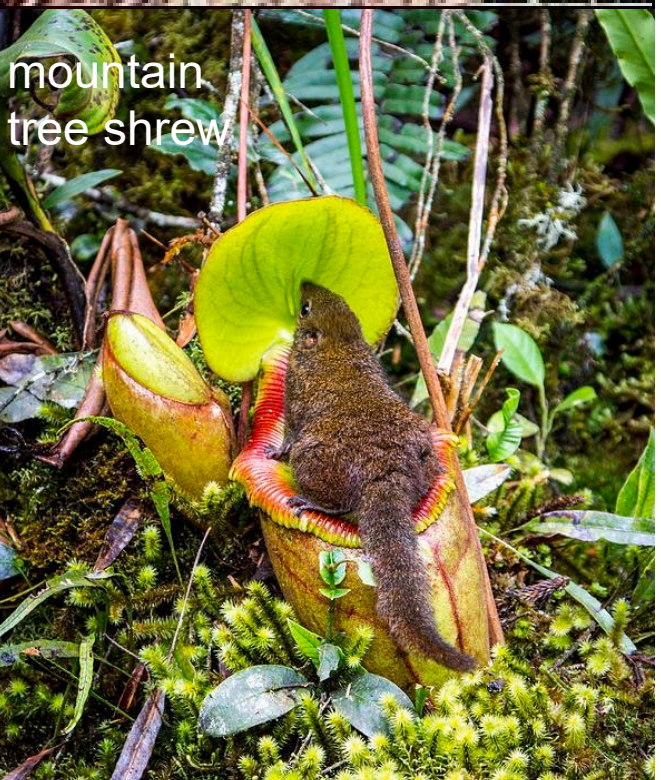


Plant of the day!

Nepenthes rajah, the largest meat-eating plant in the world, growing pitchers that can hold two litres of water if filled to the brim.

It is dioecious

Pitchers have evolved 3 times in 3 independent groups, the Sarraceniaceae (the Americas), the Nepenthaceae (Asia), and the Cephalotaceae (Australia).

Such species attract, trap and digest insects, as well as small vertebrates and derive nutrients from them.

The have a mutualistic relationship with tree shrews. How does it work?

Questions

What is adaptation and local adaptation?

Why do we study local adaptation and how does it arise?

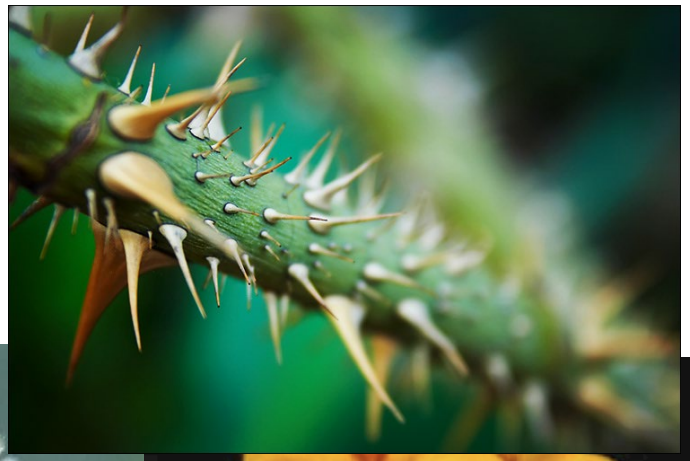
Can we measure selection in nature?

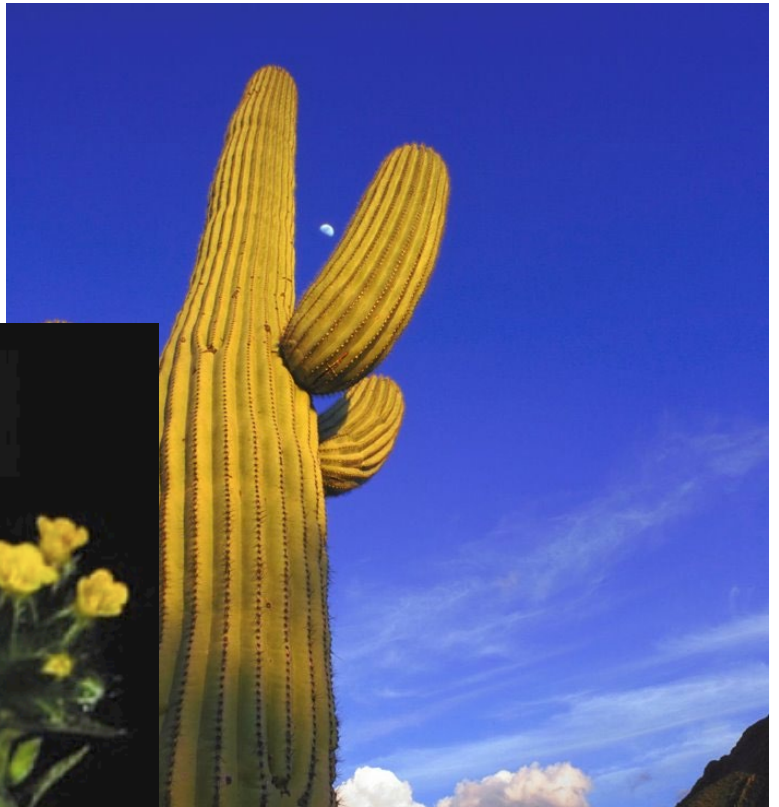
How do we assess quantitative genetic variation and why is it important?

How do we study local adaptation in nature?

Adaptation

A feature of an organism that has been favoured by natural selection because of that feature's positive effect on relative fitness





Local adaptation

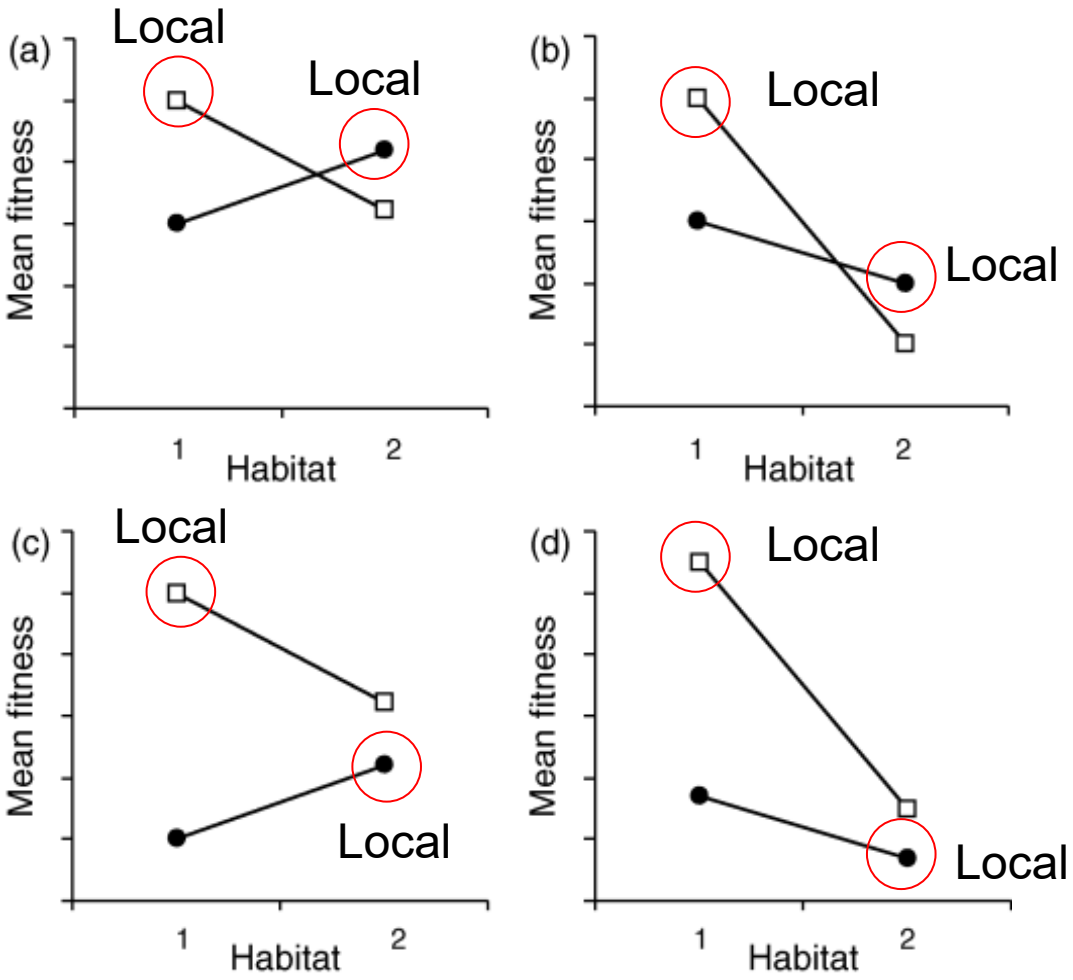
What is local adaptation?

