

# Simulation Models for Predicting Durability of Insect-resistant Germ Plasm: Hessian Fly (Diptera: Cecidomyiidae)-resistant Winter Wheat

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FORUM: Environ. Entomol. 15: 11-23 (1986)

**ABSTRACT** In an attempt to determine what strategies of resistant germ plasm deployment would most successfully inhibit Hessian fly, *Mayetiola destructor* (Say), adaptation to wheat resistance factors while offering significant crop protection, a computer simulation model was developed to mimic ecological/genetic interactions between Hessian fly populations and resistant winter wheat. Durability of the following resistant germ plasm deployment strategies was examined: 1) sequential release of two pure cultivars, each with a single resistance factor, 2) release of a random spatial mixture of these two cultivars, 3) release of a pure cultivar in which both resistance factors were present in each plant (pyramided), and 4) modification of each of the above deployment strategies by addition of totally susceptible wheat to the system. Effects of temporal and spatial characteristics of the mixtures were also explored. Interpolating a pyramided resistant cultivar with some totally susceptible plants offers the highest relative durability in most cases, and is predicted to last >400 fly generations under some conditions.

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THE HESSIAN FLY, *Mayetiola destructor* (Say), is a significant pest of wheat in the Midwest and other wheat-producing regions of the United States (McColloch 1923, Gallun et al. 1975, Morrill and Nelson 1976, Pike and Antonelli 1981). Considerable emphasis has been placed on using resistant wheat cultivars to limit the damage caused by this pest (Gallun 1977). A number of resistant cultivars have been widely planted in Indiana, but their effectiveness has been diminished by the evolution of Hessian fly biotypes that are unaffected by resistance factors in these wheat cultivars (Gallun 1977).

At least 13 wheat genes have been identified that confer resistance to some Hessian fly biotypes (Gallun 1977, Hatchett et al. 1981). Host-plant resistance programs have, in the past, recommended the sequential use of single genes from this resistant germ-plasm bank to control the Hessian fly (Gallun 1977, Gallun and Khush 1980). This sequential-use strategy involves the development and widespread deployment of wheat cultivars with one resistance-conferring gene to which the fly population is unadapted. Once the fly population adapts to the resistance factor produced by this gene, a second resistance-conferring gene is backcrossed into the wheat and released. (Often the new wheat cultivar will still possess the now obsolete resistance gene—e.g., Arthur 71.) This procedure is repeated as the fly population adapts to each sequentially released resistance gene.

There has been some controversy in the plant pathology and entomology literature concerning the merits of the sequential resistant-gene release strategy compared to pyramided or mixed resis-

tant germ plasm release strategies (Gallun 1977, Gallun and Khush 1980, Kiyosawa 1982, Gould 1984, 1986). The pyramided release strategy generally entails breeding two or more resistance factors (or genes) into a single cultivar before they are deployed. The mixed germ-plasm release strategy generally involves the development of multi-lines with a different resistance factor in each plant isolate (mixed planting of cultivars with different types of resistance are also considered).

Plant pathologists have used computer simulations to predict the length of time it will take for a pathogen to adapt to the three general deployment strategies mentioned above (see Kiyosawa 1982 and references therein). Gould (1986) developed a diploid, two-locus simulation model to explore some of the general ecological and genetic factors that could influence the durability of insect-resistant germ plasm. The factors examined included variation in: 1) method of field deployment of the resistant germ plasm, 2) selection pressure imposed on the insect population by the resistance factor(s), 3) the mode of inheritance of characteristics in the insect for adapting to the resistance factor(s), and 4) initial frequency of these adaptive characteristics in the insect population. The model was limited to exploring insect systems that had simple diploid sexual reproduction, exhibited random mating, and had one insect generation per crop planting.

The Hessian fly has a paternal gene-loss genetic system (Metcalf 1935, Gallun and Hatchett 1969, Bantock 1970), in which the males do not usually place any of their fathers' chromosomes into their sperm (but see Gallun 1978). They also exhibit

**Table 1. Heterozygote survival**

| Hessian fly genotype           | Host   |  |  |
|--------------------------------|--|--|--|
|                                | Seneca wheat   | Monon wheat  | Knox wheat   |
|                                | Allele <i>s</i> causes adaptation  | Allele <i>m</i> causes adaptation  | Allele <i>k</i> causes adaptation  |
| <i>Ss, MM, KK</i> <sup>a</sup> | 1.7% survivorship if <i>s</i> is paternally derived, 14.0% survivorship if <i>s</i> is maternally derived (Hatchett and Gallun 1970) |  | —  |
| <i>Ss, Mm, KK</i>              | —  | 0% survivorship; no maternal effect (Hatchett and Gallun 1970)   | —  |
| <i>ss, Mm, KK</i>              | —  | 50–60% survivorship, but survivors generally smaller than those with <i>mm</i> genotype; no maternal effect (Gallun and Hatchett 1969) | —  |
| <i>ss, Mm, Kk</i>              | —  | No growth if <i>m</i> is paternally derived, intermediate growth if <i>m</i> is maternally derived (Gallun 1978)                       | No growth if <i>k</i> is paternally derived, intermediate growth if <i>k</i> is maternally derived (Gallun 1978) |

<sup>a</sup> Alleles *s*, *m*, *k* code for adaptation to Seneca, Monon, and Knox wheat, respectively. Alleles *S*, *M*, *K* code for lack of adaptation to Seneca, Monon, and Knox wheat, respectively.

maternal effects on fitness in some cases (Table 1). Hessian flies may mate randomly in a small area (<100 m<sup>2</sup>) (Cartwright 1922), but certainly exhibit nonrandom mating among subpopulations in different fields. Normally, there are two Hessian fly generations per winter wheat planting in northern areas; one initiated in the fall and a second in the spring (McColloch 1923). In other areas there may be more generations per planting (e.g., Pike and Antonelli 1981). These aspects of Hessian fly biology significantly violate the assumptions of the general model (Gould 1986).

A modification of the general model is presented here that mimics more precisely the Hessian fly/winter wheat system. I believe that this model will help address, quantitatively, the question of how best to deploy wheat resistance against the Hessian fly in the future.

### Model Development

The basic framework of this model is discussed in Gould (1986). It is assumed that there are two independently acting resistance factors that can be incorporated singly or together in wheat cultivars. It is further assumed that there are two loci (which may or may not be linked) that modify the effect of the two resistance factors on fly fitness. Allele *a* at locus I codes for adaptation to resistance factor I, while allele *A* codes for lack of adaptation. Allele *b* at locus II codes for adaptation to resistance factor II. Allele *B* codes for lack of adaptation. The empirical literature on Hessian fly generally supports the validity of these assumptions (Gallun 1978).

To simulate the paternal gene-loss system and maternal effects with a two-locus model, 16 male and 16 female two-locus genotypes were assigned (see Table 2). In this manner it was possible to

keep track of which alleles each parent contributed to heterozygous offspring. This also allowed simulation of normal meiosis in females and male elimination of the genes inherited from their fathers during spermatogenesis. Since fly mortality due to resistance genes in the wheat occurs during the larval stage, male and female fitness is influenced by paternally inherited genes (Gallun and Hatchett 1969).

