Outline of the course

Day 1:

- Lecture: Introduction into quantitative genetic variation
- Practical1: Calculation of variance components
- Practical 2: Decomposition of phenotypic variance: ANOVA

Day 2:

Lecture/Practical:
- Population genetics
- Diversity estimation
- Selection scans

- Download data and scripts and slides:

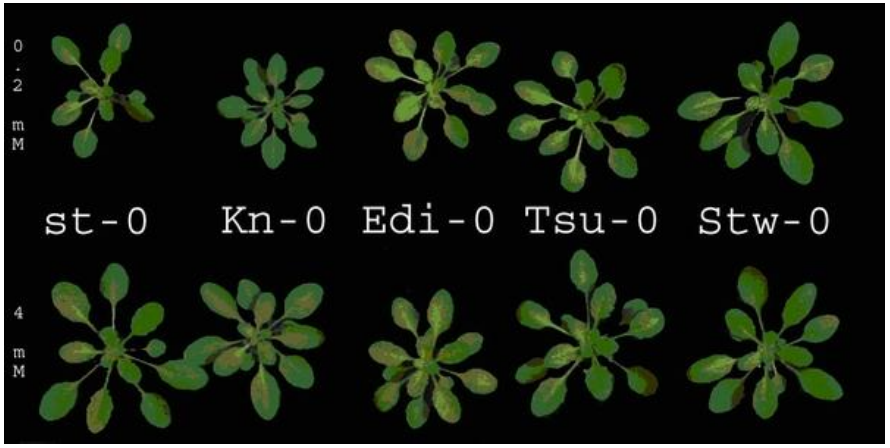
- https://github.com/ArtemPankin/ceplas_diversity_exercises

Genetic variation

Decomposition of phenotypic variance

Maria von Korff
Ceplas course 23.5-24.5.2017

Genetic variation: the raw material of evolution and breeding



Leaf shape in Arabidopsis

# of individuals

Yield distribution

- How much variation is within and between populations?
- Which factors determine quantitative variation of a trait?

Sources of phenotypic variation

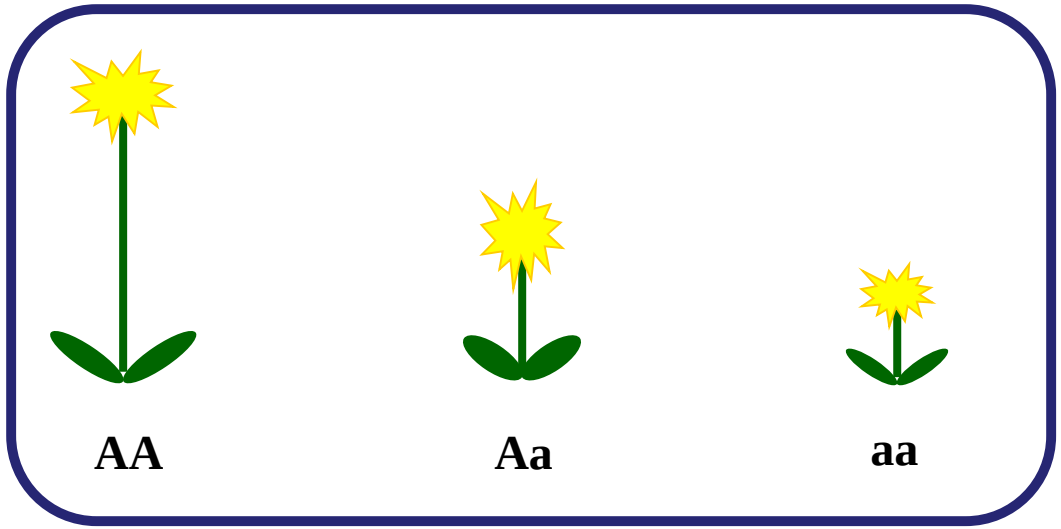
1. **Differences in genotype – Different genotypes produce different phenotypes**

2. **Differences in environment – The phenotypes produced by different genotypes depend on the environment**

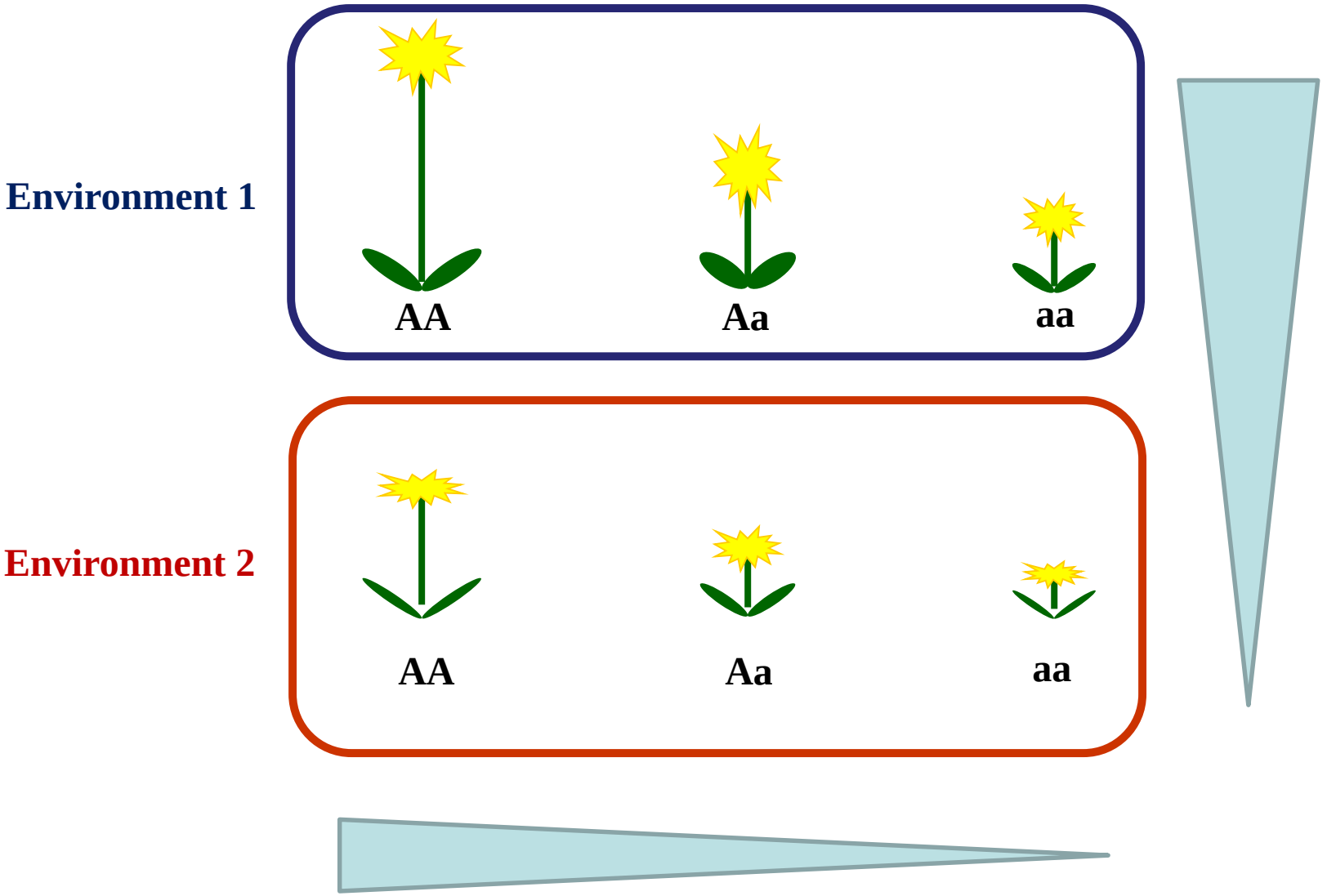
3. **Interactions between genotype and environment – The relative values of phenotypes produced by different genotypes depend on the environment**