Evolution, through *divergent* natural selection, of traits that have high fitness in the environmental conditions specific to a population.

These adaptations are local in that they are NOT found throughout the whole species

e.g. populations of sunflowers around the Great Salt Lake are highly salt tolerant there, but not elsewhere.

Which of these shows local adaptation?



"local" genotypes must do better than "immigrant" at each site

Why study local adaptation?

Many adaptations are ancient, making it difficult to understand the selection pressures that led to their origins.

Local adaptation should be due to current or recent selection related to differences in environmental conditions experienced by different populations

- Can infer rate of adaptive evolution
- Is a mechanism that maintains genetic variation
- Can be crucial for initiating speciation

What might prevent local adaptation?

Weak/no divergent selection

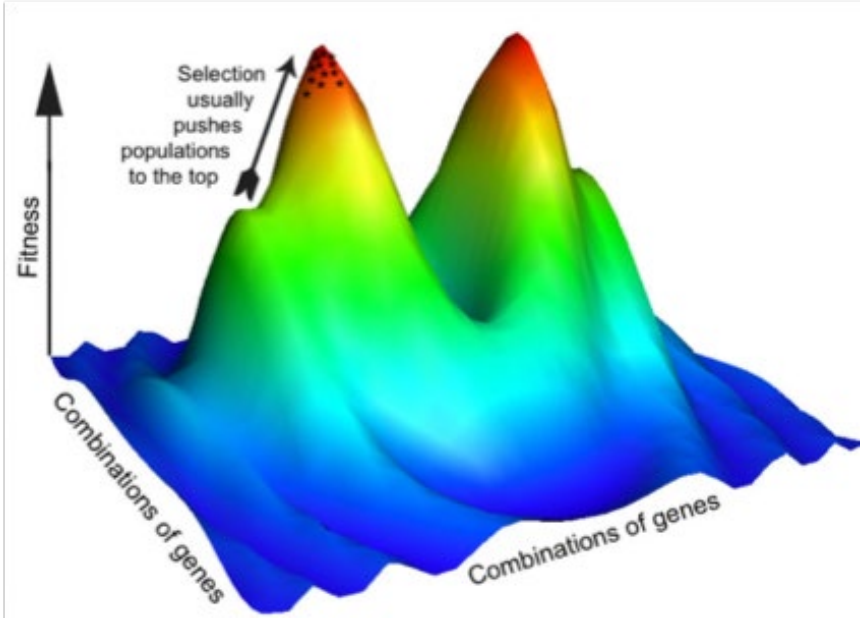
Gene flow can prevent divergence due to selection (e.g. center to edge)

Temporarily varying selection may lead to a “generalist” strategy

Drift can oppose selection

Multiple adaptive peaks

Lack of genetic variation



Natural selection

Natural selection: Individuals vary in traits that lead to differential fitness.

Fitness: An individual's contribution to the next generation. Determined by the probability of survival to reproduction and the number of offspring an individual produces. It is often expressed as a relative measure.

How can we measure fitness?
-difficult to measure in the field (especially for perennial and outcrossing plants)

Selection coefficient: A measure of the reduction in fitness compared with the best genotype in the population

Natural Selection

Natural selection:

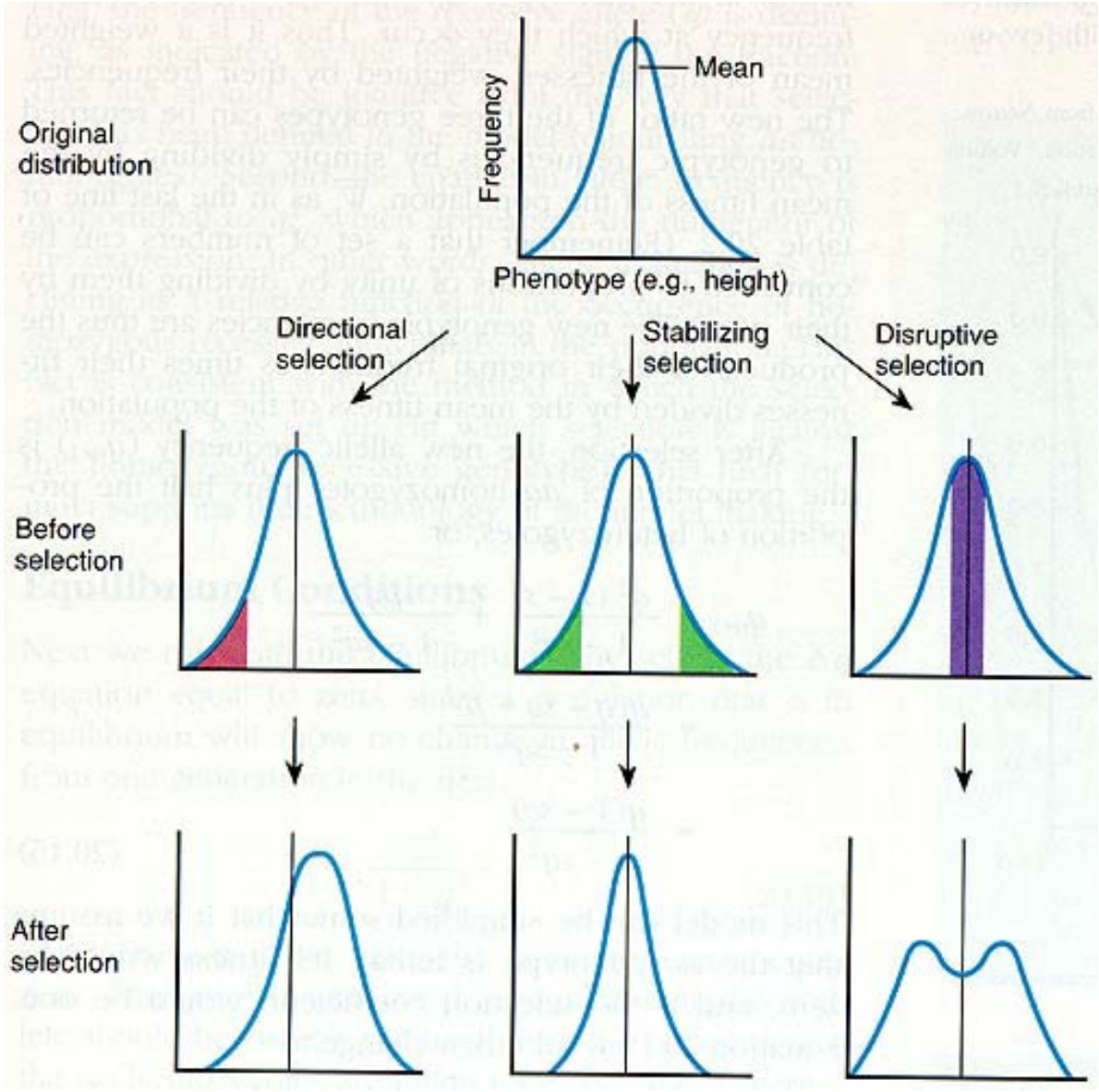
More offspring are produced than can survive
Phenotypic variation in a trait
Differential fitness among phenotypes

What else is required for a response to selection?