Data from some of the experiments reported in Hatchett and Gallun (1970) and Gallun (1978) indicate that for two biotypes, heterozygous flies that were derived from matings of homozygous adapted females (*aa* or *bb* in the model) and homozygous unadapted males (*AA* or *BB*) had higher survival or faster growth rates than flies derived from matings of homozygous adapted males and homozygous unadapted females. It is difficult to determine from the data whether maternal effects occurred when the mother was heterozygous. In other experiments, no maternal effects were found (Gallun and Hatchett 1969, Hatchett and Gallun 1970). These results are summarized in Table 1 in terms of the genotypic backgrounds of the flies involved in the crosses. This summary indicates that maternal effect varies among some experiments involving the same heterozygous locus. Since the rest of the genetic make-up of the stocks used in these experiments differed, it is possible that presence or absence of maternal effect depends on modifier genes. Alternately, the maternal effect could be entirely extra-chromosomal with its expression depending on specific greenhouse conditions. Maternal effects were incorporated into the simulation model by a 10% increase in the fitness of heterozygote offspring that received their adapted alleles from their mothers. This approximately reflected the experimental data in Hatchett and Gallun (1970).

**Table 2. Recurrence equations for 2-loci, with random mating and paternal gene loss**

|   |   |                 |                 |                 |                 |                 |                 |                 |
|---|---|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Gametic types:  | <i>AB</i>   | <i>Ab</i>       | <i>aB</i>       | <i>ab</i>       |                 |                 |                 |                 |
| ♂ gametic frequencies:  | $X_{1m}$  | $X_{2m}$        | $X_{3m}$        | $X_{4m}$        |                 |                 |                 |                 |
| ♀ gametic frequencies:  | $X_{1f}$  | $X_{2f}$        | $X_{3f}$        | $X_{4f}$        |                 |                 |                 |                 |
| Parental genotypes (maternally derived alleles above line. Paternally derived genes below line) | $\frac{AB}{AB}$   | $\frac{AB}{Ab}$ | $\frac{Ab}{AB}$ | $\frac{Ab}{Ab}$ | $\frac{AB}{aB}$ | $\frac{aB}{AB}$ | $\frac{AB}{ab}$ | $\frac{ab}{AB}$ |
| Genotype frequency  | $X_{1f}X_{1m}$  | $X_{1f}X_{2m}$  | $X_{2f}X_{1m}$  | $X_{2f}X_{2m}$  | $x_{1f}X_{3m}$  | $X_{3f}X_{1m}$  | $X_{1f}X_{4m}$  | $X_{4m}X_{1f}$  |
| ♂ fitness   | $w_{11m}$   | $w_{12m}$       | $w_{21m}$       | $w_{22m}$       | $w_{13m}$       | $w_{31m}$       | $w_{14m}$       | $w_{41m}$       |
| ♀ fitness   | $w_{11f}$   | $w_{12f}$       | $w_{21f}$       | $w_{22f}$       | $w_{13f}$       | $w_{31f}$       | $w_{14f}$       | $w_{41f}$       |
| Parental genotypes  | $\frac{Ab}{aB}$   | $\frac{aB}{Ab}$ | $\frac{Ab}{ab}$ | $\frac{ab}{Ab}$ | $\frac{aB}{aB}$ | $\frac{aB}{ab}$ | $\frac{ab}{aB}$ | $\frac{ab}{ab}$ |
| Genotype frequency  | $X_{2f}X_{3m}$  | $X_{3f}X_{2m}$  | $X_{2f}X_{4m}$  | $X_{4f}X_{2m}$  | $X_{3f}X_{3m}$  | $X_{3f}X_{4m}$  | $X_{4f}X_{3m}$  | $X_{4f}X_{4m}$  |
| ♂ fitness   | $w_{23m}$   | $w_{32m}$       | $w_{24m}$       | $w_{42m}$       | $w_{33m}$       | $w_{34m}$       | $w_{43m}$       | $w_{44m}$       |
| ♀ fitness   | $w_{23f}$   | $w_{32f}$       | $w_{24f}$       | $w_{42f}$       | $w_{33f}$       | $w_{34f}$       | $w_{43f}$       | $w_{44f}$       |
| New frequency of <i>AB</i> ♀ gametes = $X'_{1f}$  | $\bar{w}_f X'_{1f} = X_{1f}X_{1m}w_{11f} + \frac{1}{2}[(X_{1f}X_{2m}w_{12f}) + (X_{1f}X_{3m}w_{13f}) + (X_{3f}X_{1m}w_{31f}) + (X_{1f}X_{3m}w_{13f}) + (X_{4f}X_{1m}w_{41f}) + (X_{1f}X_{4m}w_{14f})](1 - r) + [(X_{3f}X_{2m}w_{32f}) + (X_{2f}X_{3m}w_{23f})](r).$ |                 |                 |                 |                 |                 |                 |                 |
| New frequency of <i>AB</i> ♂ gametes = $X'_{1m}$  | $\bar{w}_m X'_{1m} = X_{1f}X_{1m}w_{11m} + X_{1f}X_{2m}w_{12m} + X_{1f}X_{3m}w_{13m} + X_{1f}X_{4m}w_{14m}.$  |                 |                 |                 |                 |                 |                 |                 |

There are two or more Hessian fly generations per planting of winter wheat. A heavy fall infestation of Hessian fly in a wheat mixture may alter the frequency of the different wheat types the following spring; therefore, the model allows wheat type frequency changes due to the fall Hessian fly generation. The percent change in wheat type frequency is set as a constant. It does not reflect variation in the density of the fly population and variation in its genetic composition. (It is assumed that each year's new fall planting contains the initially determined frequency of wheat types for a given cultivar mixture.)

As a consequence of assuming nonrandom mating of flies between adjacent fields, the model had to be expanded to allow the existence of two subpopulations (*X* and *Y*) with migration of mated females. (Females mate only once, just after emergence [Cartwright 1922, McColloch 1923, McKay and Hatchett 1984], and may move up to 4 km under proper wind conditions [McColloch 1917].) The model assumes that the proportion of eggs in field *Y* that are laid by females originating from field *X* is directly related to the relative density of females in the two fields at the time of adult female emergence. This is achieved by setting the percentage of females moving out of a field as a constant (i.e., not density-dependent).

As with some other Diptera that exhibit paternal gene loss (Metz 1938), a single Hessian fly female usually lays only male or only female eggs (Gallun et al. 1961). In small populations, this type of reproduction could be expected to lead to significantly less sib-mating than expected in species where each female produces a ca. 1:1 ratio of males and females. This enforced outcrossing would tend to break up the two-locus adapted genotypes when they were rare. Since the present model is deterministic and assumes a large population size, prop-

er simulation of this enforced outcrossing is not possible here.