Genetic variation

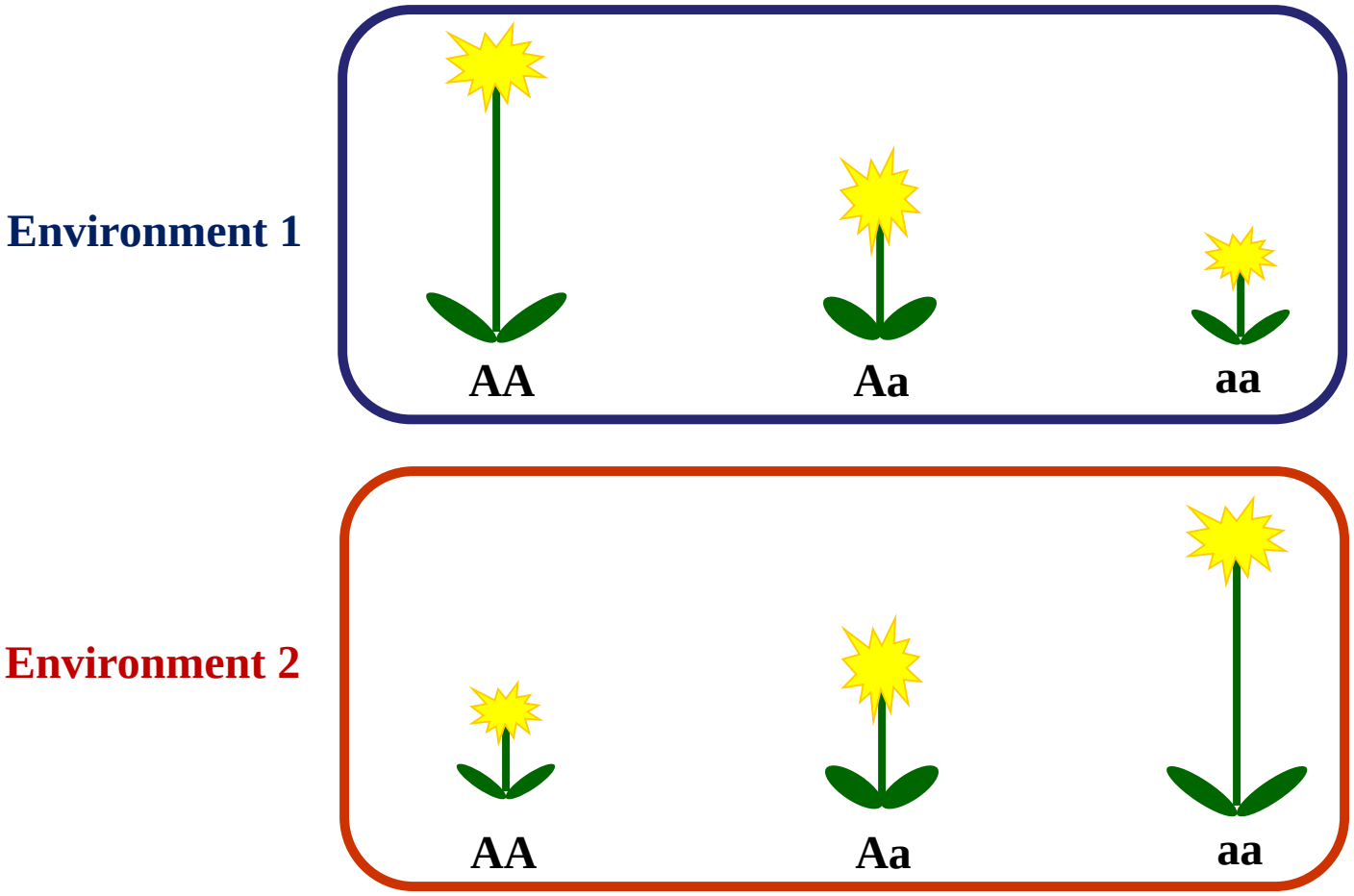
Environment 1



Environmental variation

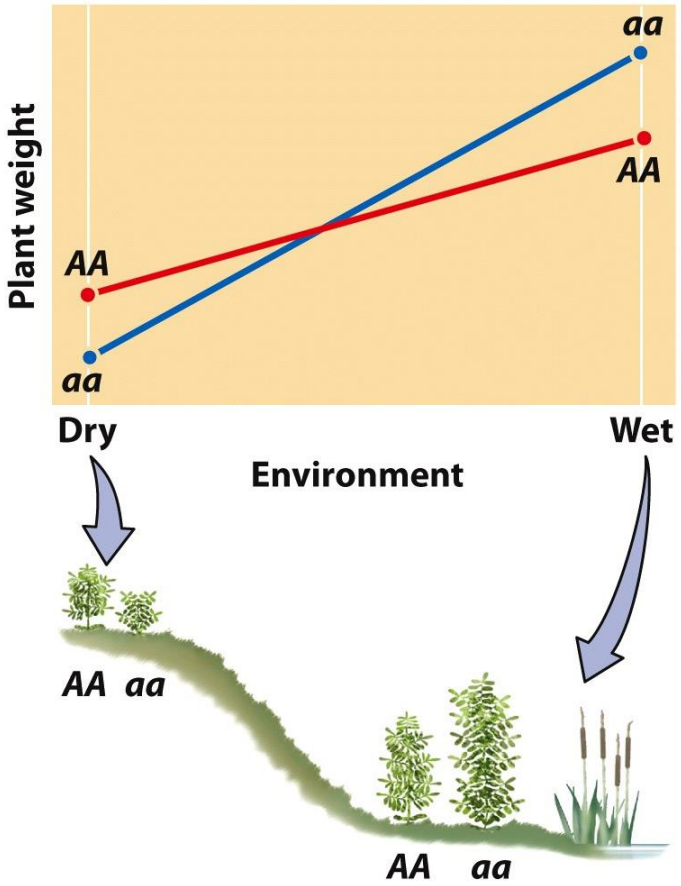


Genotype×Environment variation



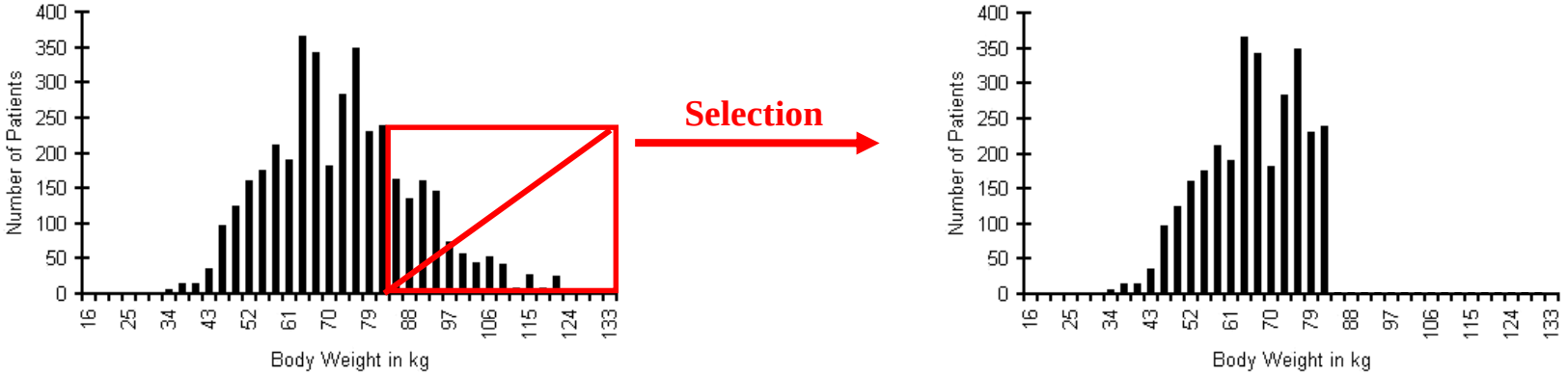
Genotype×Environment variation

Cross-over interactions: the effect of the genotye depends on the environment

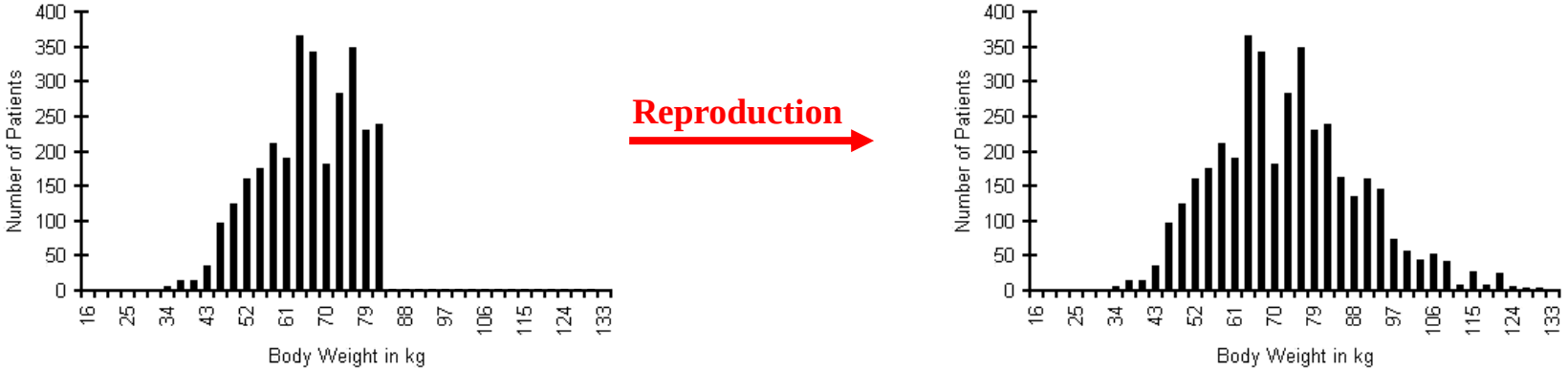


It is GENETIC variation that is essential for evolution

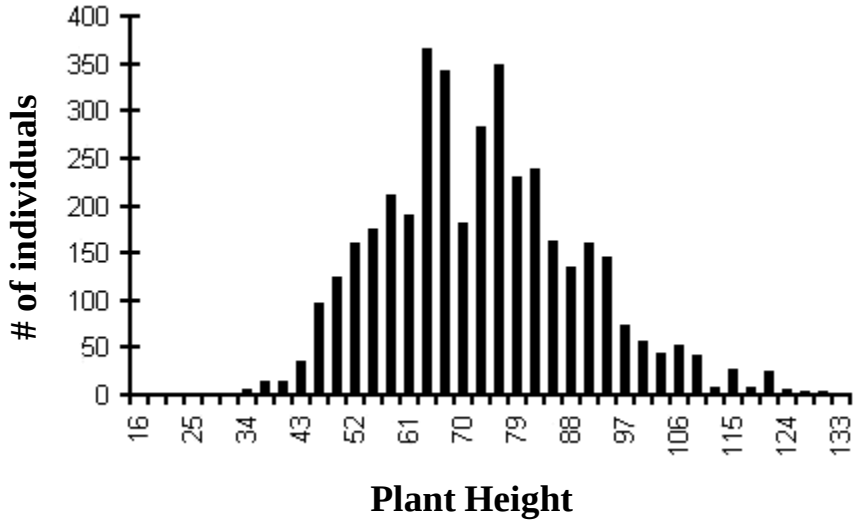
- **Selection can act on purely phenotypic variation**



- **But without genetic variation evolution will not occur**



How much genetic variation is there?