Genetic variation

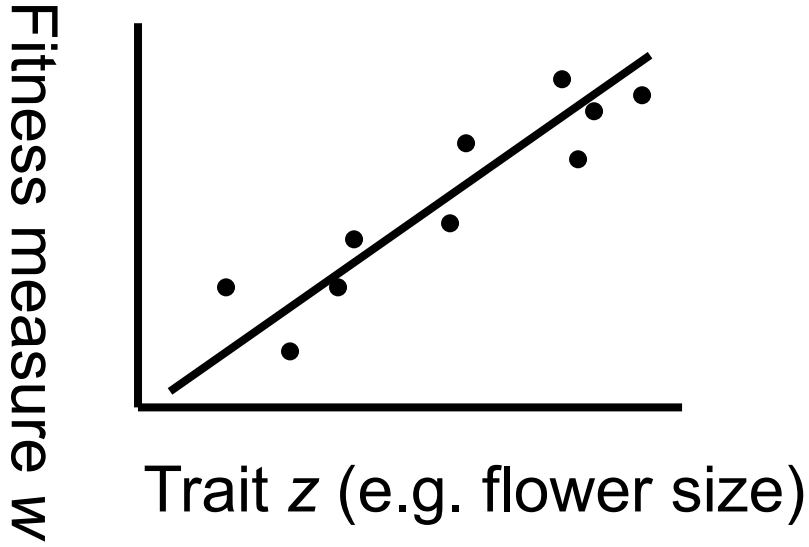
-if these traits are heritable certain genotypes will produce more offspring leading to evolutionary change

What are the different types of selection?



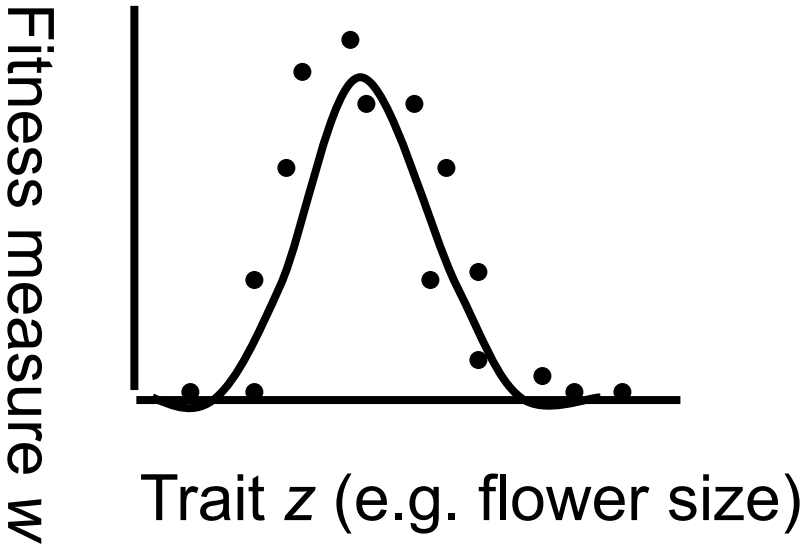
Modes of natural selection: Measuring selection on quantitative traits

Directional selection (positive selection)

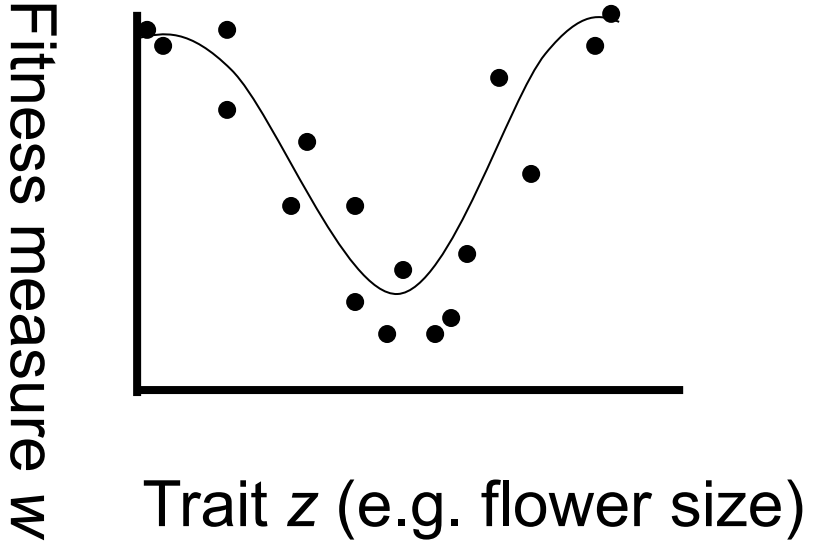


Slope of regression is estimate of strength of selection

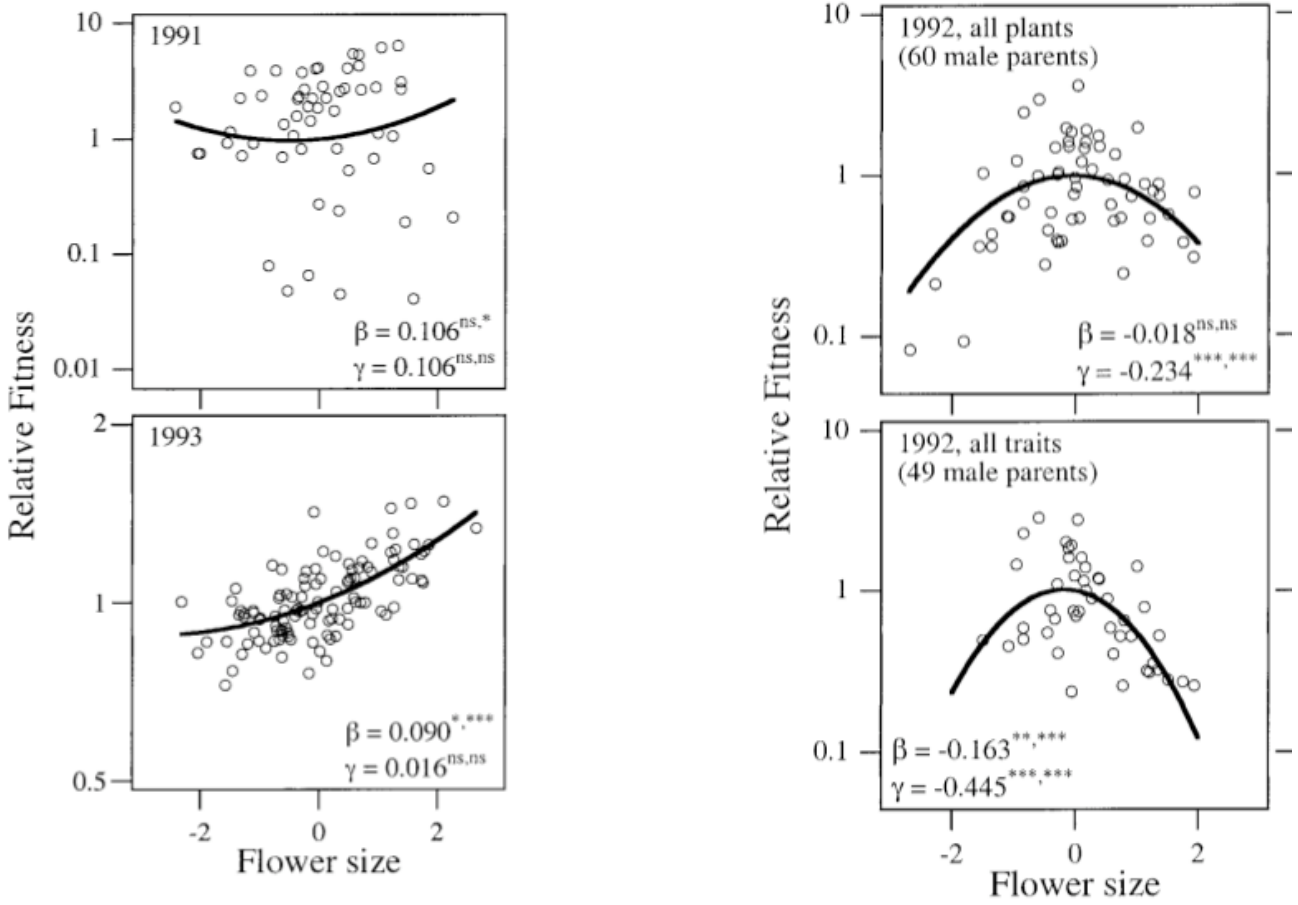
Stabilizing selection



Disruptive selection



Measuring selection in wild populations



B = linear selection gradient (measures directional selection)