The Hessian fly/winter wheat interaction is generally regarded as a case where dominance and epistasis are present (see definitions in Gould [1986]), but various papers on the topic carefully point out that the degree of dominance of the unadapted alleles is not constant from locus to locus, or even from one laboratory experiment to the next when the genetic background of the stocks is varied (Table 1 and Sosa 1981). Variance in the degree of epistasis has not been treated quantitatively in the empirical literature, but since flies with one homozygous unadapted set of alleles at one locus (e.g., *AA*) have such low survival (0-5%) at moderate temperatures (Tyler and Hatchett 1983), epistasis is likely to be very strong when such genotypes are involved (see discussion in Gould [1986]). Except where specified, it is assumed that the fitnesses of Hessian fly genotypes *AaBB*, *aaBB*, *AABb*, and *AAbb* are all equal to the fitness of *AABB* on wheat plants having both resistance factors.

In cases where heterozygous flies survive, they are often much smaller than adapted homozygotes (Gallun 1978). This is very important in modeling resistance durability (if we assume that dominance is not always complete in the field), for we have neither an estimate of fitness of these small flies nor the knowledge of whether small male and female flies have equal fitness. It is also important to realize that the detailed data on the genetics of the Hessian fly/wheat interaction are derived from laboratory and greenhouse experiments. Since expression of resistance in wheat can be modified by temperature (Sosa 1979, Tyler and Hatchett 1983) and perhaps by other environmental conditions in the field (Sosa and Gallun 1973), these data must be interpreted with caution.

**Table 3. Hessian fly allelic frequencies derived from biotype surveys in the midwestern and southeastern United States**

| Year                   | Area              | Inferred allelic frequencies <sup>a</sup> |                       |                       | No. of ♀♀ surveyed |
|------------------------|-------------------|---|-----------------------|-----------------------|--------------------|
|                        |                   | <i>m</i> <sup>b</sup>                     | <i>k</i> <sup>c</sup> | <i>s</i> <sup>d</sup> |                    |
| 1966-1967 <sup>e</sup> | Mich.             | 0.18                                      | 0.18                  | 1.00                  | 725                |
|                        | Mo.               | 0.18                                      | 0.18                  | 1.00                  | 410                |
|                        | Eastern Kans.     | 0.21                                      | 0.17                  | 0.83                  | 520                |
|                        | Western Kans.     | 0.0-0.16 <sup>g</sup>                     | 0.0-0.16 <sup>g</sup> | 0.26                  | 470                |
|                        | Ind.              |   |                       |                       |                    |
|                        | (Posey County)    | 0.97                                      | 0.36                  | 1.00                  | 276                |
|                        | (Vigo County)     | 0.52                                      | 0.22                  | 1.00                  | 500                |
|                        | (Hamilton County) | 0.94                                      | 0.24                  | 1.00                  | 300                |
| Tenn.                  | 0.25              | 0.22                                      | 1.00                  | 300                   |                    |
| 1967-1968 <sup>f</sup> | Ga.               | 1.00                                      | 0.0-0.13              | 0.27                  | 800                |

<sup>a</sup> Allelic frequencies presented are estimates based on an analysis of values for biotype frequencies found in the literature. It is assumed that alleles for adaptation are completely recessive. If they are not completely recessive, the values given are overestimates of their frequencies.

<sup>b</sup> Allele *m* codes for adaptation to the *H*<sub>3</sub> gene of Monon wheat.

<sup>c</sup> Allele *k* codes for adaptation to the *H*<sub>6</sub> gene of Knox 62 wheat.

<sup>d</sup> Allele *s* codes for adaptation to Seneca wheat.

<sup>e</sup> Hatchett and Gallun (1968).

<sup>f</sup> Hatchett (1969).

<sup>g</sup> No flies homozygous for *m* or *k* were found in these samples. The high estimate of the frequency is based on the frequency at which one homozygote fly would on average be expected to be found in the samples.

The initial allele frequencies explored in this paper were set at relatively high values, partially based on calculations from regional surveys of the fly biotypes found in western Kansas, Missouri, and Michigan during 1966 and 1967 (Hatchett and Gallun 1968), and Georgia in 1968 (Hatchett 1969). By assuming no linkage disequilibrium (Gallun 1978) and complete dominance of the unadapted alleles, it was possible to derive the approximate frequency of alleles contributing to these biotype frequencies (Table 3). For example, if biotype A frequency was 0.01, *s* allele frequency would be 0.10, the square root of biotype A frequency. To the extent that linkage disequilibrium or incomplete dominance was present, some of the derived estimates could be too high or too low. The higher frequencies in Table 3 are the obvious result of Hessian fly adaptation to widely planted resistant cultivars, but the frequency of *m* and *k* of 0.18 in Michigan and Missouri may be considered reasonable starting points with only 3% of the flies unaffected by wheats with *H*<sub>3</sub> or *H*<sub>6</sub> resistance factors. The fact that Cartwright and Noble (1947), Gallun et al. (1961), and Sosa (1978) were able to select between 1 and 4 biotypes from single laboratory colonies also argues for relatively high initial frequencies of some adaptive alleles (Gould 1983), but less classic causes of this initial variation must be considered (Temin and Engels 1984).

### Model Exploration

The relatively detailed information from the literature allows for less broad exploration of this model compared with the exploration of the general model (Gould 1985). It is possible to focus on details of variation in specific characteristics of the

Hessian fly/wheat interactions that could affect the durability of a particular deployment strategy.

#### All Plants with at Least One Resistance Factor.

If we examine the three basic strategies (sequential release of two pure cultivars with one factor each, pyramiding both factors in one pure cultivar, mixtures of 50% seed with resistance factor I and the other 50% with resistance factor II), we find that durability is always less than nine fly generations (4.5 years) when we assume no dominance (unadapted homozygote fitness = 0.04, heterozygote fitness = 0.52) and initial gene frequencies of 0.1 (Fig. 1A and 2A). Under these conditions, the pyramiding strategy is slightly less durable (about one generation) than the sequential release due to the fact that paternal gene loss makes the system operate as if there were slight gene linkage (see below). As we increase the dominance of the A and B alleles (Fig. 1A and 2A), this situation is reversed and the pyramiding strategy becomes the most durable (ca. 16 generations).

As was seen in the results with the general diploid model (Gould 1985), when alleles *a* and *b* are at low frequencies, dominance of A and B and epistasis between loci I and II tend to slow down the rate of Hessian fly adaptation. This occurs because these nonadditive genetic components of variance lower the relative contribution of additive genetic variance to the insect population's phenotypic variation in fitness (Falconer 1981). (Paternal gene loss in the Hessian fly decreases the negative effect of epistasis on the rate of adaptation because there is little or no opportunity for recombination in the male [Gallun 1978].)

