

recomb **0.5** <-- change this value to change the recombination freq.
sa **0.3** <-- change this value to change selection against the a allele
sb **0.3** <-- change this value to change selection against the b allele
z **5** <-- change this value to 1 to get independent effects of selection on a and b
 for values > 1, the ab genotype is less fit than expected
 for values < 1, the same type is more fit than expected

There are two haploid loci, each with two alleles
There are four genotypes: AB, Ab, aB, ab

genotype-->					Freq of	
	A-----B	A-----b	a-----B	a-----b	A	B
N. individuals before selection	25	25	25	25	100	
pij = Freq before selection	0.25	0.25	0.25	0.25	1	0.50
Wij = fitness of genotype	1	0.7	0.7	0.03		
Calculation of Wij	1	(1 - sb)	(1 - sa)	[(1-sa)(1-sb)]^z		

Freq after selection: Wij*pij	0.250	0.175	0.175	0.007	0.61	0.70	0.70
Normalized freq= Wij/Wbar	0.412	0.288	0.288	0.012	1.0	0.70	0.70

Freq, after free recombination	equal to (1-r)*pij + r*pi*pj						
	0.451	0.249	0.249	0.051	1.0	0.70	0.70

Linkage disequilibrium D

$$p(ab)*p(AB) - p(aB)*p(Ab)$$

or

$$p(ab) - p(a)*p(b)$$

0.000

-0.0783

-0.0392

Epistasis E

$$\ln([Wab*WAB]/[WaB*WaB])$$

or

$$\ln(Wab) - \ln(WaWb)$$

-2.8534

-0.0783 -0.0783111

Note, the effect of free recombination was to reduce linkage disequilibrium.
 In, general, $D' = D(1-r)$, where r is the rate of recombination between loci.

D' calculated as $D*(1-r)$ **-0.0392** <-- this value was incorrect in the previous sheet. Thanks to Pauline for catching this error (I had $D*r$ instead of $D*(1-r)$)

Note: freq. after free recombination calculated from normalized freqs.

Things to note:

- The p(ij) frequencies before selection (line 13) assume linkage equilibrium (no covariance between alleles). See cell L13 (pink cell)
- For z = 1, there is no epistasis for fitness, and no linkage disequilibrium is generated. Change z to equal 1. D should be zero.
- For z < 1, there is positive epistasis for fitness (gray cell). Meaning, the ab genotype is more fit than expected based on selection against the a and b alleles.
- For z > 1, there is negative epistasis for fitness. Meaning, the ab genotype is less fit than expected based on selection against the a and b alleles.
- Positive epistasis for fitness gives rise to positive D (green cell)
- Negative epistasis for fitness gives rise to negative D
- Recombination reduces D. D after recombination $D' = D(1 - r)$ (see blue cells)