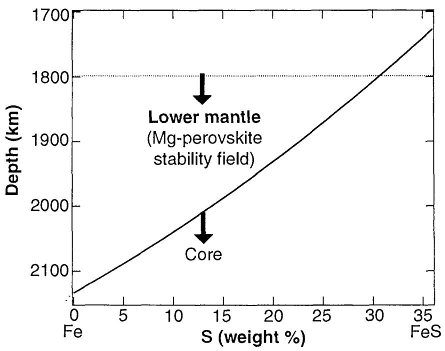

Fig. 4. Calculated relation between the depth of the martian core-mantle boundary and the sulfur content, based on our experimentally determined density data for FeS IV. Dashed line indicates the depth of Mg–silicate perovskite stability.

pure FeS core (*16*), deeper than previous calculations (*11*, *14*). The reason for this difference is that FeS IV is much more compressible than earlier assumed. For a model mantle composition of Mars (*12*) with 13.9 weight % sulfur in the core, the martian core-mantle boundary is located at a depth of 2000 km (about 24 GPa), deeper than the silicate perovskite stability field. A core with at least 30 weight % sulfur is required to eliminate a silicate perovskite lower mantle in Mars (Fig. 4). In comparison with the internal structure of the Earth, Mars may have only a thin layer of lower mantle (~200 km) but similar density discontinuities.

Melting relations in the Fe-FeS system have been used to constrain the temperatures of the interior of planets in many planetary models (*17*). The discovery of the transformation of the high-pressure phase FeS III to the high-pressure-temperature hexagonal phase FeS IV has a significant impact on the understanding of melting relations in the FeS and Fe-FeS systems and of solution behavior in systems such as Fe-S-O at high pressure and temperature. Changes in the physical properties of FeS at high pressure and temperature, such as density and chemical bonding, will lead to changes in melting temperatures and melting behavior in binary (for example, Fe-S) or ternary (for example, Fe-S-O) systems. These changes also have profound implications for the incorporation of lighter elements into iron-dominant cores of terrestrial planets (*18*).

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9. C. T. Prewitt and Y. Fei, paper presented at the 16th International Mineralogy Association Meeting, Pisa, Italy, 4 September 1994. Even with high-quality synchrotron x-ray data, it has been difficult to determine the symmetry of FeS III because diffraction patterns from different experiments are not consistent with each other, probably because of preferred orientation effects. However, it has been possible to index peaks that occur consistently in x-ray patterns at several different pressures on a monoclinic cell with $a = 5.121(2)$ Å, $b = 5.577(2)$ Å, $c = 3.328(2)$ Å, and $\beta = 95.95(4)°$ at 15 GPa (the numbers in parentheses are the errors in the last digits). The structure seems to still be related to that of NiAs but with significant distortions of the simple NiAs structure.
10. Experimental configuration for high-pressure and high-temperature experiments in a diamond-anvil cell, combined with synchrotron x-ray diffraction techniques, was described in (*8*). The FeS samples were synthesized from a mixture of iron and sulfur, sealed in evacuated silica glass tube, and heated for 4 days at 700°C. The starting materials were stoichiometric FeS, confirmed by electron microprobe analyses and x-ray diffraction.
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16. The depth of the martian core-mantle boundary was calculated by satisfying simultaneously the mass and a moment of inertia factor of the planet [G. Schubert and T. Spohn, *ibid.* **95**, 14095 (1990)] based on density profiles of the mantle (*14*) and the core. The geotherm for Mars used in the calculations is from D. H. Johnston and M. N. Toksöz [*Icarus* **32**, 73 (1977)]. Densities for the pure Fe core were calculated with compression parameters (*14*) and the thermal expansivity data [R. Boehler, N. Bargen, A. Chopelas, *J. Geophys. Res.* **95**, 21731 (1990)] of face-centered-cubic iron. Densities for the pure FeS core were from our experimental determination (Fig. 3). The density profiles used in our calculations are best fit to a moment of inertia factor of 0.367.
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Managing the Evolution of Insect Resistance to Transgenic Plants

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The evolution of resistance in pests such as the European corn borer will imperil transgenic maize varieties that express insecticidal crystal proteins of *Bacillus thuringiensis*. Patchworks of treated and untreated fields can delay the evolution of pesticide resistance, but the untreated refuge fields are likely to sustain heavy damage. A strategy that exploits corn borer preferences and movements can eliminate this problem. Computer simulation indicates that this approach can delay the evolution of resistance and reduce insect damage in the untreated fields of a patchwork planting regime.