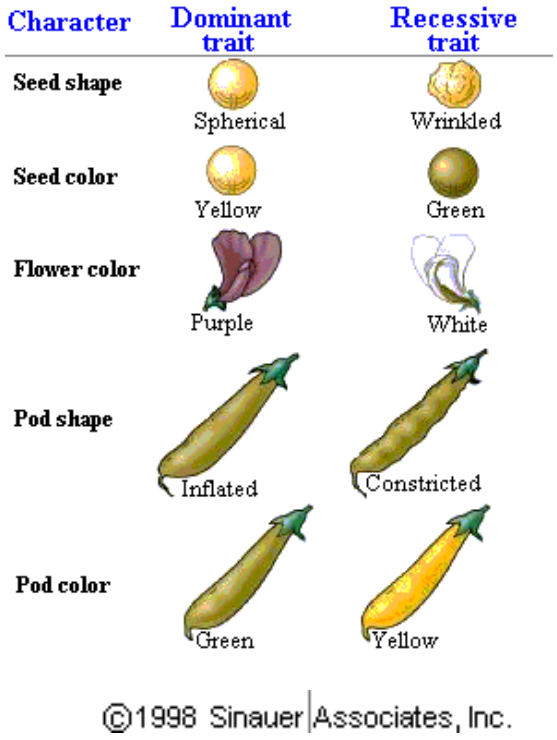


Most traits show a quantitative distribution

Qualitative and Quantitative traits

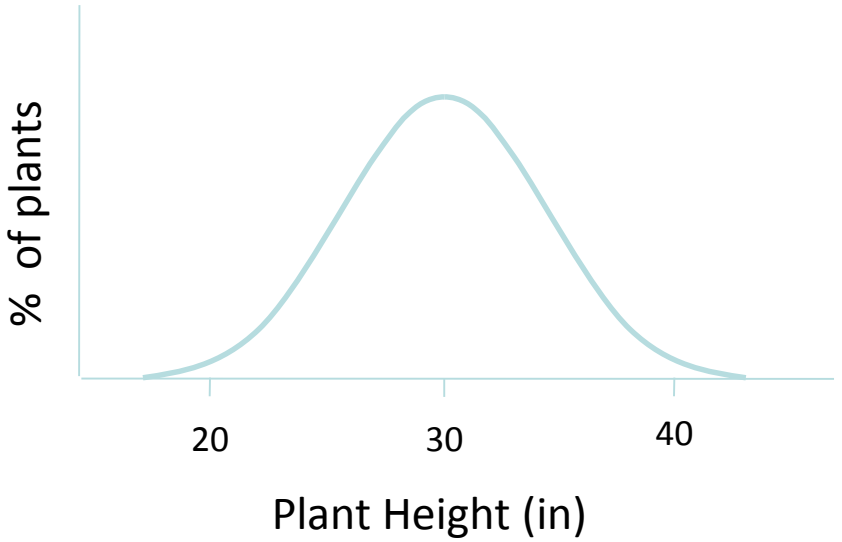
- Qualitative traits:

- Phenotypes with discrete states
- Show Mendelian inheritance (monogene)
- Little environmental effect
- Molecular markers are qualitative traits
- Examples:



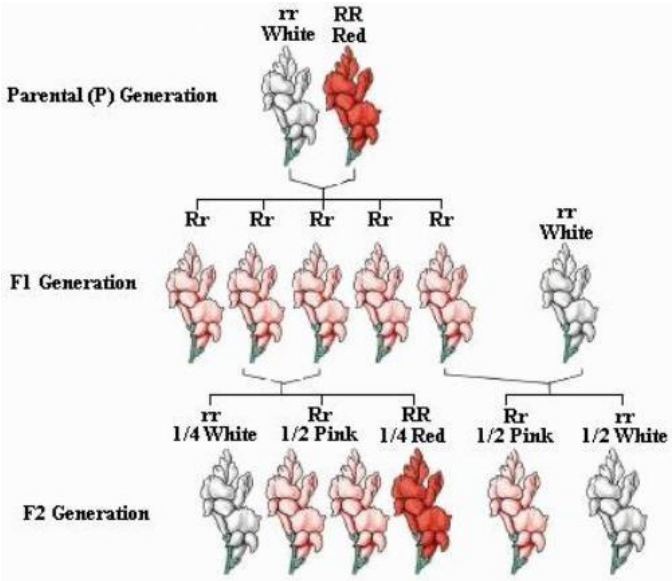
- Quantitative traits:

- Continuous range of variation
- Complex mode of inheritance (polygene)
- Moderate to great environmental effect
- Examples: Plant height, yield, disease severity, grain weight

