

recomb **0.25** <-- change this value to change the recombination freq.
sa **0.99** <-- change this value to change selection against the a allele
sb **0.99** <-- change this value to change selection against the b allele
z **0** <-- 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		
p_{ij} = Freq before selection	0.25	0.25	0.25	0.25	1	0.50	0.50
W _{ij} = fitness of genotype	1	0.01	0.01	1.00			
Calculation of W _{ij}	1	(1 - sb)	(1 - sa)	[(1-sa)(1-sb)] ^z			

Freq after selection: W_{ij}*p_{ij}	0.250	0.003	0.003	0.250	0.51	0.50	0.50
Normalized freq = W _{ij} /W _{bar}	0.495	0.005	0.005	0.495	1.0	0.50	0.50

Freq, after free recombination							
equal to (1-r)*p _{ij} + r*pi* p_j	0.434	0.066	0.066	0.434	1.0	0.50	0.50

Linkage disequilibrium D

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

or

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

0.000

0.2450

0.1838

Epistasis E

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

or

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

9.2103

0.2450 0.2450495

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) **0.1838** <-- 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)