When dominance and epistasis are both present, they act synergistically in decreasing the component of phenotypic variation that is due to additive

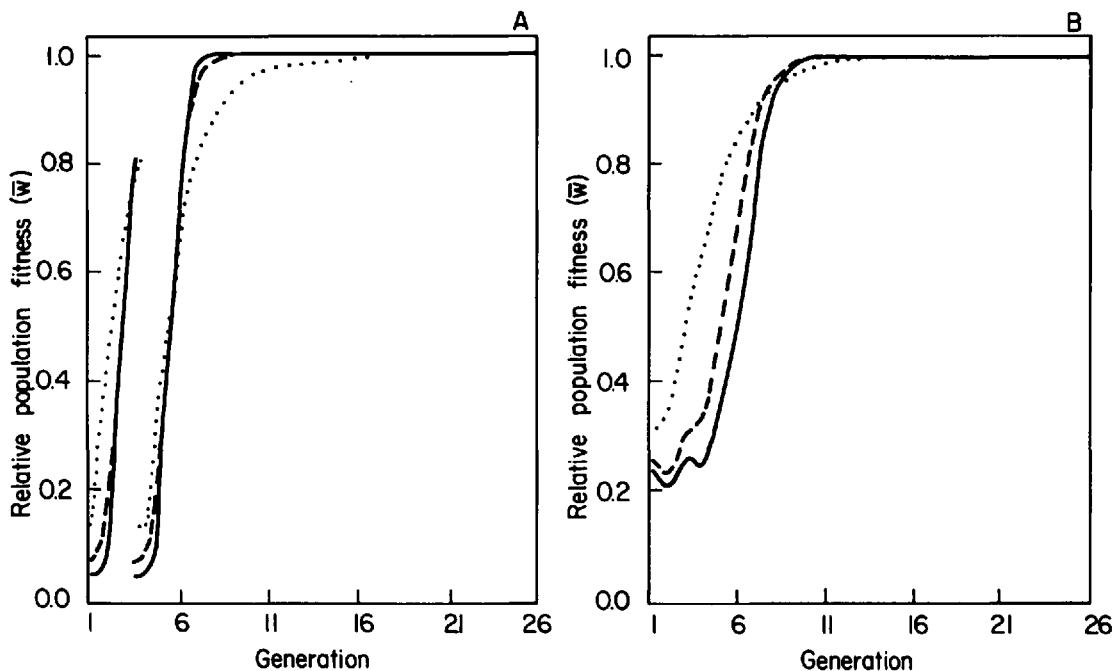


Fig. 1. Adaptation of a Hessian fly population to two resistance factors that are deployed sequentially: (A) The single-factor resistant wheat cultivars are planted as pure stands (no susceptible plants). Initial frequency of alleles  $a$  and  $b$  is 0.10. Heterozygote fly fitness on single-factor resistant plants is set at 0.52 ( $\cdots$ ) co-dominance; 0.28 ( $-\cdot-$ ); and 0.04 ( $—$ ) complete dominance of  $A$  and  $B$ . (B) Same as in A, except that the single-factor resistant wheat is combined with 20% totally susceptible wheat in a randomized seed mixture. Only adaptation to the first resistant cultivar in the sequential release is shown in B. Wavy lines in B are due to decrease in percent susceptible plants (tillers) in the spring due to Hessian fly damage the previous fall.

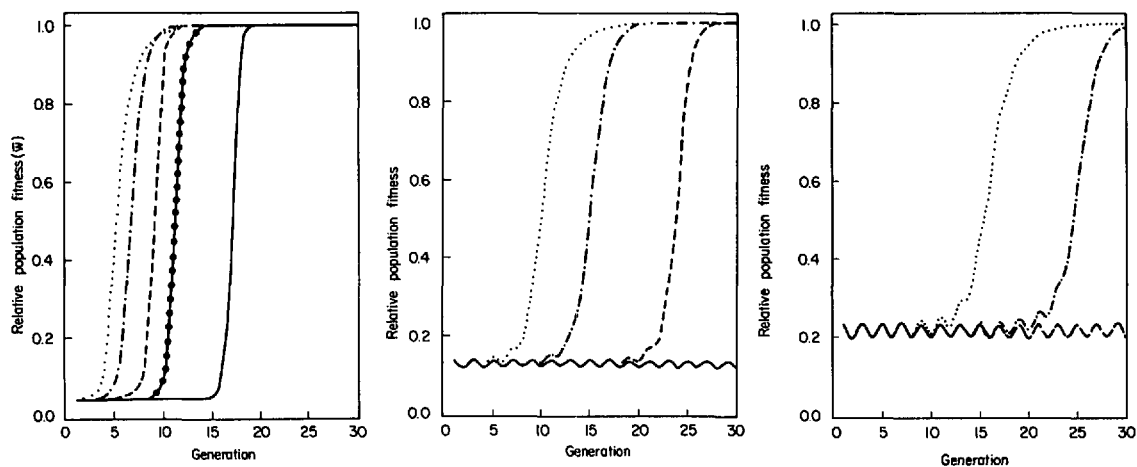
genetic variance. Thus, the pyramided release strategy is predicted to be very effective at gene frequencies slightly  $<0.10$  frequency presented in Fig. 2 (Left) (e.g., if frequency of  $a = b = 0.06$ , it takes ca. 70 generations for relative fitness of the population  $\bar{w}$  to reach 0.80). Although initial field frequencies of adapted alleles may be between 0.10 and 0.25 (Table 3), alleles for adaptation to some resistance factors may be lower. Effects of such lowered frequencies are further explored in Gould (1986) and are qualitatively applicable to the Hessian fly.

#### Effect of Adding Totally Susceptible Plants.

Lowering the selective pressure on unadapted fly genotypes within wheat fields could generally be expected to increase the durability of all of the basic deployment strategies (Gould 1986) and should be most effective when dominance and epistasis are components of fly fitness. Mixing of a small percentage of totally susceptible wheat with plants of the resistant cultivar would lower the selective pressure and could be economically practical. R. L. Gallun (personal communication) believes that a 10% loss of wheat plants in the fall would be almost totally compensated for by tillering and that a 10% loss of culms due to the spring Hessian fly generation would be below an economic threshold. If we assume that all totally susceptible plants in a field would be stunted, it would

be feasible to mix resistant seed with susceptible seed in a 9:1 ratio with little if any yield loss. Hessian flies usually stunt only a fraction of the plants in a field and oviposition choice is not correlated with antibiosis of cultivars (Gallun et al. 1961, Morrill 1982); thus, it is reasonable to expect that an 8:2 mixture of resistant-to-susceptible seed would be adequate for crop protection. This would be even more reasonable if widespread use of such resistant plantings reduced the size of Hessian fly populations and, therefore, the percentage of susceptible plants attacked. It may even be possible to breed tolerance into plants that lack antibiotic effects (Gallun and Hatchett 1969).

If the relative fitness of  $AABB$  flies on plants with one or two resistance factors is ca. 4% of their fitness on totally susceptible plants, their average fitness ( $\bar{w}$ ) in a 9:1 planting would be  $(0.9)(0.04) + (0.1)(1.0) = 0.136$ . In an 8:2 planting, it would be  $(0.8)(0.04) + (0.2)(1.0) = 0.232$ . Even if  $AABB$  flies never survived on resistant wheat, their fitness in the 8:2 planting would be 0.20. This would reduce selection pressure and cause most of the initially very rare  $aabb$  flies to mate with the common  $AABB$  genotype flies, causing the breakup of adapted genotypes. Results of simulations in which 1 out of 10, and 1 out of 5 plants are totally susceptible are discussed below and support this contention.