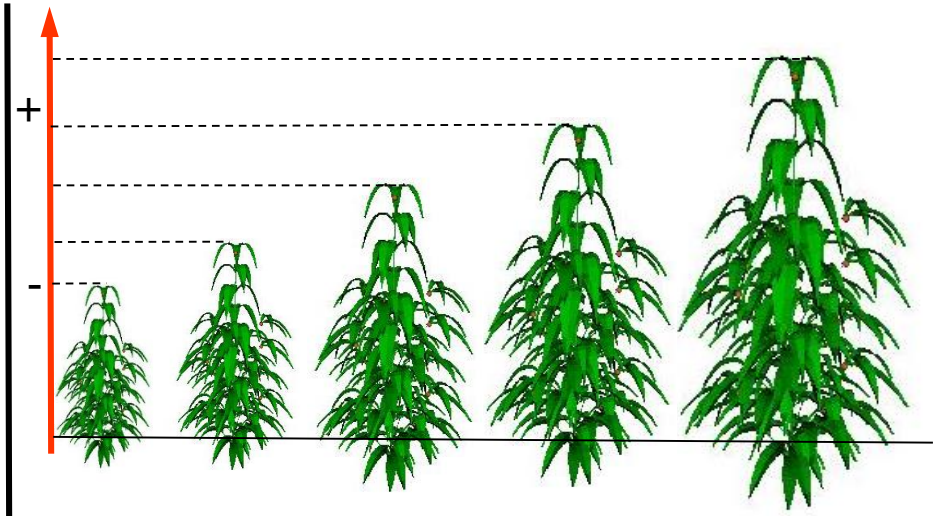


Quantification of traits

Qualitative trait

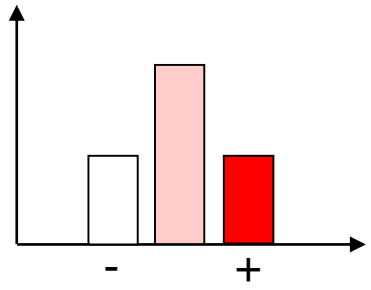


Quantitative trait



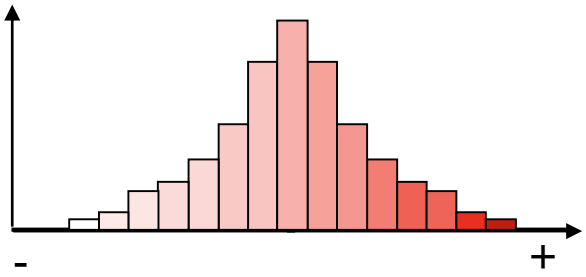
Classes

Frequency distribution in a population

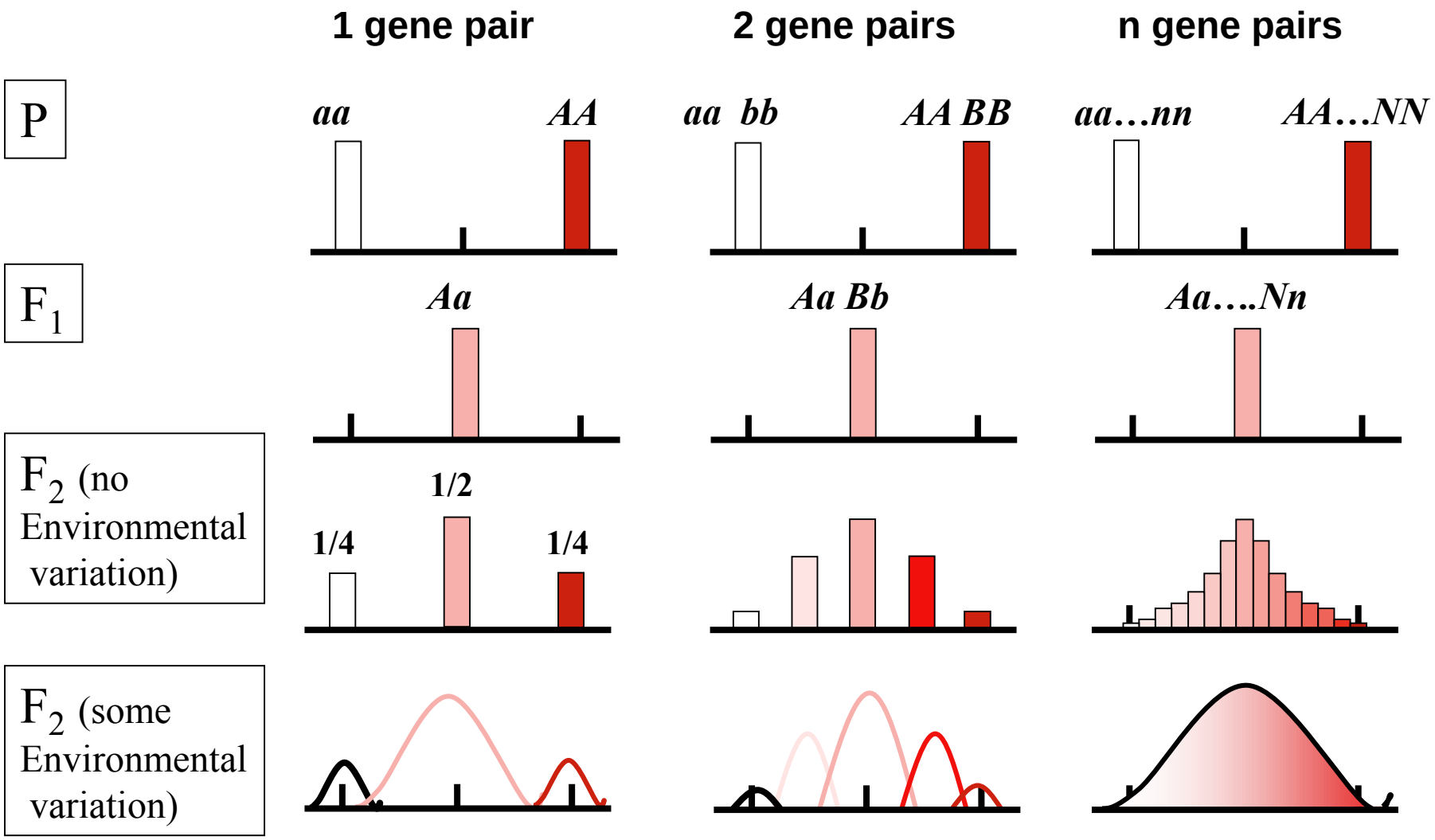


Scale

Frequency distribution in a population



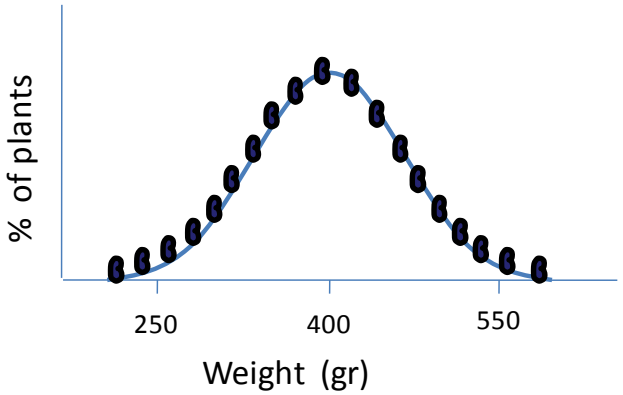
Inheritance of Complex Phenotypes



Inheritance of Quantitative traits

In 1903 the Danish botanist Wilhelm Johannsen measured the weight of seeds in the Princess variety of bean. This variety is a pure line since beans are self-fertilizing .

From a seed lot he measured and classified the beans by weight and obtained the range of distribution for that variety.



Then he selected 19 beans of different weights and self-pollinated them several generations

Doing this he got 19 pure lines (completely homozygous) in case they were not at the beginning of the experiment

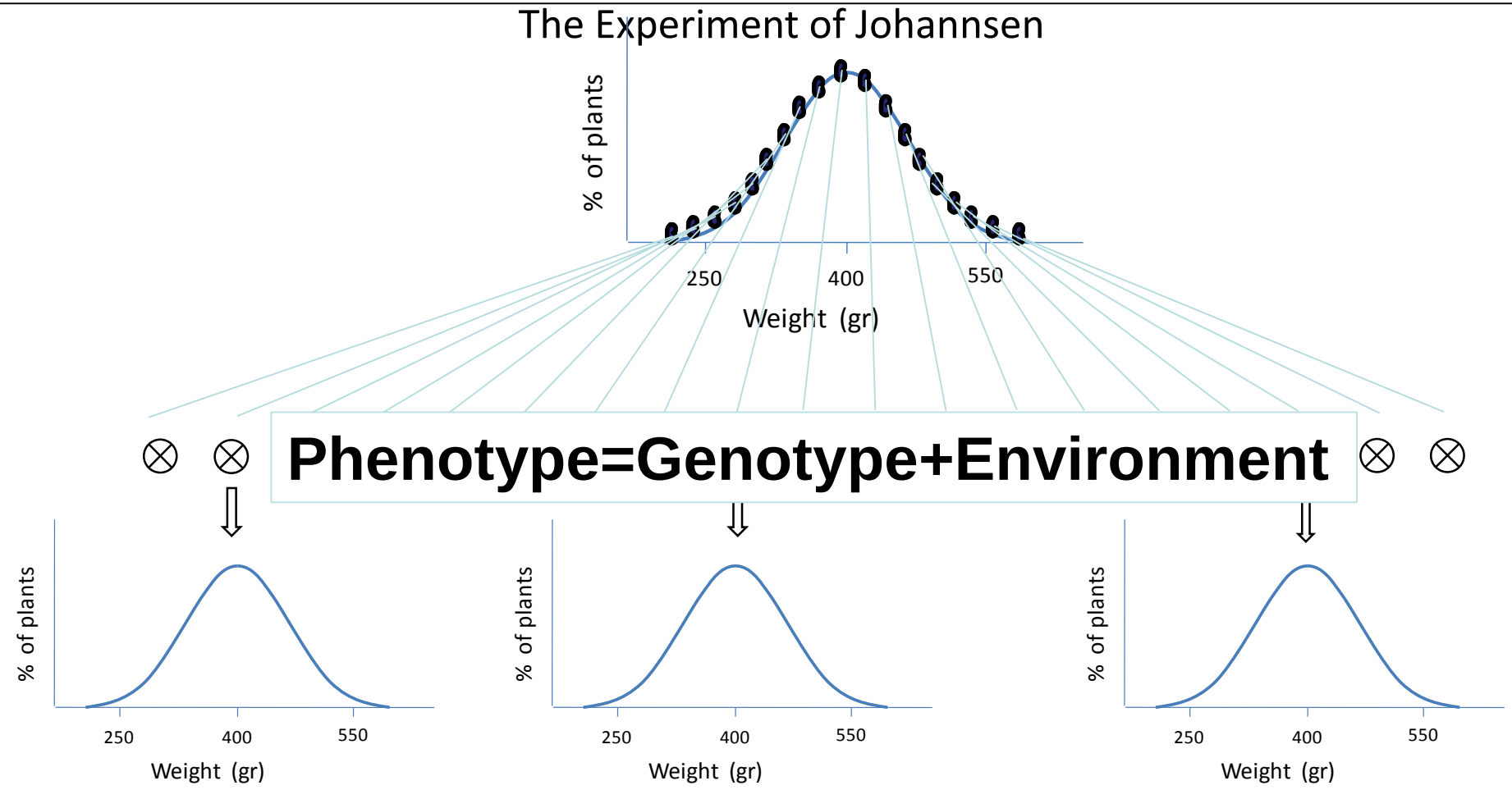
He found that:

The weight of the 5,494 beans he obtained followed a normal distribution

All lines within each of the 19 groups were genetically identical but showed also a range of variation in weights.

The average and distribution of weight in each pure line were similar to those of the original population

Inheritance of Quantitative traits



Conclusions:

- There is a genetic control that keeps the same average weight and distribution
- However not all genetically identical seeds have the same weight.
- The phenotype of each individual must be determined by the genotype and the environmental conditions
- Without genetic variability, genetic improvement is not possible

Inheritance of Quantitative traits

Johannsen showed that quantitative traits are determined by genes. However he did not find any type of Mendelian segregation.
This was studied in 1909 by Swedish **Herman Nilsson-Ehle** who studied kernel color in wheat.

He had several pure lines of red and white colored kernels. When crossing red x white he got always red F1, but different proportions of red and white kernels depending on the cross:

a) 3 red : 1 white
b) 15 red : 1 White
c) 63 red : 1 white

- Color was controlled by three loci
- Only individuals with recessive homozygous alleles at the three loci showed the white phenotype.
- When a single dominant allele (A, B or C) is present at any of the three loci the red phenotype shows up.

Inheritance of Quantitative traits

a) 3 red : 1 white
b) 15 red : 1 White
c) 63 red : 1 white

For case a), allelic variation between the two parents was present only at one locus

P1 (red) P2 (white)
AAbbcc X aabbcc

F1(red) Aabbcc

F2 (only one locus segregating)

¼ AAbbcc : ½ Aabbcc : ¼ aabbcc
(red) (red) (white)

Segregation 3 red : 1 white

Inheritance of Quantitative traits

a) 3 red : 1 white
b) 15 red : 1 White
c) 63 red : 1 white

P1 (red) P2 (white)
AABBcc X aabbcc

F1(red) AaBbcc

F2
(two loci
segregating)

1/16 AABBcc (red)
2/16 AABbcc (red)
1/16 AAbbcc (red)
2/16 AaBBcc (red)
4/16 AaBbcc (red)
2/16 Aabbcc (red)
1/16 aaBBcc (red)
2/16 aaBbcc (red)
1/16 aabbcc (white)

Segregation 15 red : 1 white

Inheritance of Quantitative traits

a) 3 red : 1 white
b) 15 red : 1 White
c) 63 red : 1 white

P1 (red) P2 (white)
AABBCC X aabbcc

F1(red) AaBbCc

F2
(two loci
segregating)

Segregation 63 red : 1 white

1/64	AABBCC	(red)	2/64 AABBCc	(red)	1/64 AABBcc (red)
2/64	AABbCC	(red)	4/64 AABbCc	(red)	2/64 AABbcc (red)
1/64	AabbCC	(red)	2/64 AabbCc	(red)	1/64 Aabbcc (red)
2/64	AaBBCC	(red)	4/64 AaBBCc	(red)	2/64 AaBBcc (red)
4/64	AaBbCC	(red)	8/64 AaBbCc	(red)	4/64 AaBbcc (red)
2/64	AabbCC	(red)	4/64 AabbCc	(red)	2/64 Aabbcc (red)
1/64	aaBBCC	(red)	2/64 aaBBCc	(red)	1/64 aaBBcc (red)
2/64	aaBbCC	(red)	4/64 aaBbCc	(red)	2/64 aaBbcc (red)
1/64	aabbCC	(red)	2/64 aabbCc	(red)	1/64 aabbcc (white)

Inheritance of Quantitative traits

However, Nilsson-Ehle not only classified the seeds by color. He also classified them by color intensity and saw that color intensity also had a defined segregation pattern

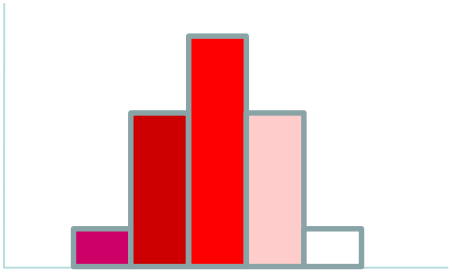
P1 (purple, very dark red) X P2 (white)

↓

F1(red)

⊗

↓



1/16 : purple
4/16: dark-red
6/16: red
4/16: light-red
1/16: red

color intensity was determined by two loci with two alleles each: one that produced red pigment (A and B) and other with no pigment (a and b).

Additive effects of the alleles depended on the number of alleles for pigment present

P1 (purple, very dark red) P2 (white)

AABB X aabb

↓

F1(red) AaBb

⊗

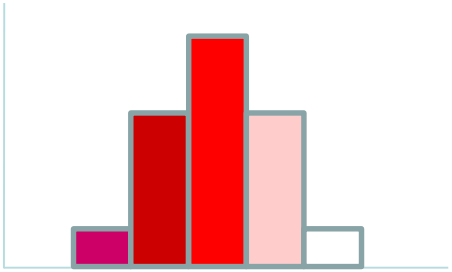
↓

1/16 AABB	(Purple)
2/16 AABb	(dark-red)
1/16 AAbb	(red)
2/16 AaBB	(dark-red)
4/16 AaBb	(red)
2/16 Aabb	(light-red)
1/16 aaBB	(red)
2/16 aaBb	(light-red)
1/16 aabb	(white)

Inheritance of Quantitative traits

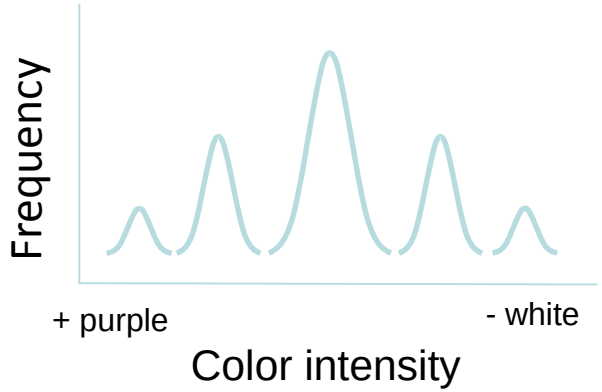
P1 (purple, very dark red) X P2 (white)

F1(red)



1/16 : purple
4/16: dark-red
6/16: red
4/16: light-red
1/16: red

Going one step further, He saw that within each of the groups there was also some variation

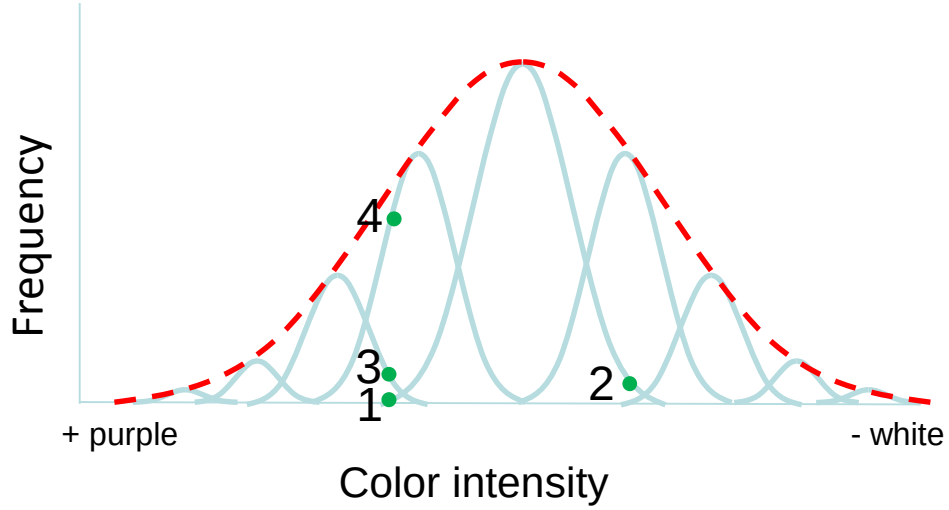


Inheritance of Quantitative traits

He deduced that many loci were involved (not only two) in the trait and taking into account Johanssen's findings:

Phenotype=Genotype+Environment

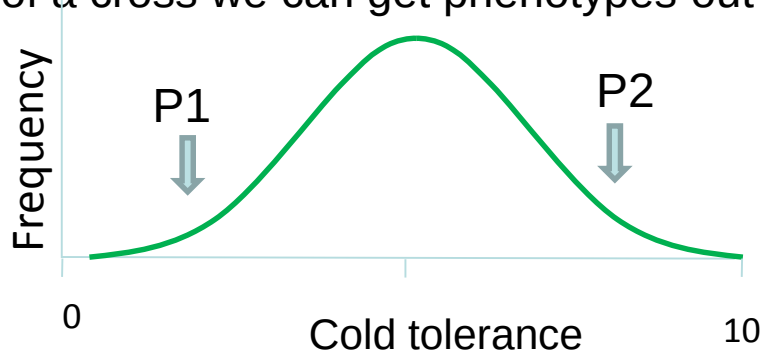
Then, the distribution of a quantitative trait would follow a normal distribution



Analysis of quantitative traits is therefore complicated:
Same genotype: 1 and 2 show different phenotype
Same phenotype: 1, 3 and 4 is the result of three different genotypes

Inheritance of Quantitative traits

The inheritance of quantitative traits also explains the phenomenon of transgressive segregation: In the progeny of a cross we can get phenotypes out of the range of the parents



Let's assume 5 loci with additive effects control the trait

P1 P2

aabbccddEE X AABBCCDDee

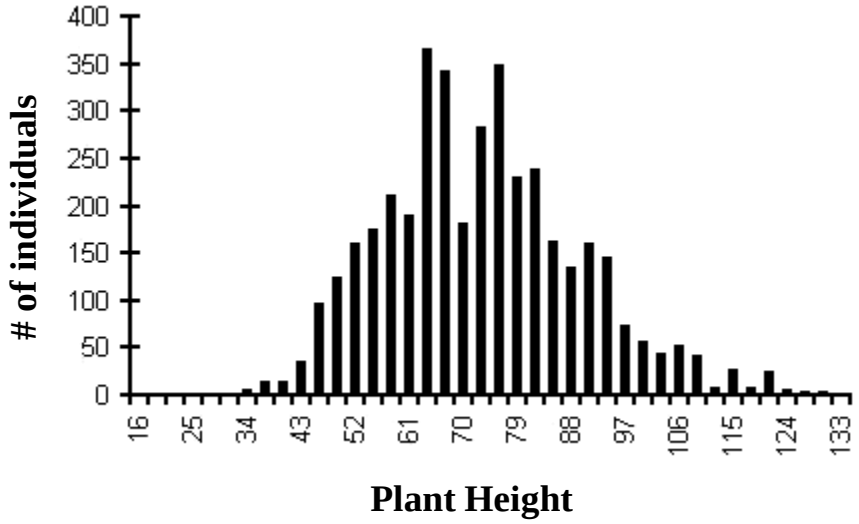
F1 AaBbCcDdEe

F2 All possible combinations of alleles at 5 loci.

Between them: AABBCCDDEE (all favorable alleles)

aabbccddee (all unfavorable alleles)

How can we quantify genetic variation?

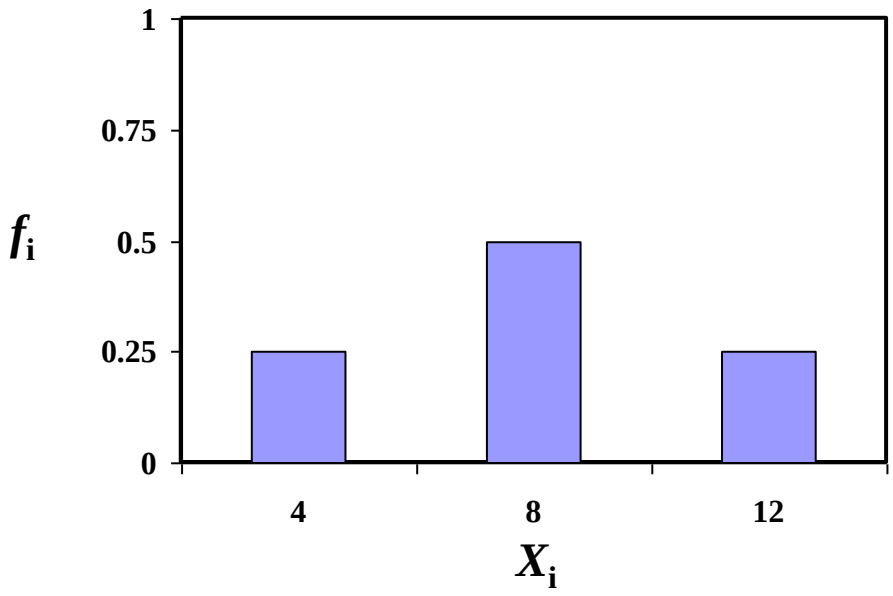


How can be describe genetic variation?