Maize, cotton, potatoes, and tobacco have now been genetically engineered to express crystal protein (*cry*) genes from *Bacillus thuringiensis*. Maize varieties nearing commercialization are toxic to many Lepidoptera, including *Ostrinia nubilalis* (Hübner) [Pyralidae], the European corn borer, one of the most injurious pests of maize in North America. A potential problem with genetically engineered crop varieties is the evolution of resistance in target pests (*1*).

Insect resistance to transgenic plants has much in common with resistance to pesticides. Potential management strategies against pesticide resistance include the application of multiple toxins in mixtures or sequences (*2*, *3*), the use of high toxin concentrations to make expression of the resistance alleles more recessive (*3–5*), and the distribution of the toxin in spatial patches interspersed with nontoxic refuges. Because the efficacy of toxin mixtures remains controversial, discussion of resistance management in transgenic crops has focused on the relative merits of the "high-dose" strategy and spatial refuges (*2–6*).

Comins and others (*3–6*) have shown that random gene exchange between select-

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ed and unselected insect populations in a patchwork can delay the evolution of resistance. For some systems, the unselected refuge may be a nonagricultural area or an alternate crop, but in the Midwest of the United States, corn borer refuges of unprotected maize will suffer yield loss. Here we outline a patchwork management strategy that incorporates insect movement and preference to protect both toxic fields and nontoxic refuges, while delaying the evolution of resistance. Although the structure and parameterization of the model are specified for *O. nubilalis* and maize, our rationale is applicable to the management of toxin resistance in other vagile pests.

European corn borers are bivoltine throughout much of the central North American corn belt. In this region, the insects overwinter as mature larvae, pupate in the spring, and eclose as June adults to mate and lay eggs. The June moths are strongly attracted to the most mature maize available for oviposition, and 10-fold differences in egg numbers can be observed between adjacent fields with differing phenologies (*7*). The offspring of June moths metamorphose into July and August adults whose progeny become mature larvae by the end of the growing season. Wintering insects experience a heavy density-independent mortality that is undercompensated by spring reproduction.

Our model simulates the evolution and population dynamics of *O. nubilalis* in a patchwork habitat of early and late-planted fields, with *cry* toxin restricted to the most phenologically advanced and attractive units. We assume that there is a diallelic locus with a resistance allele segregating at low initial frequency among the insects. We also assume that adults do not detect and avoid crop units where their developing larvae will encounter the toxin. Simulations are initialized by imposing density-independent overwinter mortality (*8*). Then, as illustrated in Fig. 1, each generation involves four steps.

In the first step, adult migration causes the introgression of susceptible alleles into the toxic maize, retarding the selective increase of resistant allele frequency. Migration also causes resistant alleles to enter the nontoxic fields, and unless resistance has a cost in the absence of *cry* toxin, it will ultimately increase to fixation under most realistic conditions. Restriction of *cry* protection to the earliest, most preferred fields causes spring migration to be strongly biased, with net movement from nontoxic fields into toxic ones (*9*). Thus, the vagility and preference of *O. nubilalis* cause phenologically advanced maize to function as a trap crop, reducing insect density on less mature varieties or later plantings in adjacent fields. Because preference differences between early and late-planted maize are more complicated during the flight period of August adults, we use a random, unbiased migration process in the second generation.

The generation's second step, reproduction, is simulated as constant per capita oviposition, and population sizes jump to reflect this recruitment (*10*).

In the third step, toxin-induced mortality affects young larvae as soon as they begin feeding on toxic plants. Changes in pest population size and the frequency of resistance alleles are determined by the

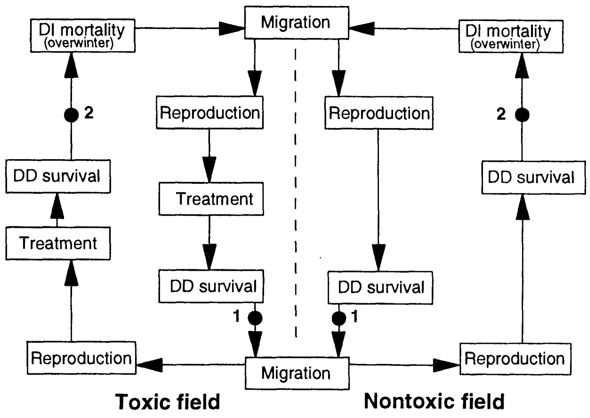

Fig. 1. Schematic of a bivoltine simulation, with toxic (left) and nontoxic (right) fields linked twice yearly by adult migration. DI, density-independent; DD, density-dependent. The first-generation densities graphed in Fig. 3 are measured at dot 1 and the second-generation densities are measured at dot 2.