γ = quadratic selection gradient (measures stabilizing and disruptive selection)

Positive selection for larger flowers in 1993
Stabilizing selection for flower size in 1992

Morgan and Conner 2000

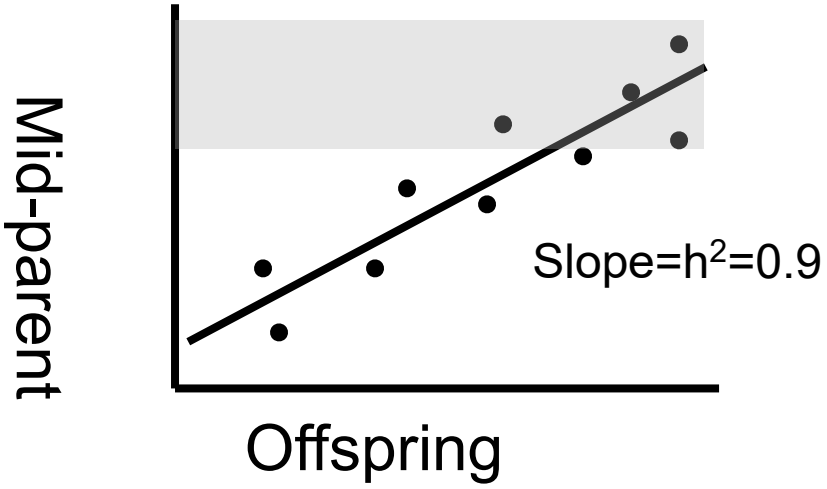
Genetic variation and response to selection

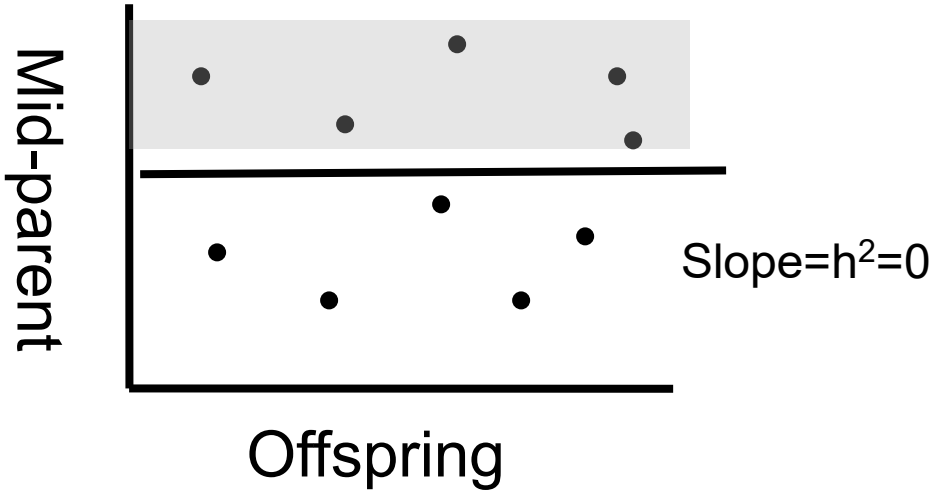
Provides the capacity for organisms to adapt

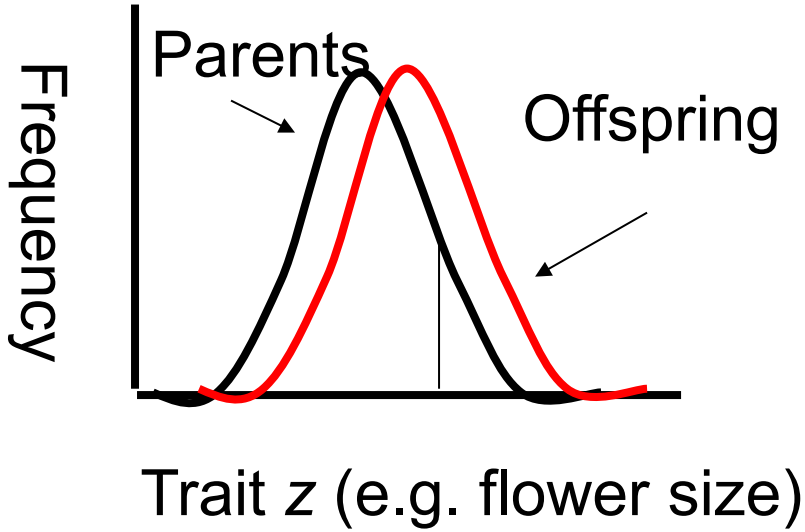
Population/species with no genetic variation can not respond to selection

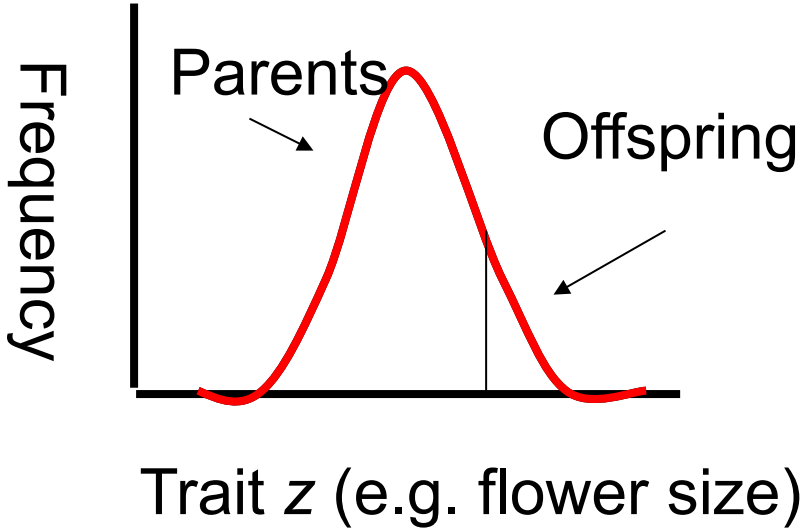
How do we measure genetic variation in quantitative traits?

Parent offspring regression









How do we measure genetic variation in quantitative traits?