**Fig. 2.** Adaptation of a Hessian fly population to two resistance factors that are deployed in a single pyramided cultivar. (Left) Resistant pyramided cultivar is planted as a pure stand (no susceptible plants). (Middle) Pyramided cultivar is interplanted with 10% totally susceptible plants. (Right) Pyramided cultivar is interplanted with 20% totally susceptible plants each fall. Initial frequency of alleles *a* and *b* is 0.10. Fitness of *Aabb* and *aaBb* flies on plants with both resistance factors are equal and set at 0.52 (····), 0.28 (---), 0.14 (— · —), and 0.04 (—). Maternal effects are simulated (— · —) by setting fitness of *Aabb* and *aaBb* flies equal to 0.04 if the *A* or *B* allele comes from the mother and 0.14 if the *A* or *B* allele comes from the father.

**Single-factor Resistance Plus Susceptible Plants.** Fig. 1B illustrates that mixing 20% susceptible seed with 80% single factor resistant wheat could extend the durability of the sequentially released germ plasm, especially if there was complete dominance of alleles *A* and *B*. Given such complete dominance, durability is almost twice that seen in plantings of 100% single-factor resistant plants. Of course, one could argue that the lower survival rate of flies when the pure resistant cultivar was released (4% compared with 23%) could cause a lag in fly population buildup, so that although survival in generation 7 for the 8:2 plantings was lower than in the pure resistant planting, the number of flies present would be equal. By extending this argument to its somewhat implausible limit, it is possible to predict that numbers of flies would be larger in generation 7 in the mixed planting than in the pure resistant-cultivar planting (Gould 1986).

**Pyramided Two-factor Resistance Plus Susceptible Plants.** The effect of initially low fly survival caused by deploying a pure, pyramided cultivar could severely lower population size and have long time-lag effects on population buildup. But when compared with the extended durability of the pyramided cultivar mixed with 10 or 20% susceptible plants (Fig. 2 Left and Right), it is impossible to argue that initially lower numbers of flies would lead to durability approximating that of the deployment with 10 or 20% totally susceptible plants. Indeed, the simulation model predicts that if we assume initial frequency of *a* and *b* of 0.10, and strong dominance and epistasis of *A* and *B*, deployment of wheat with 10 or 20% totally susceptible plants would allow resistance to last >50 and >100 generations, respectively ( $\bar{w} <$

0.40). Even with only partial dominance of *A* and *B* (heterozygote fitness = 0.14 or 0.28), durability is greatly enhanced by the pyramided strategy involving 20% totally susceptible plants. If we assume strong dominance and epistasis, with *a* and *b* initial frequency of 0.05, resistance lasts over 400 generations. This almost indefinite durability also occurs if 0.01 initial frequency is assumed with only partial dominance (heterozygote  $\bar{w} = 0.28$ ), or partial epistasis ( $\bar{w}$  on wheat with two resistance factors is 0.04 for *aaB-* or *A-bb* and 0.00 for *A-B-*).

**Maternal Effects.** Since two of the laboratory studies indicated a maternal effect on the survival of heterozygous larvae (Table 1), it was important to explore the possible effect of this characteristic on durability. By altering survival of heterozygotes, within the model, dependent on the sex of the parent contributing the adapted allele, it was possible to simulate an extra-chromosomal maternal effect. The results (Fig. 2 Left) indicate that this may cause a reduction in durability of the resistance factors similar to that caused by incomplete dominance of *A* and *B*. In this simulation it was assumed that as long as the adapted allele was contributed by the mother, there would be constant maternal effect. Indeed, this effect could vary depending on whether the allele came from a homozygous or heterozygous mother.

**Differential Effects of Resistance on Male and Female Fitness.** Laboratory studies (Hatchett and Gallun 1970, Gallun 1978) indicated that when heterozygous flies survive they usually are smaller than normal flies. This size reduction is similar for male and female flies, but it does not mean that male and female fitness are therefore equally impaired. If there is strong sexual selection on males

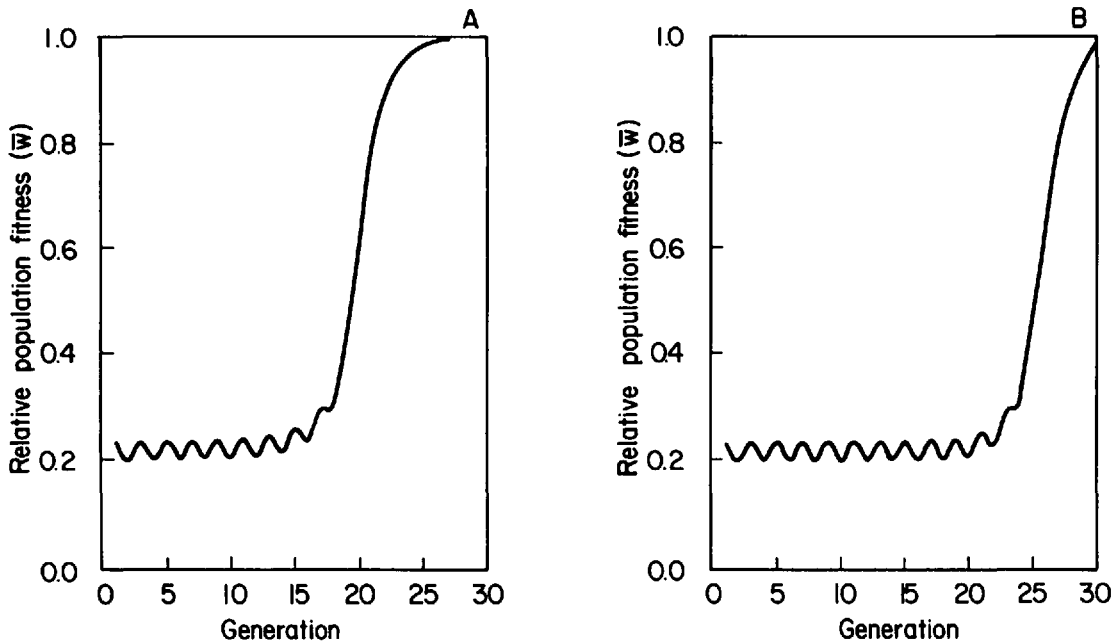


Fig. 3. Effects of varying male and female heterozygote fitness on the durability of a pyramided cultivar that is interplanted with 20% susceptible plants each fall. Initial frequencies of alleles  $a$  and  $b$  are both 0.10. (A)  $w_{aabb}$  females and  $w_{Aabb}$  females are both equal to 0.52 on the pyramided cultivar; while  $w_{aabb}$  males and  $w_{Aabb}$  males are both equal to 0.14 on the pyramided cultivar. (B) Fitness values in A for males and females are reversed.

(Arnold and Wade 1984a,b), even a small reduction in size could cause a fly to be genetically dead ( $w = 0$ ). Fitness of the small females could be related to reduction in fecundity and possibly to a decrease in the genetic fitness of her male partner, if there was assortative mating by size. Dependent on the differential strength of these selection factors, it is possible for heterozygous males or females to be more fit.

Since there is paternal gene loss in male flies, it is not possible to use mean reduction in fitness of heterozygotes in the model. Simulations indicate that increasing heterozygote female fitness reduces durability more than an equal increase in heterozygote male fitness (Fig. 3 A and B) when population fitness of 0.80 is the criteria used to measure durability. It must be understood that a further complication arises here because increasing female heterozygote fitness also increases the population growth rate, while increased fitness of male heterozygotes should have little or no effect on population growth unless it causes a significant percentage of females to remain unmated.