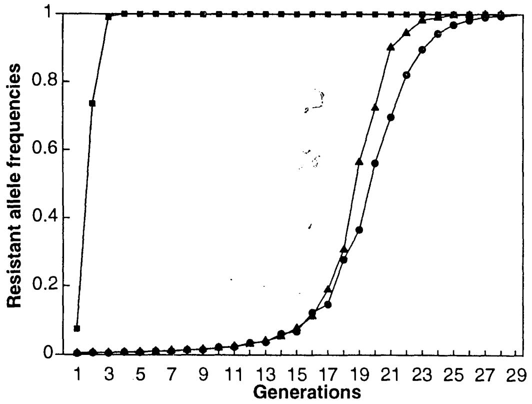

Fig. 2. Allelic frequency changes with a homogeneous toxic crop (squares), and in a patchwork of toxic and nontoxic maize varieties with random (circles) and preference-biased (triangles) migration. Parameter values (*15*) imposed moderate density-dependent mortality and overwinter survival typical in southern Minnesota. Trajectories for the two patchwork cases plot the population-wide allelic frequency, calculated as a weighted average of frequencies in the toxic and nontoxic patches.

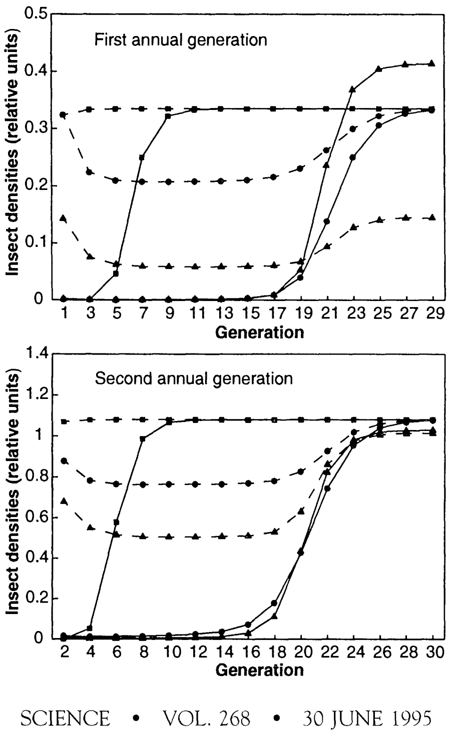

Fig. 3. Insect densities at the end of the growing season in (i) a nontoxic crop (squares, dotted line), (ii) a uniformly toxic crop (squares, solid line), and in the toxic (solid line) and nontoxic (dotted line) fields of a patchwork with (iii) random, unbiased migration of June adults (circles), and (iv) preference-biased migration (triangles). Parameter values (*15*) are identical to those used to generate Fig. 2. Ordinal units are multiples of equilibrial density. The appearance of sustained densities above equilibrium in the lower panel is an artifact of graphing only the second annual generation. In generations 9 and 10, the biased patchwork strategy lowers first- and second-generation insect densities in the nontoxic fields by 83 and 53%, respectively, relative to a uniform, nontoxic crop. Corresponding reductions for the random patchwork are 38 and 29%.

relative fitnesses of the resistant and susceptible homozygotes, by gene expression in heterozygotes, and by the toxicity of transgenic maize. Because resistance evolves more rapidly if the resistance allele is dominant (*11*), the commercial objective is to achieve extremely high levels of *cry* toxin expression (*12*) which will cause intense selection and may cause a high rate of heterozygote mortality, reducing dominance. No plant-induced mortality or selection occurs on nontoxic maize.

In the generation's final step, density-dependent larval mortality follows the mortality resulting from exposure to *cry* toxin. Because density-dependent mortality rates in *O. nubilalis* are variable (*13*), we use a two-parameter algorithm by Hassell that allows a wide range of density-dependent effects (*14*). The number of surviving larvae becomes an initial population size for August adults, and we repeat the same four simulation processes. After density-dependent larval mortality of the second summer generation, we impose density-independent overwinter mortality and begin the next seasonal iteration.

Figures 2 and 3 compare the evolutionary dynamics of resistant allele frequency and the ecological dynamics of insect density that result under our assumptions of (i) uniformly nontoxic fields, (ii) uniformly toxic fields, and a patchwork of nontoxic and toxic fields with (iii) random and (iv) preference-biased migration during the spring generation. In the patchwork simulations we assume a 1:1 areal ratio of nontoxic to toxic fields.

Our simulations show a large improvement in the duration of toxin susceptibility for a patchwork compared with uniform plantings of transgenic maize (Fig. 2). In addition, preference-biased spring migration reduces insect density in the nontoxic fields relative to other cases (Fig. 3). This qualitative pattern pertains over a wide range of parameter values. Thus, by planting only part of the land with transgenic maize and restricting these varieties to the earliest, most attractive plantings, it is possible to delay the evolution of resistance and reduce insect density in nontoxic fields.