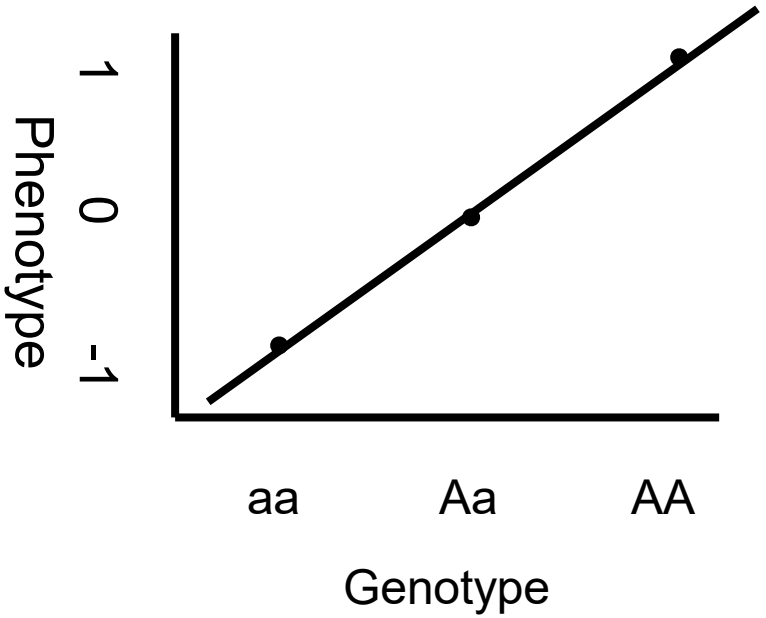
$\mathbf{V_P = V_G + V_E + V_{GE}}$

V_P = total phenotypic variation of the segregating population

V_G = genetic variation that contributes to the total phenotypic variation

V_E = environmental contribution to the total phenotypic variation

V_{GE} = variation associated with the genetic and environmental interactions



V_G includes three components:

- additive genetic variance (V_A)
- dominance genetic variance (V_D)
- interaction genetic variance (V_I)

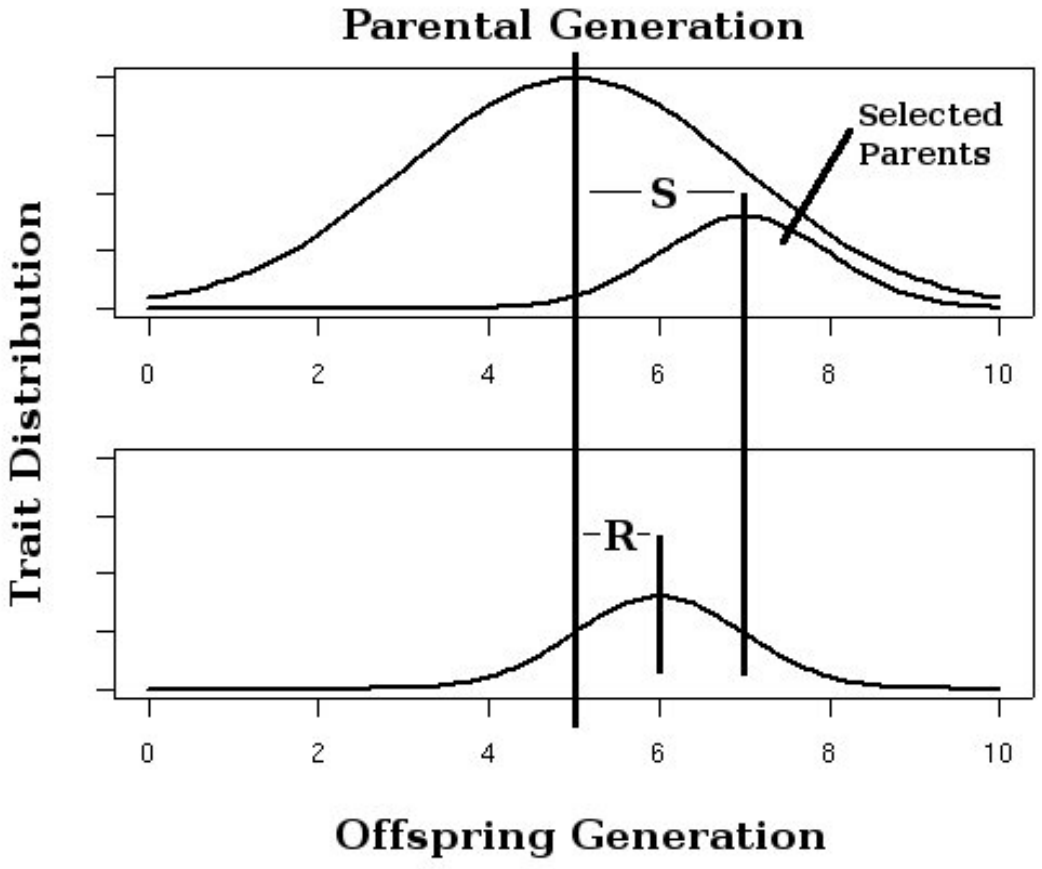
$\mathbf{V_G = V_A + V_D + V_I}$

Additive genetic variation is important for adaptation because it determines most of the correlation of relatives and the opportunities for genetic change by natural or artificial selection.

Genetic variation: quantitative traits and the breeder's equation

Narrow Sense Heritability

$$h^2 = \frac{V_A}{V_P} = \frac{R}{S} \qquad R = h^2 S$$



S = Selection differential

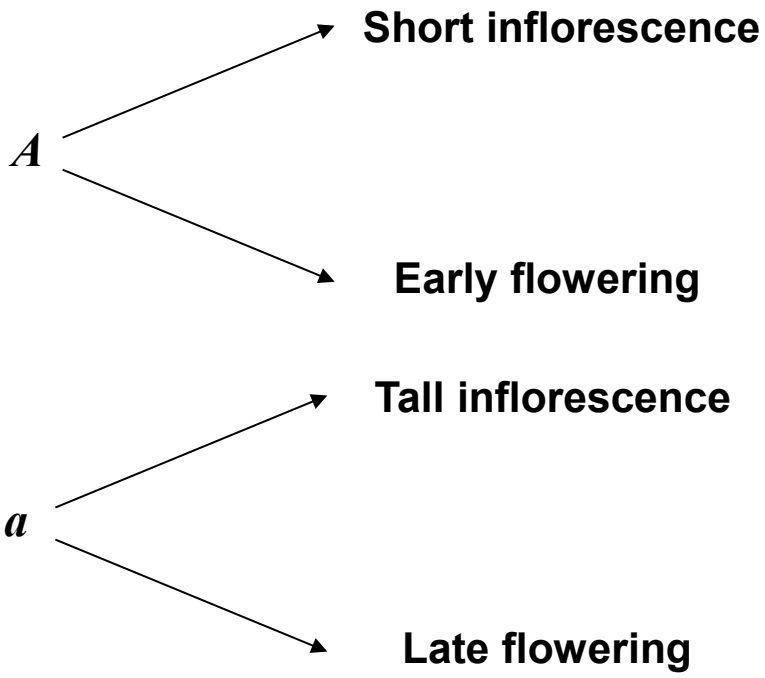
difference between selected parents and the population as a whole (within a generation)

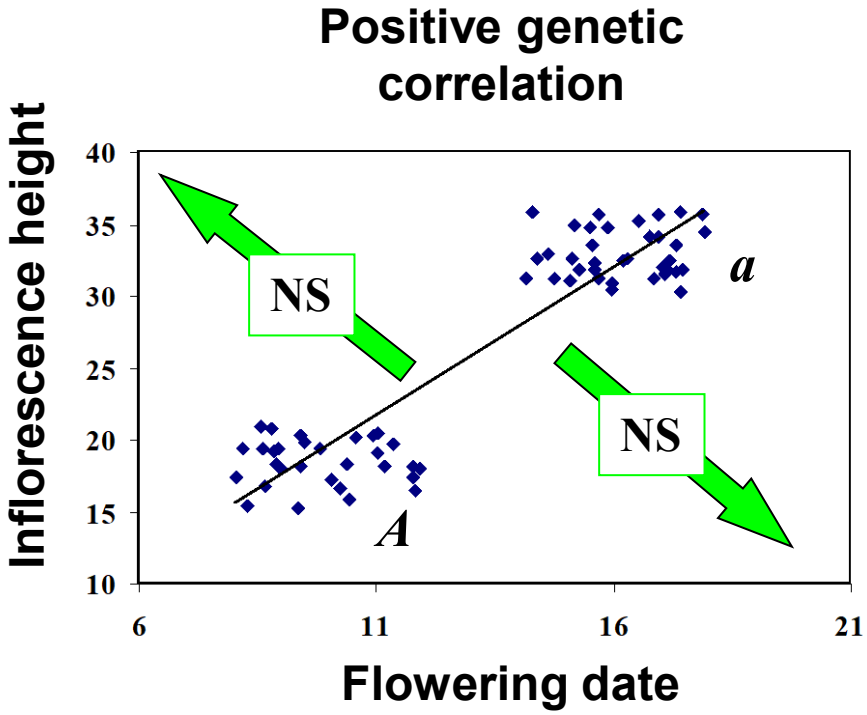
R = response to selection

difference between selected offspring and the unselected population (across generations)

