



**FIGURE 19.34.** The replacement of one allele by another involves a substitution load. Initially, the population has a mean fitness of 1.1. The environment then changes suddenly, and mean fitness falls to 0.8. An allele P, which was previously unfavorable and was held at low frequency ( $p_0 = 0.0001$ ) by selection, now becomes favorable: The fitnesses of genotypes QQ, PQ, and PP are 0.8, 0.9, and 1, respectively. After about 100 generations, this allele becomes common and sweeps to fixation. However, the population suffers a 20% drop in fitness while it waits for adaptation by natural selection. The net loss, indicated by the shaded area, is  $2 \log_e(1/p_0) = 18.4$ .