

Use Populus for this problem (<http://www.cbs.umn.edu/research/resources/populus>).

From the **Models** menu at the top left, choose **Natural Selection** and then **Two-Locus Selection**. Look over all the parameters in the model dialog. Click on the help button and read the help text for the model (admittedly, not that helpful in this case). Set the simulation model parameters as given in the table below. You may have to adjust the number of generations depending on how rapidly equilibrium is approached. 100 generations is a good starting place.

To see the graphical output, pick a radio button for one of the four possible plots and then click the **View** button at the top left of the model parameter window. (Be sure to look at each type of plot and understand its axes and the pattern it illustrates.)

Before beginning, please understand what gamete frequencies are and why there are nine (9) different fitness values.

What is a gamete and what is its expected frequency?

Gametes are haplotypes or the alleles at two (or more) different loci found on the same chromosome and therefore inherited as a unit.

Expected gamete frequencies are the product of each allele plus or minus any departure from this expected value because of mechanisms such as linkage, drift, or natural selection expressed as the gametic disequilibrium coefficient, D .

For example, if $\text{freq}(A) = p_1$ and $\text{freq}(B) = p_2$

$$\text{freq}(gAB) = p_1 p_2 + D$$

Why are there nine relative fitness values?

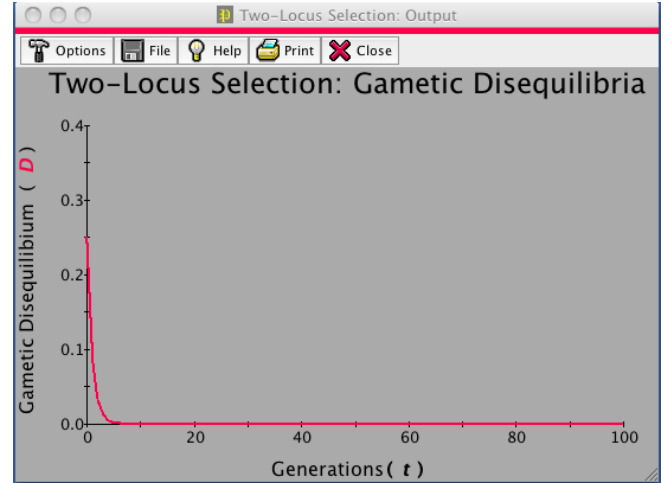
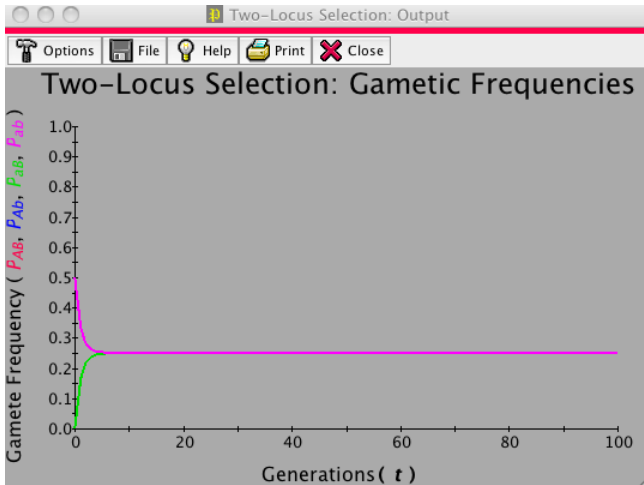
There are nine relative fitness values because there are nine possible two locus genotypes (AABB, AABb, AAbb, etc.) and each of these genotypes potentially has a unique relative fitness value.

Simulation model parameters to try:

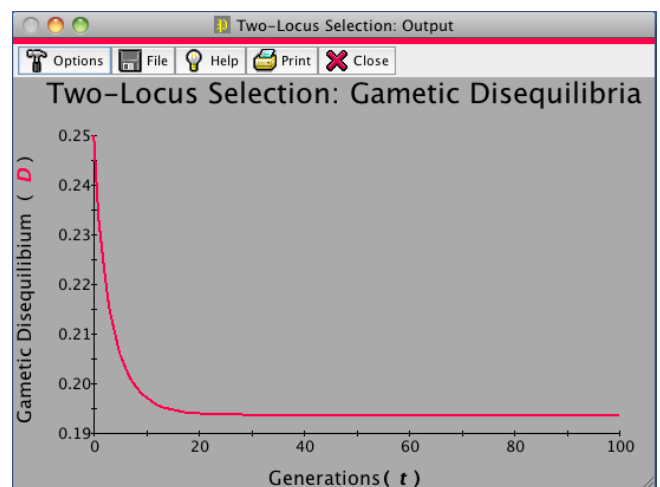
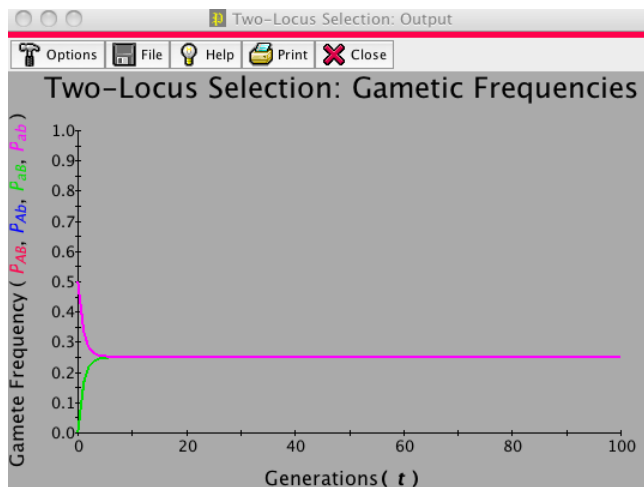
Run	pAB	pAb	paB	pab	r	relative fitness values
1	0.5	0.0	0.0	0.5	0.5	wAaBb = 1; all others = 0.5
2	0.5	0.0	0.0	0.5	0.05	wAaBb = 1; all others = 0.5
3	0.5	0.0	0.0	0.5	0.5	wAAbb = waaBB = 1; all others = 0.5
4	0.5	0.0	0.0	0.5	0.05	wAAbb = waaBB = 1; all others = 0.5

Focus your attention on the **gamete frequencies (P) vs. t** and **D vs. t** plots. Draw each below (remember to label your axes and all lines in the gamete frequency plots!).

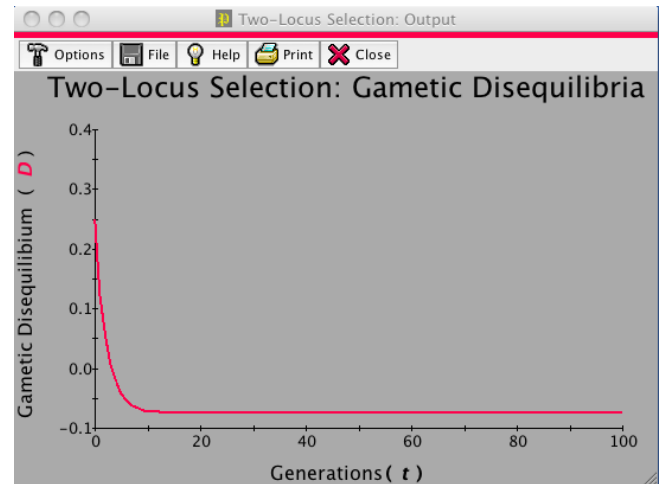
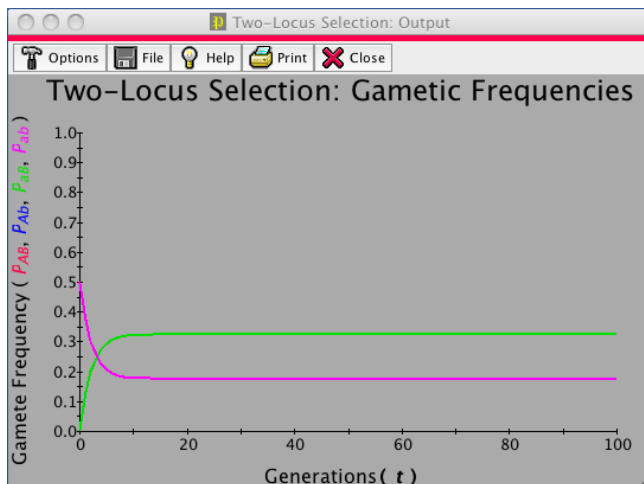
Results of simulation run 1:



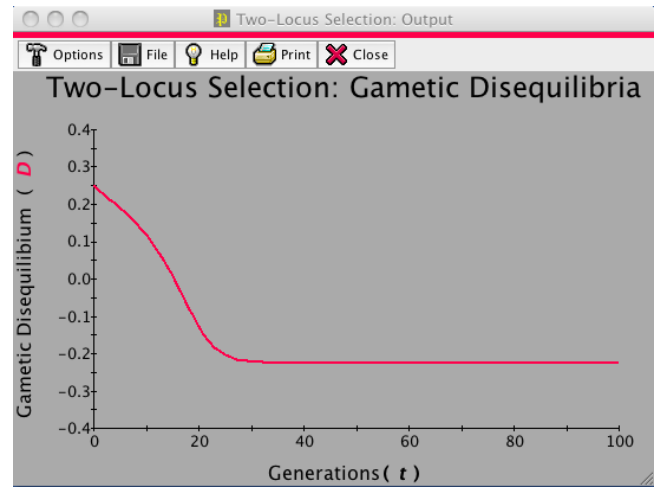
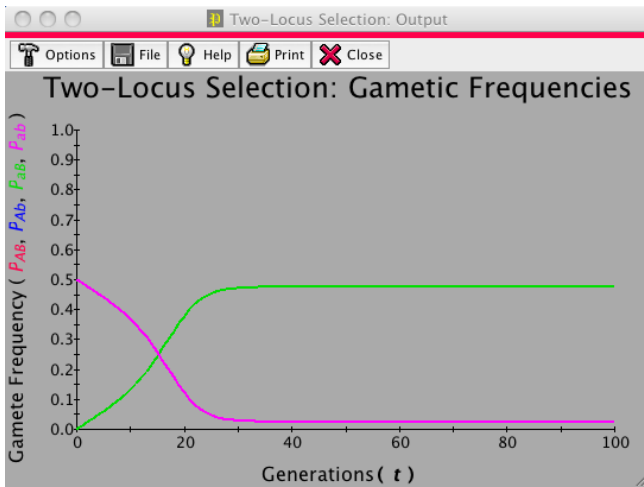
Results of simulation run 2:



Results of simulation run 3:



Results of simulation run 4:



In runs 1 and 2 how many gamete frequency trajectories are visible? [two](#)

How many gamete frequency trajectories are actually there? [four](#)

What do the relative fitness values, such as w_{AAbb} , mean?

Relative fitness values express the relative *viability* of individuals of various genotypes, or their genotype-specific relative rates of survival. For example, if two genotypes have relative fitness values of 1.0 and 0.5, for every two individuals of the first genotype that survive only one individual of the second genotype will survive. Note that genotypes have fitness values but gametes do not (at least in the standard viability model of natural selection).

What is D and what does the D vs. t plot show?

D is the coefficient of gametic disequilibrium (or coefficient of linkage disequilibrium). The plots of D versus t show the amount of gametic disequilibrium over time in a population.

Why do runs 1 vs. 2 and 3 vs. 4 differ for D ?

Simulations 1-2 and 3-4 have identical relative fitness values but contrasting recombination rates. Comparing the D vs. t plots for runs 1 and 2, for example, shows us how D behaves when there is free recombination (run 1) and limited recombination expected for loci that are physically linked (run 2).

When the recombination rate is lower, D reaches equilibrium more slowly. In both sets, the equilibrium value of D is farther from zero when r is smaller.

Why do runs 1 vs. 3 and 2 vs. 4 differ for D ?

Simulations 1-3 and 2-4 have identical recombination rates but different patterns of genotypes with high relative fitness. Comparing the D vs. t plots for runs 1 and 3, for example, shows us how D behaves when double heterozygotes have the highest fitness (run 1) or when double homozygotes for different alleles have the highest relative fitness (run 3).

In runs 1 and 2 where the double heterozygote have high fitness, individuals with that AaBb genotype are able to generate all four types of gametes. D decays to zero for free recombination in this case. But with $r=0.05$ the AaBb makes mostly coupling gametes and D reaches a positive equilibrium value and does not decay to zero.

In runs 3 and 4 where double homozygotes have high relative fitness, D does not decay to zero even with free recombination. This occurs because the genotypes with high fitness make only two of the four possible gametes (recombinant gametes) and genotypes that are the result of other gamete combinations (or make other gamete combinations) do not survive as well. Even with free recombination as in run 3, strong natural selection maintains negative D at equilibrium because recombinant gametes are more frequent.

Runs 1 and 3 show us how natural selection alone impacts D over time in a population since those runs have free recombination between loci.

Is the level of gametic disequilibrium in a population only a function of the rate of recombination?

The amount of gametic disequilibrium is not simply a function of the recombination rate! In these simulations we see how natural selection acting on genotypes can alter rates of change in D as well as equilibrium D . Any equilibrium gametic disequilibrium other than zero is maintained by mechanisms that are working against recombination.