Genetic correlations can constrain adaptation

• Imagine a case where a single diallelic locus controls both inflorescence height and date of first flower

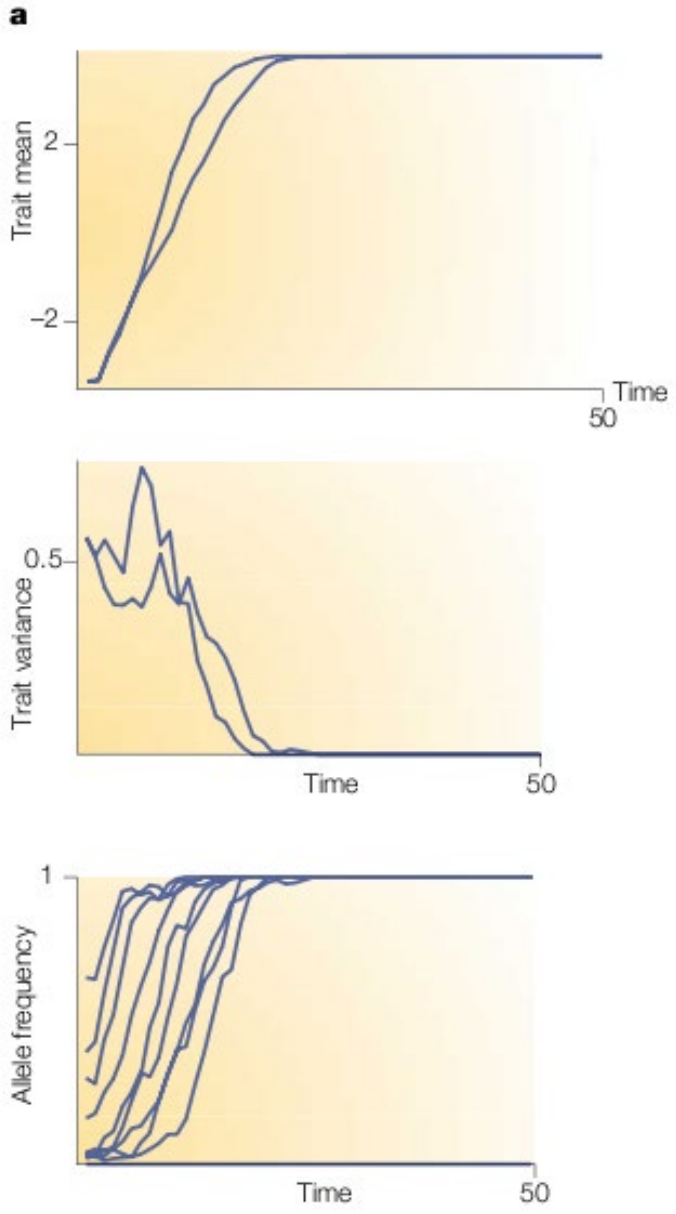




• Can natural selection lead to late flowering plants with short inflorescences?

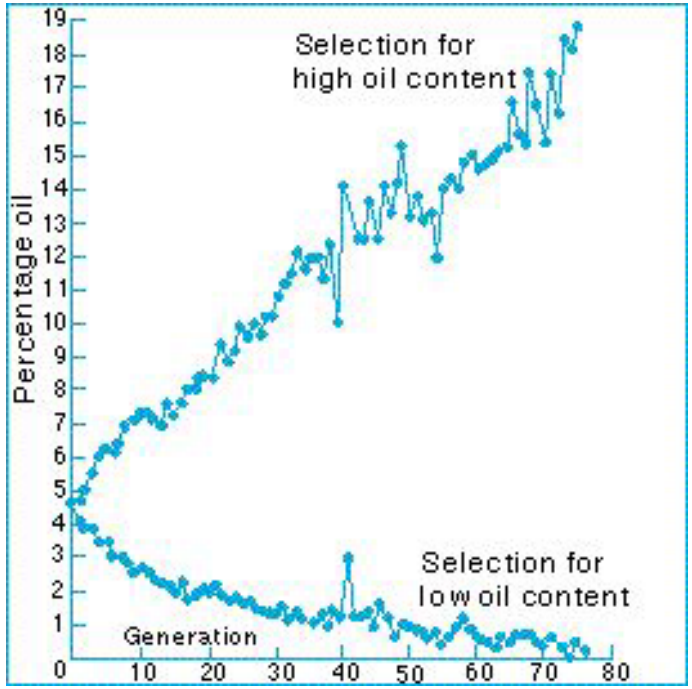
• Can natural selection lead to early flowering plants with tall inflorescences?

The depletion of genetic variation



Over time additive variance for a trait is expected to be used up by selection

Evolution relies on new, beneficial mutations which may occur more frequently than expected as suggested by sustained responses to artificial selection



Dudley and Lambert 1992

Finding evidence for local adaptation

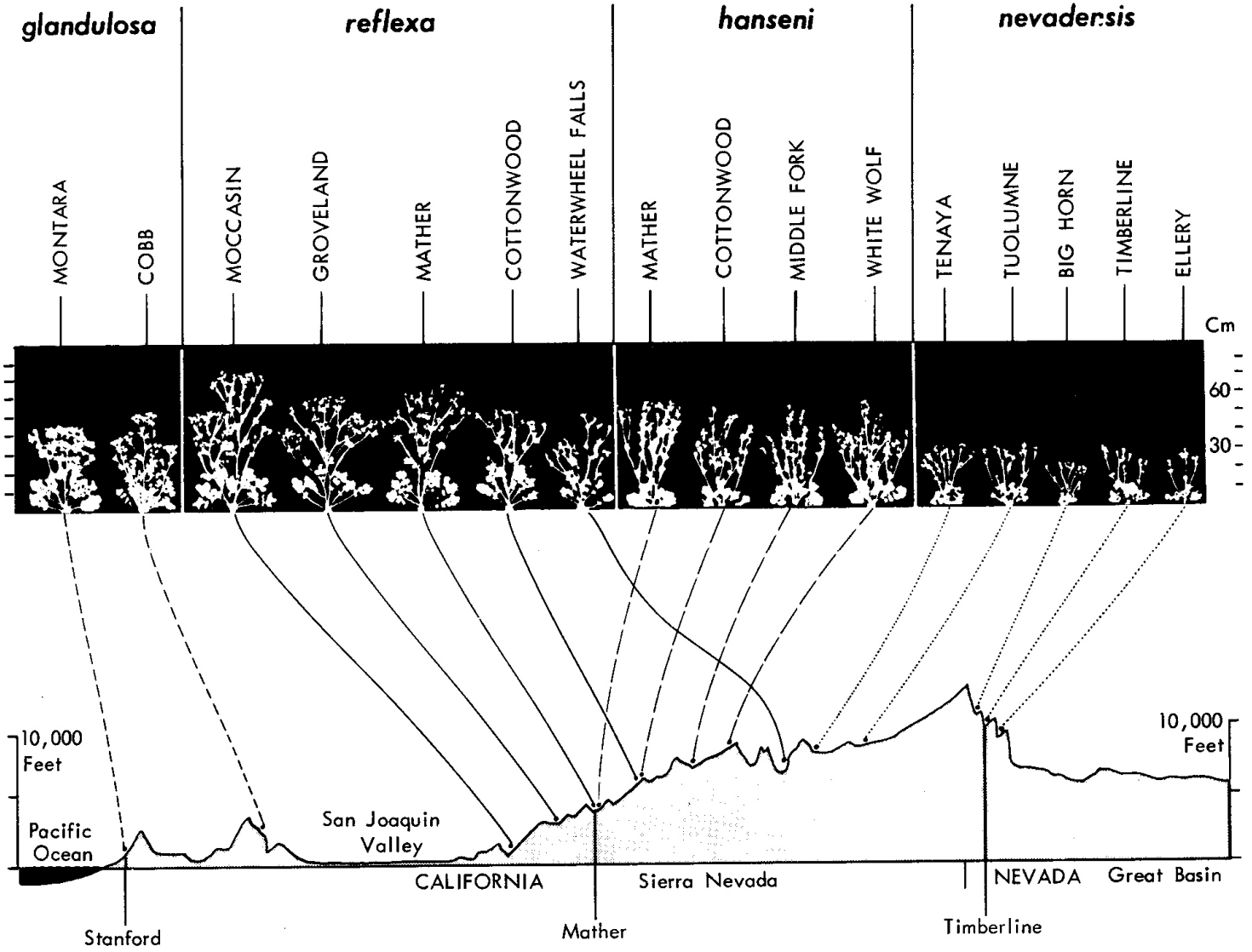
Common garden experiments/ reciprocal transplants

