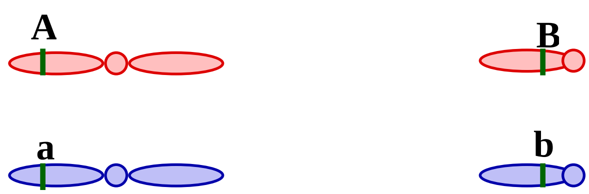
Evolution at Multiple Loci
Chapter 7

I) Linkage Equilibrium/Disequilibrium

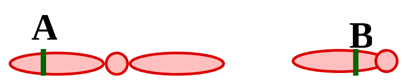
A) Definition – Linkage disequilibrium is the non-random associations of alleles at different loci.

1) Equilibrium:

	Locus 1		Locus 2	
	A	**a**	**B**	**b**
Frequency	**0.23**	**0.77**	**0.65**	**0.35**

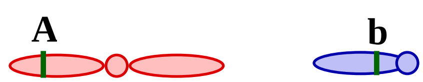


F(AB) = F(A) x F(B) =



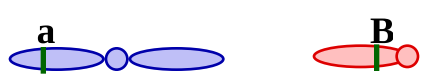
= 0.23 x 0.65 = 0.1495

F(Ab) = F(A) x F(b) =



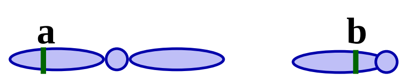
= 0.23 x 0.35 = 0.0805

F(aB) = F(a) x F(B) =



= 0.77 x 0.65 = 0.5005

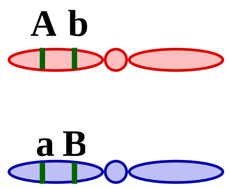
F(ab) = F(a) x F(b) =



= 0.77 x 0.35 = 0.2695

2) Disequilibrium:

	Locus 1		Locus 2	
	A	**a**	**B**	**b**
Frequency	**0.25**	**0.75**	**0.75**	**0.25**



Expect:

F(AB) = 0.25 x 0.75 = 0.1875

F(Ab) = 0.25 x 0.25 = 0.0625

F(aB) = 0.75 x 0.75 = 0.5625

F(ab) = 0.75 x 0.25 = 0.1875

Observe:

F(AB) = 0.00

F(Ab) = 0.25

F(aB) = 0.75

F(ab) = 0.00

3) Coefficient of Disequilibrium (D)

Case 1, Equilibrium:

D = F(AB) x F(ab) – F(Ab) x F(aB)

= 0.1495 x 0.2695 – 0.0805 x 0.5005

= 0.0403 – 0.0403

= 0.0

Case 2, Disequilibrium:

$$D = F(AB) \times F(ab) - F(Ab) \times F(aB)$$
$$= 0.00 \times 0.00 - 0.25 \times 0.75$$
$$= 0.00 - 0.1875$$
$$= -0.1875$$

Note:(book says $-0.25 \leq D \leq 0.25$ which is true if and ONLY if F(Ab) = 0.5 and F(aB) = 0.5

$$D' = \frac{D}{D_{max}}$$

if D is positive:

$$D_{max} = \min[F(A)F(b), F(a)F(B)]$$

if D is negative:

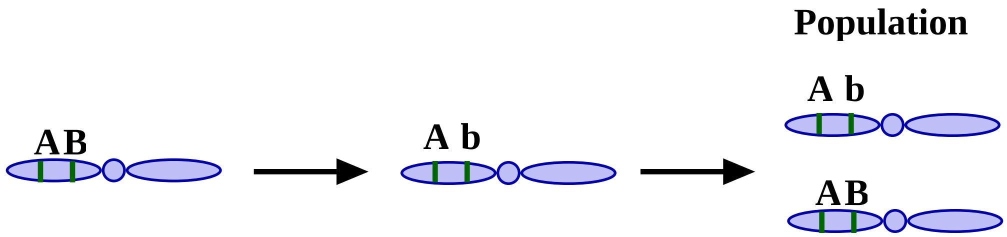
$$D_{max} = \min[F(A)F(B), F(a)F(b)]$$

$$D' = \frac{-0.1875}{0.1875} = -1.0$$

$$-1.0 \leq D' \leq 1.0$$

B) Creation of Linkage Disequilibrium

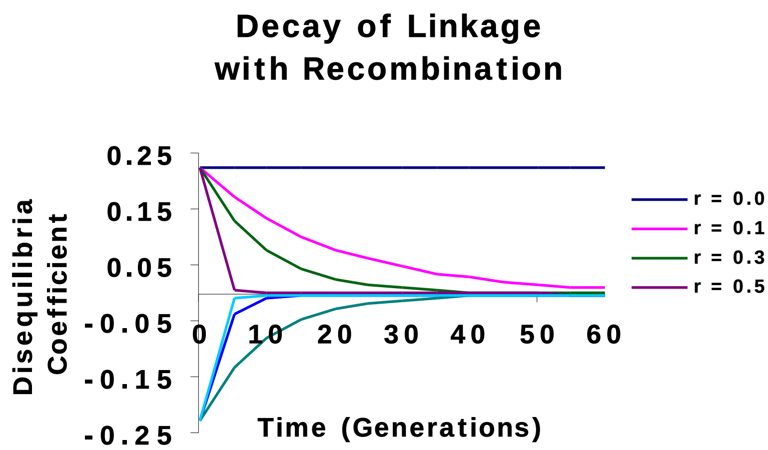
1) Mutation/Genetic Drift – since populations are finite not all mutations happen at the same time. When mutation creates a new haplotype, it is, from the start, in linkage disequilibrium.



2) Selection on multilocus genotypes: In the same way that selection can cause a population to be not in Hardy-Weinberg Genotype Frequency Equilibrium, it can also cause linkage disequilibrium.

3) Mixture of two populations – when populations in linkage equilibrium but with different allele frequencies mix. (i.e., inbreeding within populations relative to between)

C) Elimination of Linkage Disequilibrium – sexual reproduction and associated genetic recombination (r) quickly reduces linkage



D) Importance of Linkage Equilibrium

1) **Can be an indication of admixture**

2) **Can be an indication of selection acting on more than one locus**

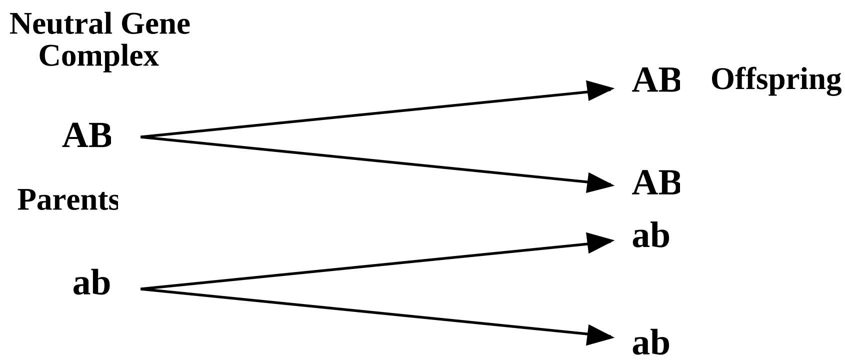
3) **Can mislead conclusions concerning a single neutral locus if linked to a selected one.**

II) Sexual Reproduction

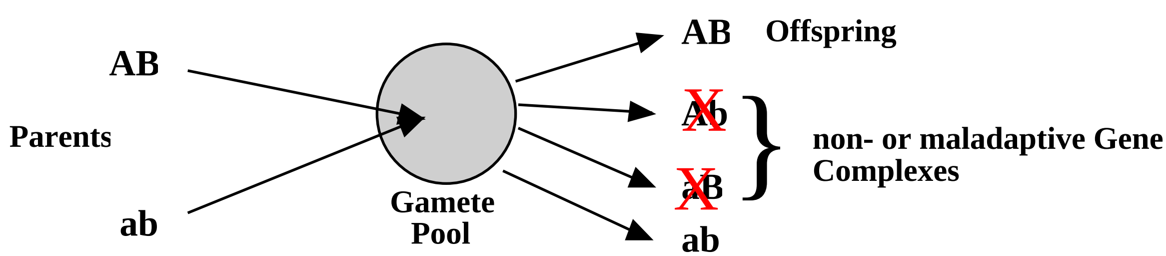
A) Sexual Reproduction is Disadvantageous

1) Adaptive gene complexes – sexual reproduction and recombination breaks up coadapted gene complexes.