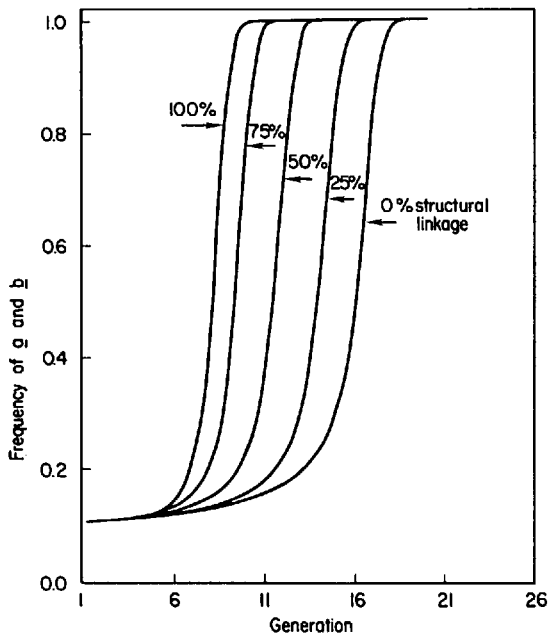
**Gene Linkage.** The previous conclusions are based on the assumption that there is no structural gene linkage among loci, but since this model assumes that males generally do not use their fathers' genetic complement in producing sperm, the mothers' genetic component in the male is assumed to be passed on without effects of recombination. This factor in the model will have an effect on gene frequency change similar to weak structural gene linkage. For example, if there were

no paternal gene loss and the mother was  $AABB$ , while the father was  $aabb$ , 25% of the sperm in the male offspring would be  $ab$ . Given paternal gene loss, 0% of the sperm would be  $ab$ . Paternal gene loss would lessen the rate of formation of genotype  $aabb$  when  $a$  and  $b$  were rare, but would tend to preserve them once formed. A comparison of results from the general diploid model (Gould 1986; fig. 7) with those of the Hessian fly model (Fig. 4) indicates that paternal gene loss causes slightly more rapid adaptation of the fly population in the pyramided deployment system when structural gene linkage is absent (21 generations, general diploid model; 17 generations, Hessian fly model).

When the rate of recombination in the model is decreased from random to no recombination, the durability of the pyramided system is substantially decreased. Fig. 4 illustrates the effects of varying linkage when a pure pyramided cultivar is used. When there is total linkage of the two fly loci, but no initial linkage disequilibrium between alleles  $a$  and  $b$ , the pyramided cultivar will last 3-fold as long as each single cultivar with one resistance factor.

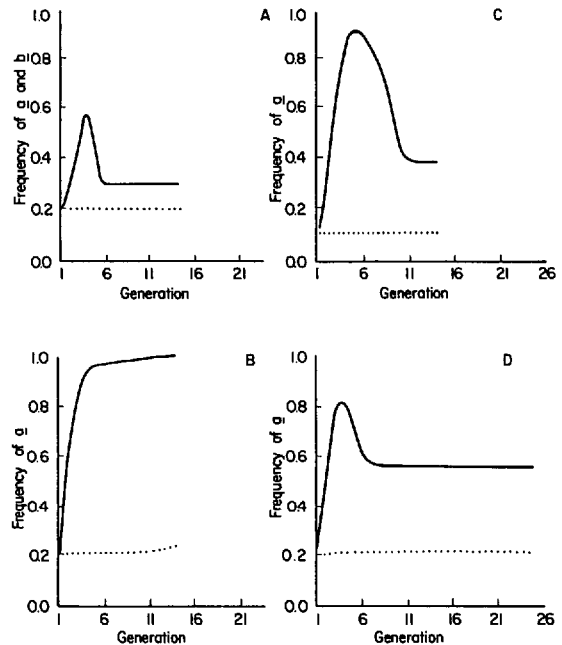
Initial linkage disequilibrium of the  $a$  and  $b$  alleles would affect the durability of the pyramided cultivar and that of the second cultivar in the sequential release. If  $a$  and  $b$  were in coupling disequilibrium, durability would decrease; if they were in repulsion disequilibrium, durability would increase.

**Two-field Model with Migration.** Up to this



**Fig. 4.** Effects of structural gene linkage on durability of a pure planting of the pyramided cultivar. Since the Hessian fly exhibits paternal gene loss, there is always some effective gene linkage. When structural gene linkage is also present, durability is decreased. Initial frequency of alleles *a* and *b* is 0.01; dominance and epistasis are strong ( $D = 1.0$ ,  $E = -1.0$ );  $w_{AABB} = 0.04$ . This figure should be compared to fig. 7 of Gould (1986), which gives effects of linkage in a diploid organism. When there is complete linkage, results are identical, but when there is no linkage, the diploid organism adapts more slowly.

point, the deployment strategies considered involved pure cultivars or mixtures where wheat plants of differing resistance were randomly distributed in the field. In some cases, such plantings may not be preferred, based on harvesting considerations. If mixtures are therefore planted as matrixes of pure cultivar plots that are larger than ca. 100 m<sup>2</sup>, random mating of the flies emerging from the different wheats is not assured (Cartwright 1922). Since the most reasonable spatial unit for pure cultivar plots is a field, mating of flies emerging from the different cultivars will probably be rare. The extent of within-generation interbreeding of the subpopulations in adjacent fields will depend upon movement behavior of male flies over their entire reproductive lives and movement of females during their first few hours of adult lives (before their first and only mating). If development of flies takes longer on one cultivar than on the other, random mating would be further disrupted, as it would be if there was any assortative mating based on the fly's host type. (Resistant cultivars presently used do not change the adult emergence time of homozygous adapted flies [R. L. Gallun, personal communication].) Females



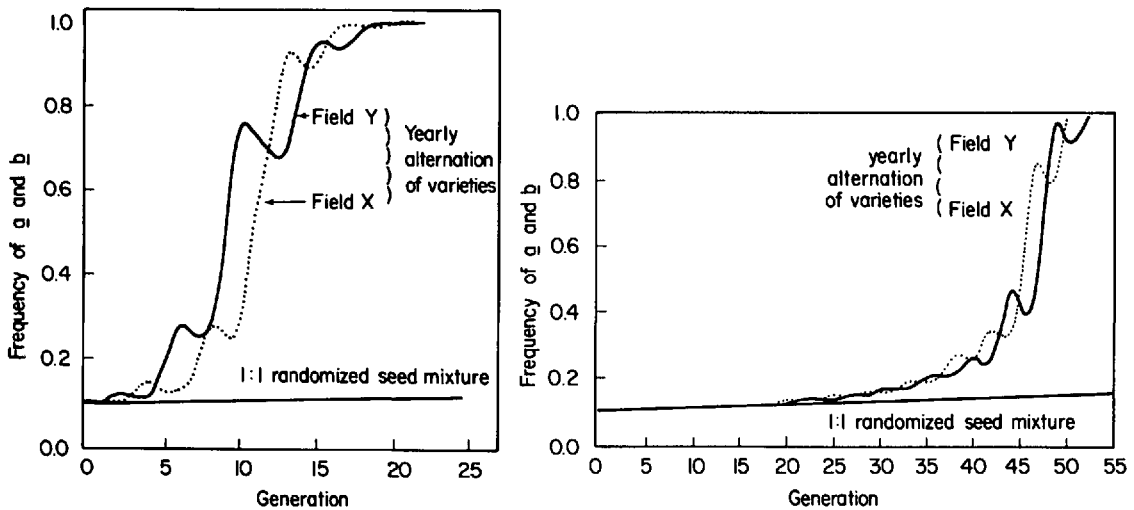
**Fig. 5.** Two-field model with variable migration. Solid lines indicate allelic frequencies of *a* or *a* and *b* in the field with resistant plants. Dotted lines indicate allelic frequencies in the fields with susceptible plants,  $D = 1.0$ ,  $E = -1.0$ . (A) Pyramided cultivar with 1% migration of residents from each field to the opposite field. Initial frequency of *a* and *b* is 0.2. (B) Same as A, except resistant cultivar has only one resistance factor. (C) Same as B, except initial frequency of *a* is 0.1. (D) Same as B, except migration is 10% instead of 1%.