Statistical methods – Based on changes in phenotypic variance

Some basic statistics: The mean

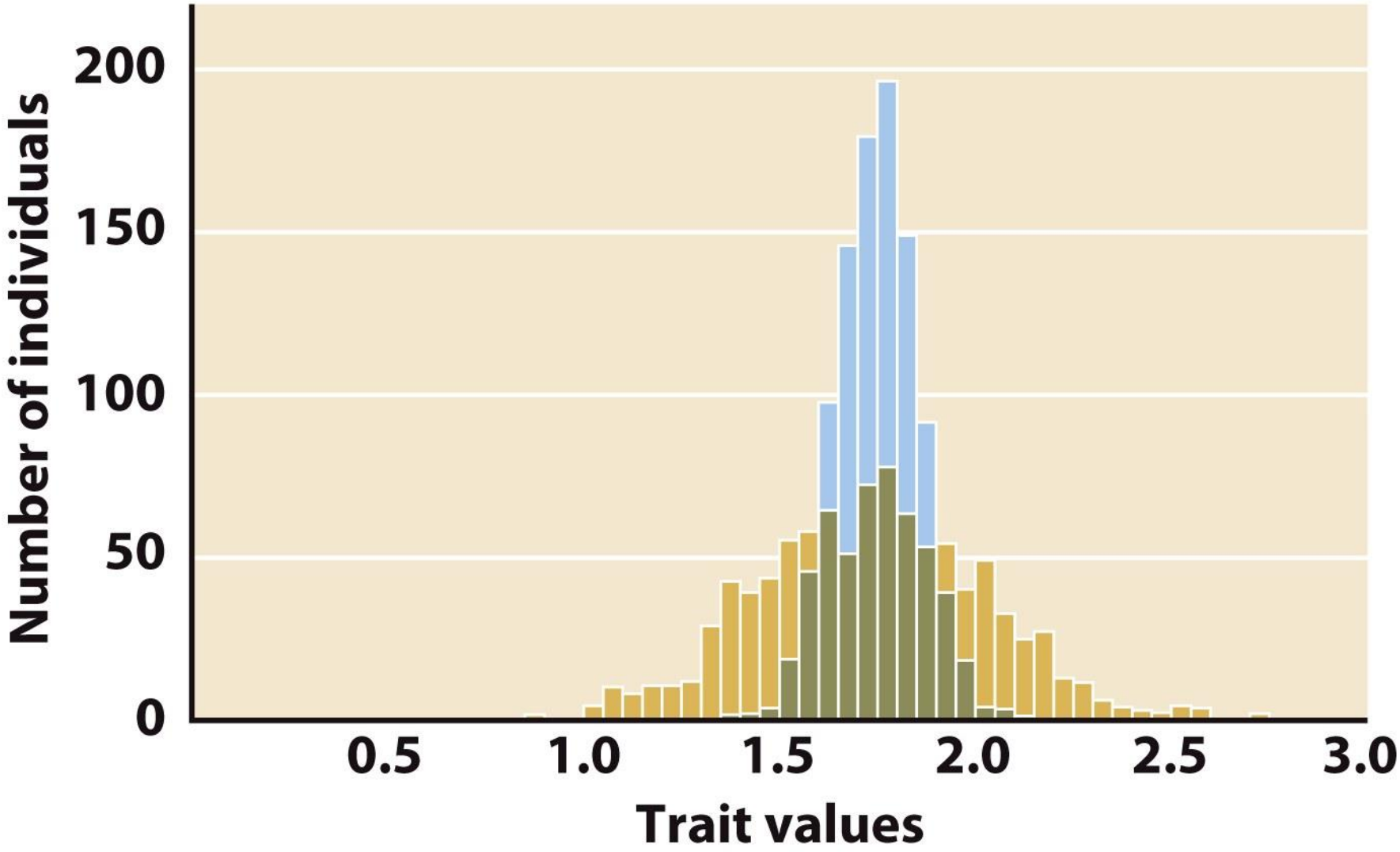
$$\bar{x} = \sum_{i=1}^{n} f_i X_i$$



$$\bar{x} = .25(4) + .5(8) + .25(12) = 8$$

Where *n* is the number of different phenotype classes

Basic statistics: The variance



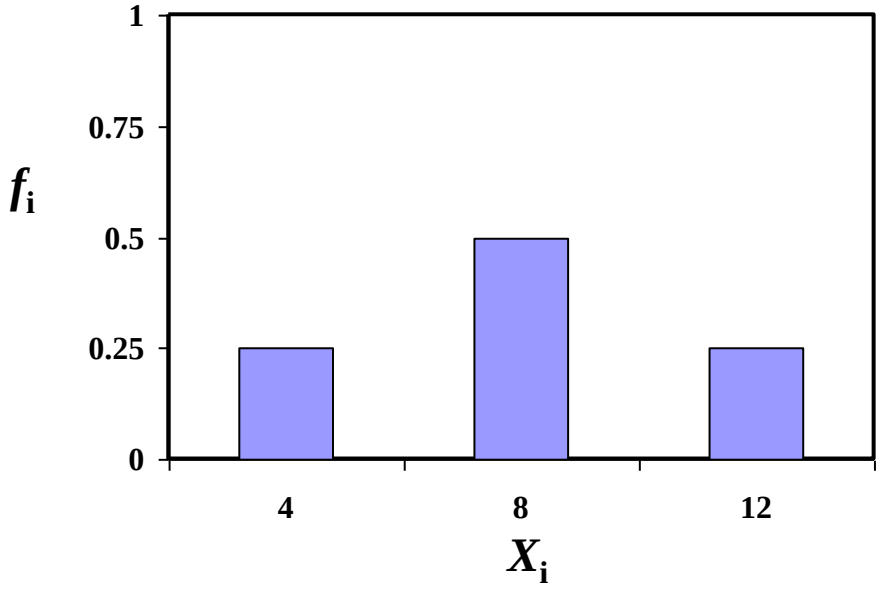
Evolution, 1/e Figure 9.33a

Basic statistics: The variance

(measures the amount of variation)

$$V = \sum_{i=1}^{n} f_i (X_i - \bar{x})^2$$

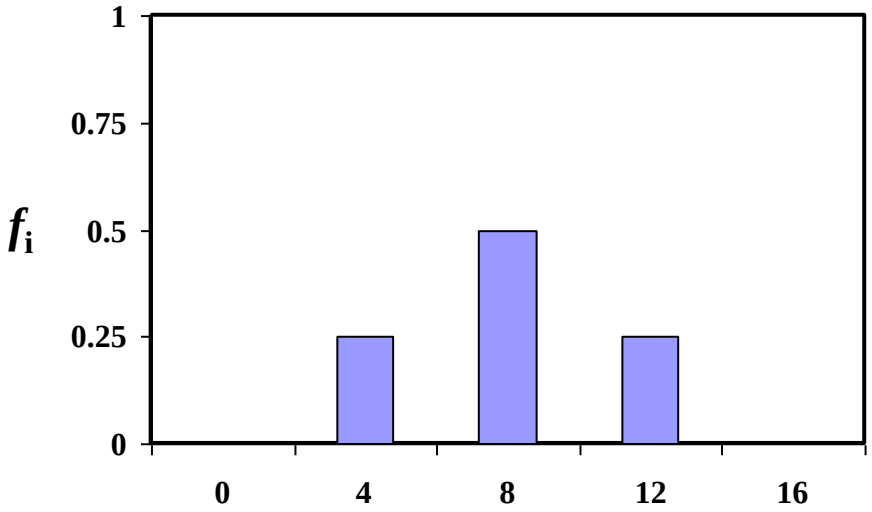
The average of the *squared* differences from the Mean



$$V = .25(4-8)^2 + .5(8-8)^2 + .25(12-8)^2 = 8$$

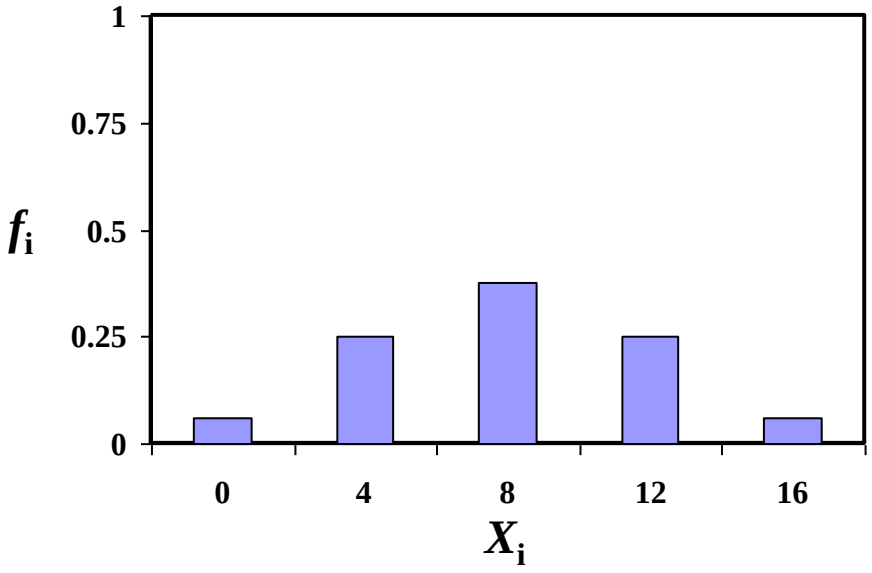
Where *n* is the number of different phenotype classes

Basic statistics: The variance



Population with variance = 8

$$V = 0(0-8)^2 + .25(4-8)^2 + .5(8-8)^2 + .25(12-8)^2 + 0(16-8)^2 = 8$$



Population with variance = 16

$$V = .0625(0-8)^2 + .25(4-8)^2 + .375(8-8)^2 + .25(12-8)^2 + .0625(16-8)^2 = 16$$

USEFUL PARAMETERS FOR QUANTITATIVE GENETICS

- **Mean:** The sum of all measurements divided by the number of measurements

$$\bar{x} = \frac{x_1 + x_2 + \ldots + x_n}{N} = \frac{1}{N}\sum x_i$$

- **Variance:** The average squared deviation of the observations from the mean

$$Variance = \frac{(x_1 - \bar{x})^2 + (x_2 - \bar{x})^2 + \cdots + (x_n - \bar{x})^2}{N} = \frac{1}{N}\sum (x_i - \bar{x})^2$$

COMPONENTS OF PHENOTYPIC VARIATION

$$V_P = V_G + V_E$$

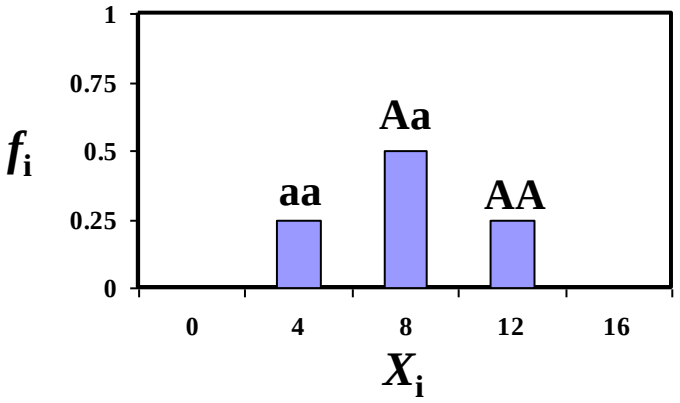
- The total *phenotypic* variance for a character (V_P) is a function of:
- **Genetic variance** (V_G)– the variance among the mean phenotypes of different genotypes
- **Environmental variance** (V_E)– the variance among phenotypes expressed by replicate members of the same genotype

- Differences between monozygotic twins are due to environmental factors.