Asexual Reproduction



Sexual Reproduction



2) Game of Numbers – consider a population of equal mix of sexual females and male. Females (regardless of type) produce two offspring each. Sexual females produce equal numbers of males and females.

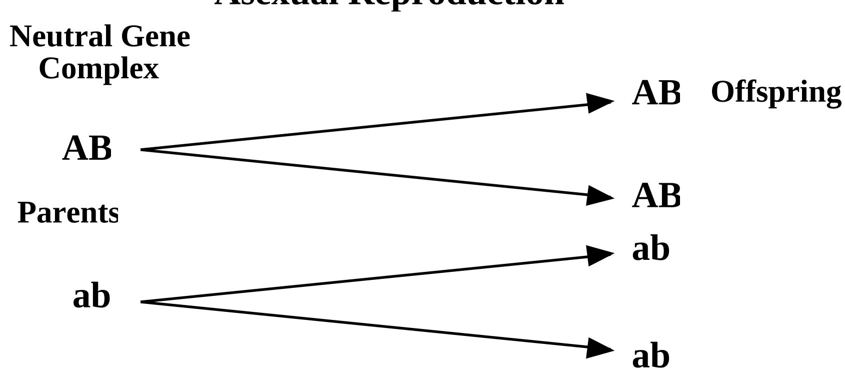
		Generation		
	Start	**1**	**2**	**3**
Sexual female	100	100	100	100
Sexual male	100	100	100	100
Asexual	100	200	400	800
% Asexual	0.333	0.500	0.667	0.800

B)

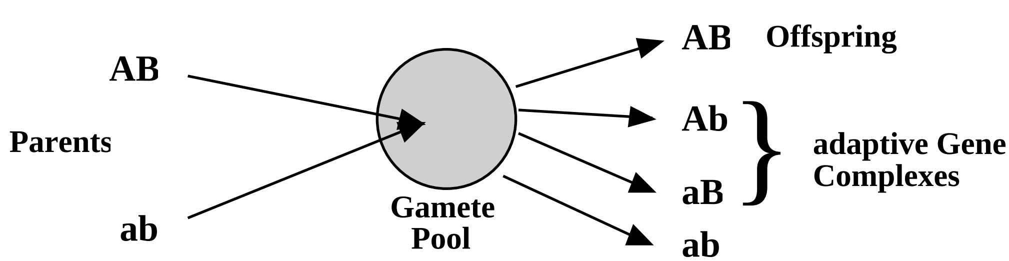
Sexual Reproduction is Advantageous

1) Adaptive Complexes Form.

