample, but the difference was not significant at site 5. Several other loci were heterogeneous for single site comparisons (Table 1) but did not display the consistent patterns seen in *Acon-2* and *Had*. Differences in host-associated loci between this study and that of Feder *et al.*[6] reflect a strong latitudinal allele frequency cline at several enzyme genes in *R. pomonella* (J. L. Feder, C. A. Chilcote and G. L. Bush, personal communication and ref. 7).

Significant intrahost differentiation among both apple- and hawthorn-associated flies (Table 1) was of insufficient magnitude to obscure the patterns of interhost differences. Similar microgeographic heterogeneity has been demonstrated previously among flies from individual trees for another hawthorn-infesting *R. pomonella* population in Urbana, Illinois[8]. Cases of significant intrahost heterogeneity in our data were primarily

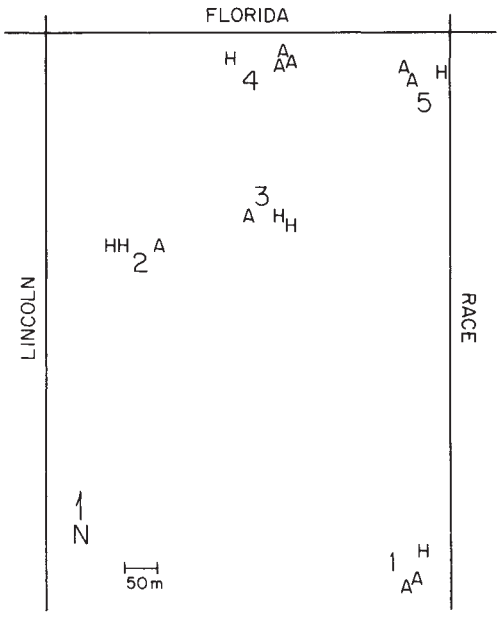

Fig. 1 Spatial arrangement of the five collecting sites in Urbana, Illinois. The symbol A refers to individual apple trees and the symbol H refers to individual hawthorn trees.

Methods. Infested fruit were collected from beneath five paired sets of apple (*M. pumila*) and hawthorn (*C. mollis*) trees. Apple collections were made in mid-August, 1985, and hawthorn collections followed in mid-September, 1985. Fruit were held under controlled conditions in the laboratory until larvae emerged and pupated in moist vermiculite. Pupae were then stored at 6 °C for six months to break diapause. Adult flies eclosed between one to three months following exposure to 24 °C at 20:4 light:dark. One hundred frozen adult flies from each host at each site were analysed by standard horizontal starch gel electrophoresis[7,8,15–17] for 17 loci: aconitase-1, aconitase-2, adenylate kinase, alcohol dehydrogenase-1, aldolase, arginine kinase, aspartate aminotransferase-2, NADH-dependent diaphorase-2, fumarate hydratase, α-glycerophosphate dehydrogenase, β-hydroxyacid dehydrogenase, isocitrate dehydrogenase, mannose phosphate isomerase, phosphoglucomutase, phosphoglucose isomerase, trehalase, and triose phosphate isomerase. Mendelian inheritance of significantly variable loci has been demonstrated (refs 15 and 17; J. L. Feder, C. A. Chilcote and G. L. Bush, personal communication). Allele designations are by mobility relative to the most common allele at a locus (=100). χ^2 analysis of these loci revealed only five deviations from Hardy–Weinberg equilibrium out of 134 tests, a level expected from chance alone.

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