Clines

Qst (phenotypic differentiation) versus Fst (genetic differentiation at neutral molecular markers)

Population genomic approaches

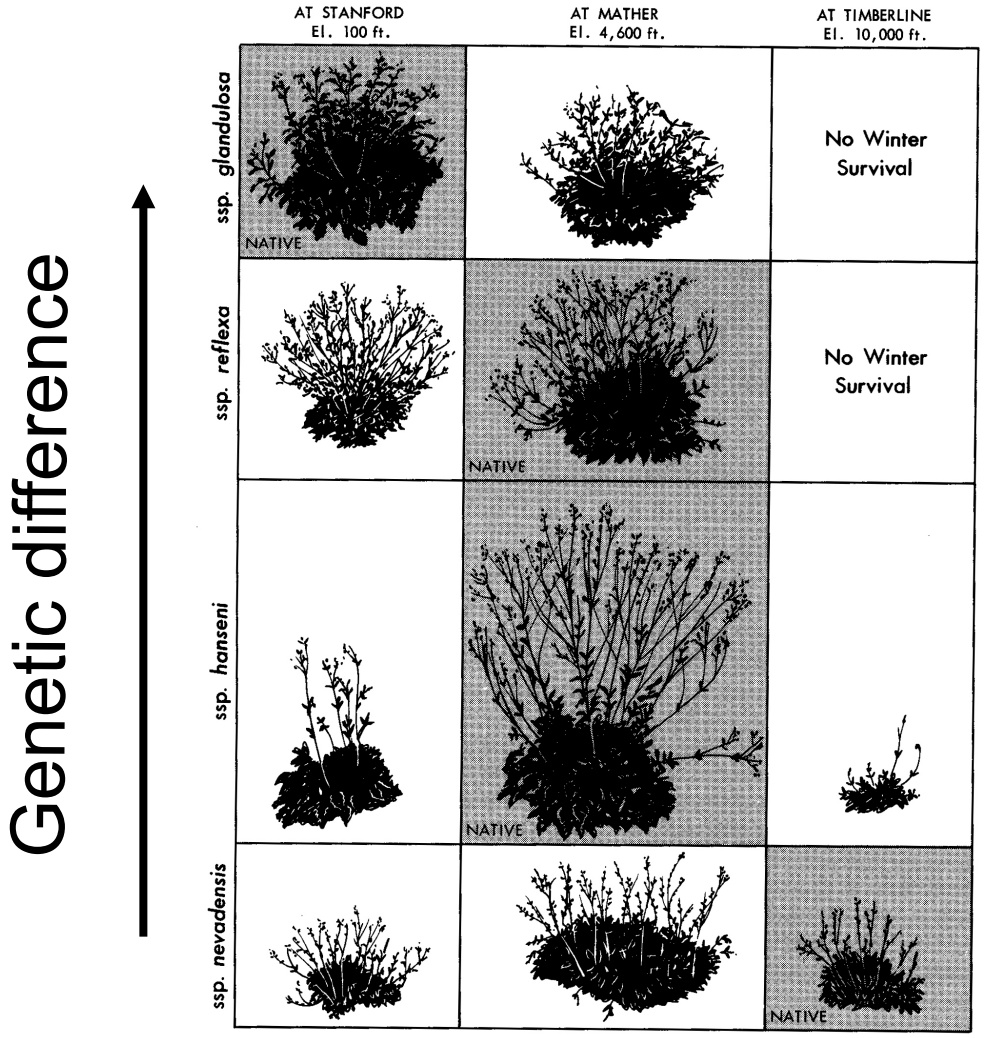
Common garden experiments



Potentilla glandulosa

Clausen, Keck, & Hiesey

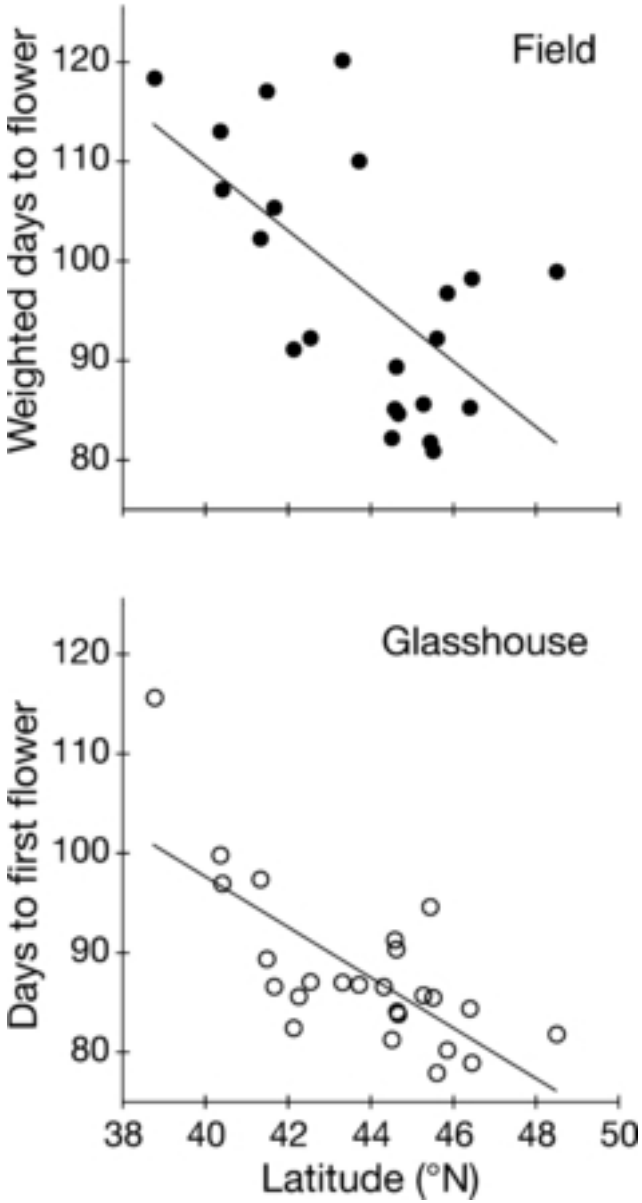
Common garden experiments



Genetic differentiation for traits related to fitness

Suggests local adaptation

Identifying local adaptation: clinal variation



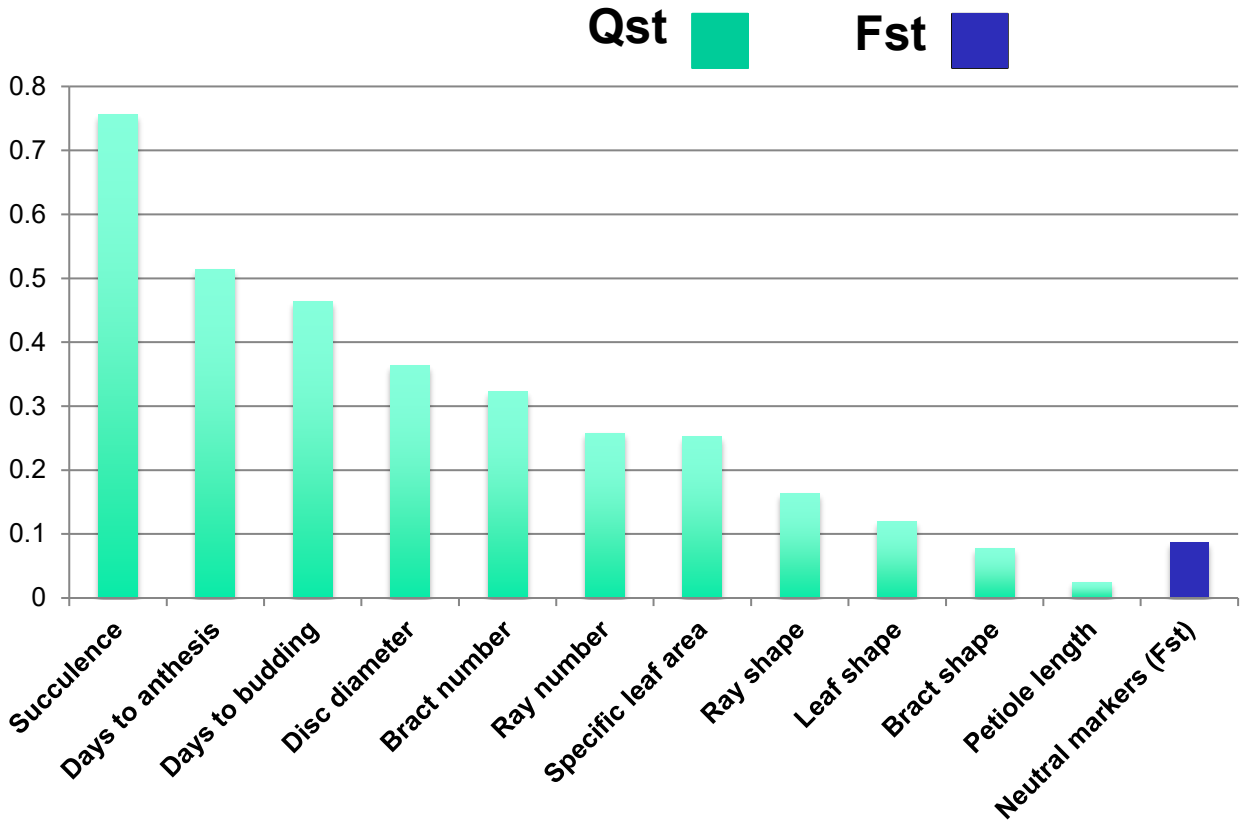
Clinal variation in traits (e.g. flowering time in purple loosestrife)

-suggests adaptation to local conditions

Why would we expect an earlier flowering time at higher latitudes?

MONTAGUE et al 2008

Is drift or selection driving patterns of phenotypic differentiation?



FST and QST values along latitudinal cline in common sunflower

FST=among population divergence in molecular markers

QST=among population variation in quantitative traits

QST>FST?

Suggests divergent selection rather than drift causing differences

QST<FST?

Suggests stabilizing selection

Identifying local adaptation: reciprocal transplants

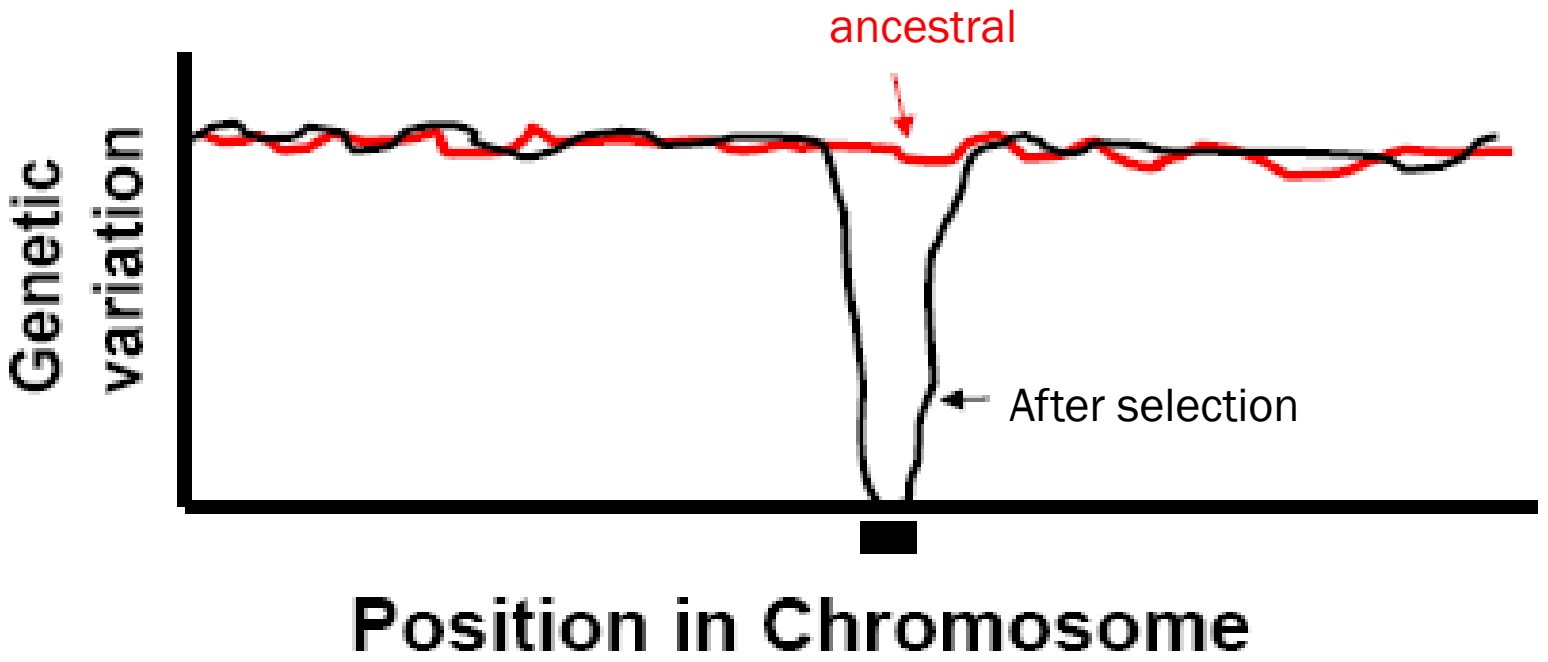
Table 6.2. Population mean (standard error) reproductive biomass (g) of six populations of *Lythrum salicaria* grown at each of three common garden field site (South = Blandy, Mid = Newmarket and North = Timmins) in 2008. The population with the highest fitness at each field site is indicated in bold font.