Asexual Reproduction

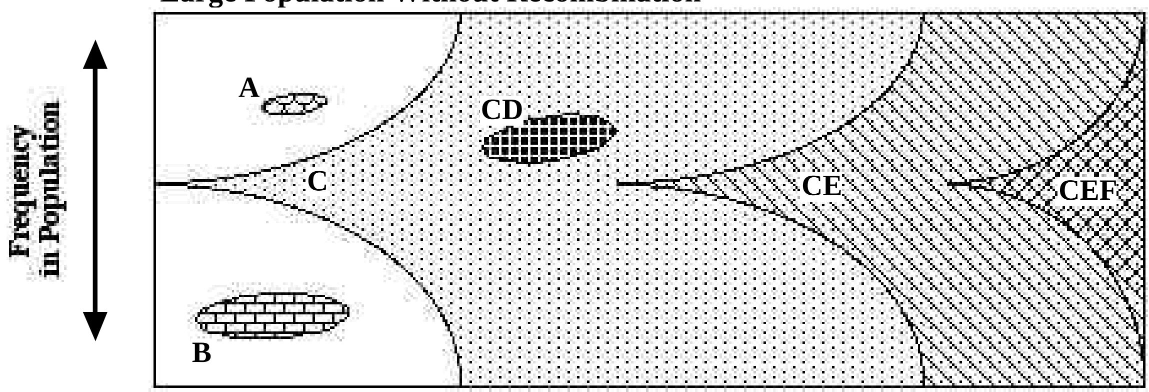


Sexual Reproduction

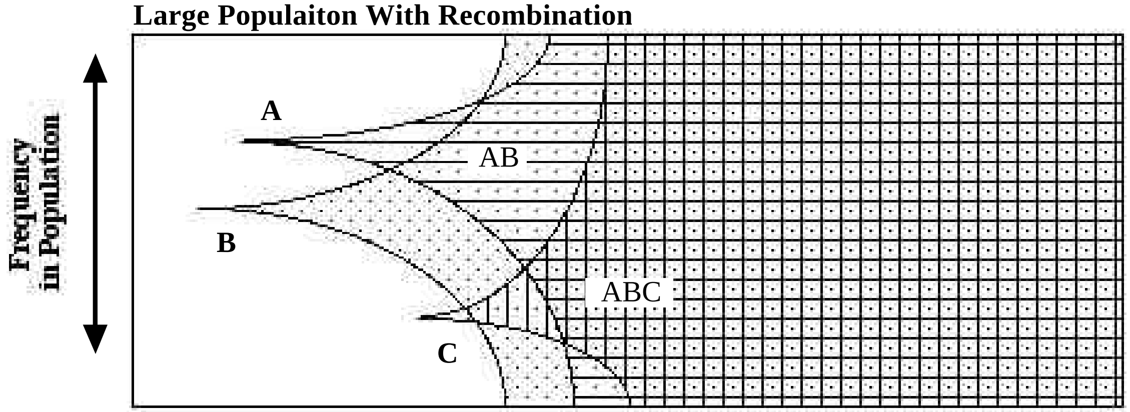


2) Fixation of Rare, Beneficial Mutations

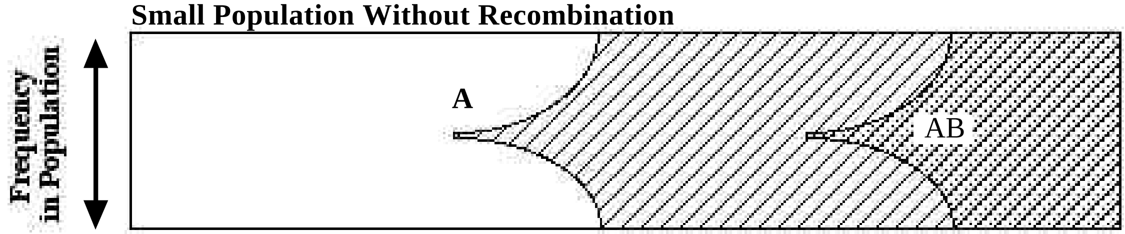
Large Population Without Recombination



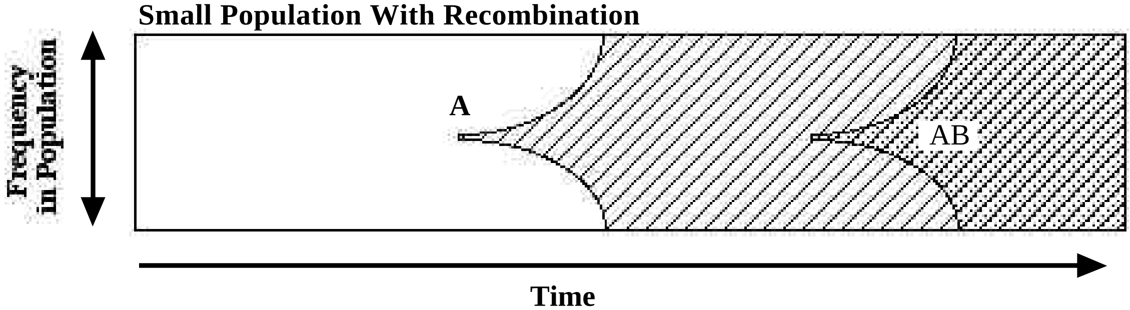
Large Populaiton With Recombination



Small Population Without Recombination



Small Population With Recombination



3) Combinations made by recombination can be neutral (or equally fit) but provide protection against a changing environment

4) Asexual Lineages Accumulate Deleterious Mutations (Muller's Ratchet)

# of Deleterious Mutation

Increasing Time

0	1	2	3	4	5	6	…
100							
90	10						
80	15	5					
⋮							
50	30	10	7				
⋮							
0	60	20	10	5	5		

Lost through drift
Recreated by mutation

Lost through drift
AND by mutation

Sexual populations can recreate classes of lower numbers of mutations by recombination.

Sexual populations also can purge deleterious mutations faster by creating double mutant strains that go extinct