FIGURE 23.2. The mutation rate evolves as a compromise between the mutation load and the cost of lowering mutation rates. (*A*) In an asexual population, overall fitness (*black curve*) is the product of the effect of mutation on fitness (exp(–*U*); *blue curve*) and the physiological cost of reducing the rate of mutation (*purple curve*). (*B*) A sexual population will evolve a higher mutation rate than is optimal. The diagram shows the effect of a modifier allele that increases mutation rate (*blue circles*). Over time, deleterious alleles caused by this allele accumulate on the same genome (*left column*). However, recombination carries the mutations onto other genomes, which carry the low-mutation-rate allele at the modifier locus (*green circles*). Eventually, an equilibrium is reached in which the high-mutation-rate modifier may be associated with only a modest increase in the number of deleterious mutations (*bottom row*). It is this difference that causes indirect selection against high mutation rates.

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