Population	(°N)	Field Site		
		North	Mid	South
North	48.48	9.8 (1.32)	14.3 (1.26)	13.6 (1.30)
	46.43	**16.3 (1.20)**	33.9 (1.19)	22.5 (1.20)
Mid	45.49	6.3 (1.23)	22.1 (1.19)	8.9 (1.22)
	43.69	4.7 (1.22)	**53.1 (1.20)**	37.2 (1.20)
South	40.34	1.3 (1.23)	15 (1.20)	**46.2 (1.21)**
	38.75	2.6 (1.28)	15.6 (1.26)	23.3 (1.30)

This demonstrates local adaptation

But was is the mechanism underlying local adaptation? Can you think of some experiments to determine this?

Identifying local adaptation: population genomic approaches



Summary: local adaptation

Local adaptation is where local genotypes do better (have higher fitness) than immigrant genotypes

Divergent selection drives local adaptation but other factors such as gene flow can oppose it

Determining the traits underlying local adaptation and the agents of selection can be challenging

Additive genetic variation is required for an evolutionary response to selection

Unanswered Questions

How rapidly can populations evolve?

What sets the geographic limits of a species range?

What is the genetic architecture of adaptation?

- how many genes?
- what is the magnitude of their effects
- what is the relative importance of regulatory versus protein-coding changes?
- how repeatable is adaptation?