Random, unbiased patchworks delay resistance with damaging insect densities in the nontoxic refuges, and any manipulation that lowers refuge populations will increase the average selection pressure on the pest, accelerating its evolution. Our preference-biased migration strategy mitigates this tradeoff, because larval mortality acts disproportionately against resistant insects concentrated in the trap crop, lowering the population-wide frequency of resistant alleles, delaying the evolution of resistance, and reducing the density differential between toxic and nontoxic fields.

Because our strategy requires toxic and refuge fields within flight range of adult corn borers on individual farms, its implementation will require significant educational effort. Economic incentives will favor adoption of the strategy when farmers understand that they gain protection in two fields for the price of one. Seed companies could facilitate implementation by restricting *cry* toxin to long-season varieties that are planted earliest and will be most attractive to corn borers. The strategy will also create a market for late-planted, nontransgenic refuge varieties. Ultimately, proportions and arrangements of treated and refuge fields could be adjusted to the maize phenologies and corn borer dispersal patterns in different regions. This optimization will require simulation with empirical measures of local selection and gene flow.

The qualitative results of our model suggest that preference-biased patchwork strategies will have important advantages over uniform use of toxic maize varieties or unbiased patchworks by prolonging toxin susceptibility in the pests and lowering the costs of corn borer management.

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8. Initial adult densities per unit area are set in the toxic (X) and nontoxic (Y/G) regions (where the nontoxic region is G times as large as the toxic region; total population sizes in the toxic and nontoxic areas are X and Y). If insects have achieved equilibrial density preceding first exposure to toxic plants and the density-independent overwinter survival rate is μ, then surviving spring populations at the outset of each simulation are μX and μY, respectively.
9. We define r as a proportion of the population that moves from its natal site and s as a preference factor, where toxic maize is s times more attractive than nontoxic maize. After migration the new densities are

$$X' = (1-r)X + \frac{srX}{s+G} + \frac{srY}{s+G} \qquad (1)$$

$$Y' = (1-r)Y + \frac{GrY}{s+G} + \frac{GrX}{s+G} \qquad (2)$$

Migration will also affect the frequencies of resistance alleles in both the toxic (p) and nontoxic (w) regions. The new frequencies after migration will be

$$p' = \frac{(1-r)pX + \frac{srpX}{s+G} + \frac{srwY}{s+G}}{X'} \qquad (3)$$

$$w' = \frac{(1-r)wY + \frac{GrwY}{s+G} + \frac{GrpX}{s+G}}{Y'} \qquad (4)$$

10. We increase population size from adult to egg stage by a factor F, interpretable as the average fertility of adults. With a balanced sex ratio, F will be half the number of eggs produced per female.

$$X'' = FX' \qquad (5)$$

$$Y'' = FY' \qquad (6)$$

11. If A alleles are resistant and a alleles are susceptible, we define the genotypic survival rates as L for AA (resistant homozygotes), $hL + (1-h)K$ for Aa (heterozygotes), and K for aa (susceptible homozygotes), where h sets the dominance of the resistant allele (when $h = 0$, resistance is fully recessive; when $h = 1$, the resistant allele is dominant). If p' and p'' are frequencies of the resistant allele in the toxic region before and after *cry* toxin exposure (and if $q = 1 - p$), then the recursion equations for surviving insect density and resistant allele frequency in the toxic region are

$$X''' = \{Lp'^2 + [Lh + K(1-h)]2p'q' + Kq'^2\}X'' \qquad (7)$$

$$p'' = \frac{\{Lp'^2 + [Lh + K(1-h)]p'q'\}X''}{X'''} \qquad (8)$$

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$$X'''' = X''(1 + aX''')^{-b} \qquad (9)$$

$$Y''' = Y''\left(1 + \frac{aY''}{G}\right)^{-b} \qquad (10)$$

Note that we assume the density-dependent processes to be unaffected by resistance genotype and maize variety. If density-dependent mortality increases in the toxic unit, then the relative performance of our preference-biased patchwork will improve.

15. Parameter values for the simulations in Figs. 2 and 3 are as follows: $X_0 = 1$, $Y_0 = 1$, $p_0 = w_0 = 0.003$, $F = 100$, $L = 1$, $K = 0.001$, $h = 0.025$, $G = 1$, $a = 4$, $\mu = 0.01$, $b_1 = b_2 = 0.7$, $s_1 = 10$, $s_2 = 1$ (for the preference-biased patchwork) or $s_1 = s_2 = 1$ (for the random, unbiased patchwork), and $r_1 = r_2 = 0.95$ (for the patchwork runs with migration), or $r_1 = r_2 = 0$ (for the uniform run without migration).

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