generally move farther than males (McColloch 1923), and the most important contribution to gene flow between fields may come from female movement after mating. McColloch (1923) indicated that fall-generation adult females moved more than spring-generation females, and infestation of newly planted fields indicates that between-field movement may sometimes be significant (McColloch 1917, Foster and Taylor 1974).

A detailed model of mating and gene flow would be useful, but would require quantitative data on aspects of Hessian fly ecology that have not been studied to date. By making a number of simplifying assumptions, an algorithm was developed that allows migration of mated females between two fields (*X* and *Y*) of equal size. Fine-tuning of the model based on biological data will be essential for more realistic predictions. The proportion of mated females in field *X* that developed in field *Y* is set as follows:

$$A_x = \frac{D_y(M_y)}{D_y(M_y) + (D_x(1 - M_x))}$$

where  $A_x$  = frequency of mated females in field *X* that developed in field *Y*;  $M_y$  = probability that a female that developed in field *Y* will move to



**Fig. 6.** Two-field model with alternate planting of a pyramided two-factor resistant cultivar and a susceptible cultivar in the fields compared to a 1:1 random mixture of resistant-susceptible plants in both fields. (Left) Initial frequency of *a* and *b* is 0.10;  $w_{aaBb}$  and  $w_{Aabb}$  on resistant plants are 0.28; bottom line depicts the slow change in allelic frequencies when a 1:1 random seed mixture is used. With 1:1 mixture, 92 generations are required before  $w$  reaches 0.80. (Right) Same as A, except that  $w_{aaBb}$  and  $w_{Aabb}$  are equal to  $w_{AABB} = 0.04$ . With a 1:1 mixture, 435 generations are required before  $w$  reaches 0.80.

field X;  $1 - M_x$  = probability that a female that developed in field X will stay in field X;  $D_Y$  = density of females in field Y before migration;  $D_x(1 - M_x)$  = density of nonmigrant females in field X after migration. By setting  $M_x$  and  $M_y$  as constants, the probability of migration is assumed to be density independent. This assumption is parsimonious, but further empirical studies are warranted. It is likely that not all flies in one field have an equal probability of migration to the second field. Flies at field borders may make this move more frequently. Additionally, such migrants may be likely to remain at the border of the fields they entered. Such a gradient in movement would affect resistance durability, but the present simplified model does not take this into account.

In the two-field model, initial population density in each field is equal. Population growth and decline is based on a simple exponential model with discrete generations in which  $R_0$  (replacement rate) is directly related to the average survival of larvae in a field. (Since no estimates of  $R_0$  or carrying capacity are available from the literature, arbitrary values were chosen for illustrative purposes.) Maximum  $R_0 = 2$  when relative population fitness is 1.0 (i.e., no decrease in fitness due to resistance). Growth of the population is truncated if the density in a field reaches 20-fold the original density. Population decline is truncated if the density in a field reaches 0.005 of the original density. The growth model is overly simplistic and must be examined cautiously. Again, we lack the data for a more detailed model.

**Effects of Spatial Scale of Interplanting on Durability.** Let us assume that half of the wheat in

an area is planted to a single-factor or pyramided resistant cultivar, and the other half to a totally susceptible cultivar. At least two types of plantings are possible. One involves half of the fields being planted with resistant wheat and half with susceptible wheat (Fig. 5). The second involves all fields being planted with a randomized seed mixture, half of which is resistant, half susceptible. When the two-field model, incorporating migration, is used to compare the durability of these two deployment strategies, the deployment of a seed mixture is always more durable. The 1:1 seed mixture of the pyramided cultivar and a susceptible wheat type is especially advantageous, leading to almost indefinite resistance in some cases (see Fig. 6 Left and Right). The durability of the field level "mixture" (Fig. 5) is strongly linked to the migration rate (1–10%) and the interaction of migration rate with the decreasing fly population size in the field with resistant wheat. (The longer flies with unadapted genotypes persist in the field planted to resistant wheat, the lower the fly population size.) Since fly population size in the susceptible field becomes relatively much higher, flies emigrating from the susceptible field swamp out the uncommon adapted genotypes in the resistant field. This can even lead to a decrease of percent survival in the resistant field (Fig. 5).

It should be noted that in some areas Hessian flies attack susceptible hosts other than wheat (McColloch 1923, Jones 1939). In such areas the evolution of adaptation to pure widespread plantings of resistant wheat may be envisioned to proceed in a manner similar to that of field level mixtures of resistant and susceptible wheat, except that

field X would have resistant wheat and field Y would have a susceptible nonwheat host plant.

**Alternating Resistant and Susceptible Plantings.** In the discussion above, resistant wheat was always planted in field X and susceptible wheat planted in field Y. This leads to low fly abundance in field X and no population size-reducing factors in field Y (aside from effects of unbalanced migration). Given this situation, a farmer might decide to limit Hessian fly damage on his farm by rotating the use of resistant cultivars among fields. Such rotation would decrease the durability of resistance (Fig. 6), because flies with some resistant alleles would be allowed to increase every other generation. Additionally, population size in each field would be approximately equal, so migration would be less important. Of course durability in this situation would be higher than it would be where widespread pure plantings of resistant wheat were used (Fig. 2), but would be far lower than the >90 to >400 generations of durability expected in the 1:1 random seed mixture (Fig. 6 Left and Right).

The fact that farmers have different cultivar preferences could lead to a resistance deployment arrangement without temporal field alternation if farmers of adjacent farms happened to plant cultivars that differed in fly resistance and there was sufficient migration between farms. An integrated pest management (IPM) system in which resistant cultivars were planted only in fields with a high probability of fly damage (e.g., irrigated or no-till [Pike and Antonelli 1981]) could help increase resistance durability.

### Discussion

Computer simulation models have recently been used to explore options for pesticide-use strategies that would inhibit development of insecticide resistance (e.g., Comins 1977, Taylor and Georghiou 1979, Tabashnik and Croft 1982, Knipling and Klassen 1984, Mani 1985). Results of these models have suggested some obvious tactics and others that were not so obvious. The most limiting constraints on utilizing tactics suggested by these models are economic costs and problems involved in technical implementation of the often complex tactics suggested. Another equally important problem pointed out by Taylor (1983) is that most of the present models are too general and do not realistically reflect the biological and genetic attributes of specific pests with precision or accuracy (Levins 1972).

If we are to use simulation models effectively in developing host-plant resistance deployment strategies, it is important for us to realize that similar problems will appear. Indeed, some of the economic and implementation constraints on host-plant resistance deployment strategies may be less severe than is the case with insecticide-use strategies. In our present crop-improvement system, the

researcher has considerable control over the types of resistance that are investigated. Once resistance is moved into commercial cultivars, its cost to the farmer is small and any significant degree of pest suppression is acceptable (assuming no pleiotropic yield reduction).

Some problems in implementing resistant germ plasm deployment strategies are obvious. For example, it is more difficult to breed pyramided cultivars and it is more difficult to register a seed mixture than it is to register a pure cultivar (Mundt and Browning 1985). If resistance of a crop to a number of pests is necessary, the optimal deployment strategies become further complicated. Perhaps the most significant constraint on host-plant resistance deployment strategies that does not constrain pesticide use is the fact that the resistant cultivar usually has to be purchased and planted well before the farmer can judge that season's pest population size. There is therefore no option for density-dependent pest management. Selection pressure on the pest becomes a constant, not a variable that can be adjusted, based on actual need.

Results of the simulations explored in this paper and in Gould (1986) point out how sensitive durability may be to the specific genetic and ecological properties of the system. Thus general models can only give a rough idea of the pros and cons of a specific deployment strategy. Development of specific models will require a considerable amount of basic empirical research on the pest/crop interaction. Even with the Hessian fly, a pest for which we have more biological information than average, much remains unknown. The present model points out how important migration and sexual selection could be to the durability of certain strategies, but we have no quantitative estimates of these parameters. We also lack an understanding of Hessian fly population dynamics, which is essential in defining durability.

The model points out how changes in relative fitness of Hessian fly genotypes can affect durability. Compared with genetic data on other pests, the data on Hessian fly are extremely good, but all of our information to date on dominance and epistasis comes from experiments with laboratory strains of flies tested in greenhouse and laboratory environments. Field tests are needed to confirm and extend this information. Although relative fitness estimates are available for fly genotypes reared on resistant seedlings, we do not know whether or not the same relationship holds on maturing wheat plants. Although we have knowledge about the alleles that have adapted flies to past host-plant resistance programs, we cannot say with certainty that a fly population faced with a pyramided cultivar would evolve by the same genetic mechanisms that arose when it was faced with single resistance factors. To date, Hessian flies have never been shown to discriminate between wheat cultivars based on antibiotic factors (some resistant

wheat is preferred over susceptible [Gallun et al. 1961]), but such discrimination could evolve (Gould 1984) and could influence durability.

The present model is deterministic and is applicable to fly populations of 1,000 or more individuals. We must at least consider the possibility that the effective breeding size of Hessian fly populations may become very small when a successful host-plant resistance program is in force. Indeed, a preliminary electrophoretic analysis of North Carolina flies (A. Massey and F. Gould, unpublished data) supports the hypothesis of small breeding populations. If this is confirmed, stochastic factors will change the relative effects of various parameters in the model (e.g., dominance and epistasis). In general, such stochastic effects would have more pronounced effects on lowering durability of pure plantings of resistant cultivars than mixtures that include some totally susceptible plants. (Although not addressed in this model, the highly skewed sex ratio of each female's offspring would tend to increase the positive effects of dominance and epistasis by enforcing outcrossing.) J. Schneider (personal communication) has found that small population size would increase the variance in initial fly gene frequency. This would decrease durability. The extent to which it decreases durability would depend on movement patterns among fly populations.

While we can never expect to build totally accurate models for quantitatively predicting durability in a specific crop/pest system, qualitative predictions can be useful. The present model certainly indicates that in the future it should be worth pyramiding two or more wheat genes for Hessian fly resistance into one cultivar and then planting seed of this cultivar mixed with seed of a totally susceptible cultivar. Chances of increased durability would be highest if care was taken to pick resistance genes in the wheat for which Hessian fly virulence genes did not appear to be structurally linked (as with the *M* and *K* loci) and were initially at low frequency. Although most of the work presented in this paper involves mixtures containing at least 80% resistant plants, it should be noted that use of 50% resistant plants can lead to much higher durability (>90 generations in Fig. 6 Left, and >400 generations in Fig. 6 Right). Given that Hessian fly is only a sporadic pest in most areas of the United States (Riley 1881, Packard 1883), the use of 50% resistant plants over an extended period of time may significantly decrease the frequency of pest outbreaks and would offer moderate protection when outbreaks did occur.

Development and deployment of resistant germ plasm in the manner suggested above would not be simple, but would be likely to repay the effort invested. Three problems can be readily anticipated. One involves problems of backcrossing double gene resistance into high yielding cultivars.

Although more laborious than backcrossing single-gene resistance, this may be accomplished by using existing stocks of various Hessian fly biotypes. Once a pyramided resistant cultivar is produced, distributing it as a mixture with a susceptible isolate or cultivar would require unusual but not unrealistic registration procedures. Indeed, rust-resistant mixtures of wheat have been registered in the Northwest United States (Allen et al. 1983), so cooperative programs may be feasible. A third problem would arise if farmers were producing their own seed for many years and used fields that were heavily infested with Hessian fly for seed production. This practice could lower the proportion of susceptible seed that they plant each year. In areas where fly populations were of moderate density, this would not be too much of a problem, and the fact that wheat plants rarely outcross would maintain the integrity of the resistant and susceptible components of the cultivar.

We have seen the rapid loss of two Hessian fly resistance genes in parts of the Midwest where up to 90% of the wheat acreage was planted to pure single-gene resistant cultivars (Sosa 1981). These biotypes are still in low frequency in many areas of the United States where predominantly fly-susceptible wheat is grown (e.g., Table 3 and Pike and Antonelli [1981]). Some of these areas have more fly generations per year than in the Midwest; thus, durability of sequential releases of single factor resistant wheat would be predicted to be shorter than in the Midwest. Unless we are confident that we will always be able to find new sources of Hessian fly resistance in coming centuries, we must act responsibly in attempting to preserve the utility of our Hessian fly resistance germ plasm bank. We must at least consider alternatives to the widespread release of pure cultivars with single factor resistance that initially cause close to 100% fly mortality. Given the sporadic nature of Hessian fly outbreaks, such absolute control may rarely be necessary. Pyramided or sequential releases of antibiotic resistance factors mixed with 20-50% susceptible plants will probably offer adequate protection, especially when combined with cultural and biological control practices.

#### Acknowledgment

The efforts of B. Weir, C. Laurie-Ahlberg, and K. Leonard in reviewing the genetic model are much appreciated. H. Alexander, S. Cox, R. Gallun, G. Kennedy, D. Landis, M. Rausher, R. Roush, P. Saks, J. Schneider, K. Suiter, M. Waldvogel, and J. Wolfson made helpful suggestions. This article is Paper No. 9748 of the Journal Series of N.C. Agric. Res. Serv., Raleigh.

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*Received for publication 28 February 1985; accepted 15 October 1985.*

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