Using basic statistics to decompose phenotypic variation

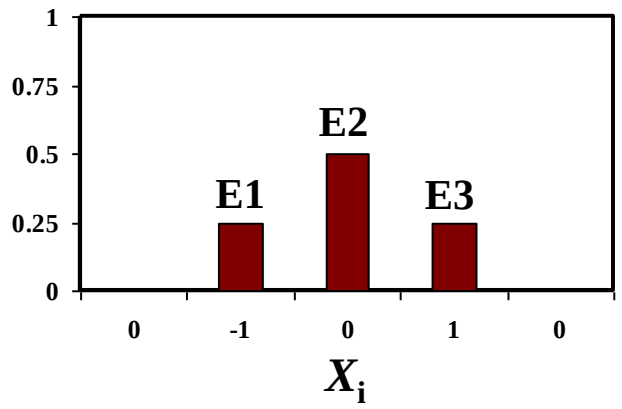
$$V_P = V_G + V_E$$

Genetic Variance

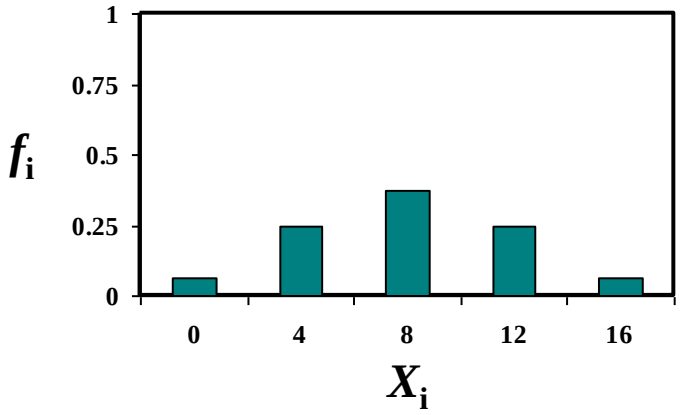


+

Environmental Variance



Phenotypic Variance



COMPONENTS OF GENETIC VARIATION

$$V_G = V_A + V_D + V_I$$

- The total *genetic* variance for a character (V_G) is a function of:

- **Additive genetic variance** (V_A) – variation due to the additive effects of alleles

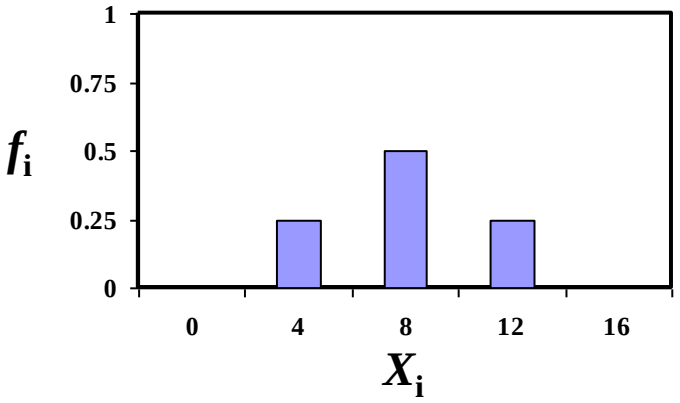
- **Dominance genetic variation** (V_D) – variation due to dominance relationships among alleles

- **Epistatic genetic variation** (V_I) – variation due to interactions among loci

Genetic variation can be further decomposed

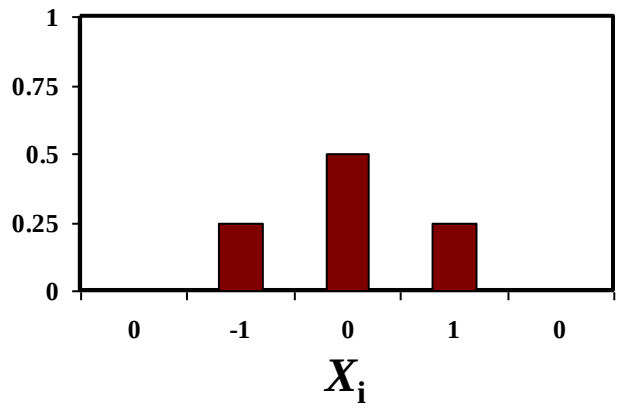
$$V_G = V_A + V_I + V_D$$

Additive Genetic Variance

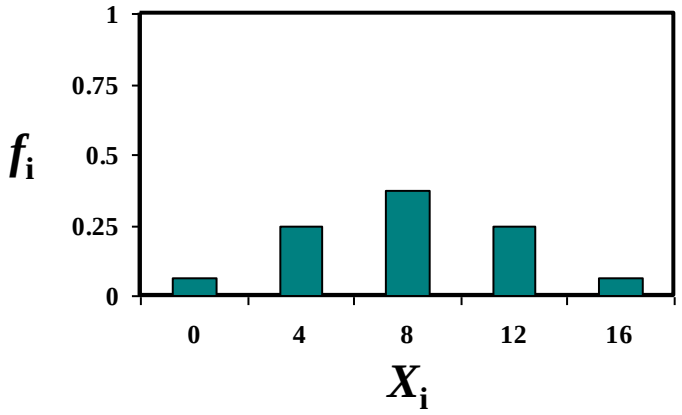


+

Epistasis and Dominance Variance



Genotypic Variance



What is the source of each component of genetic variance?

Additive genetic variance (V_A) – Due to the additive effects of alleles

Genotype	Phenotype
AA	2
Aa	1
aa	0

Dominance variance (V_D) – Due to dominance

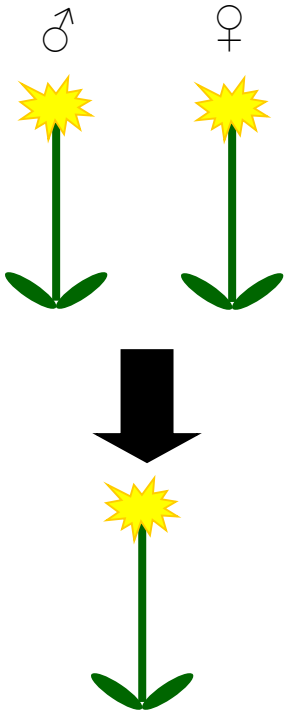
Genotype	Phenotype
AA	2
Aa	1
aa	2

Interaction variance (V_I) – Due to epistasis

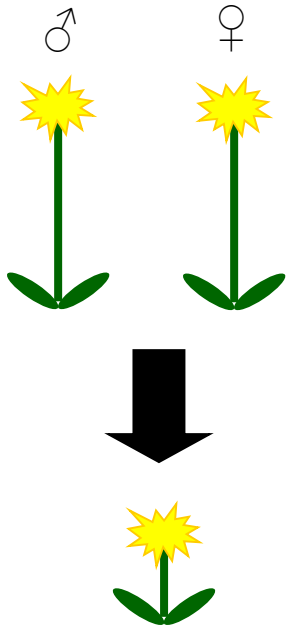
Genotype	Phenotype
AA (BB)	2
AA (Bb)	1
AA (bb)	2

It is additive genetic variance that determines the resemblance of parents and offspring

Additvity



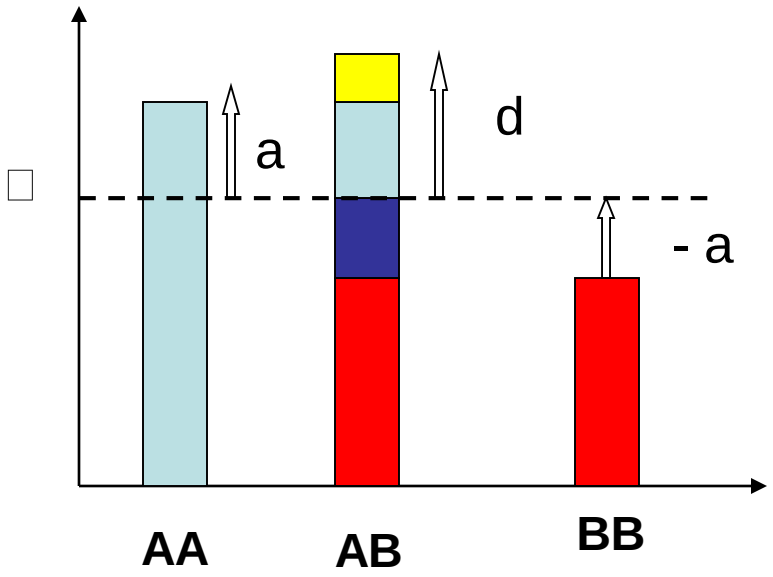
Epistasis or Dominance



Offspring need not look like parents!

How do we know how much additive genetic variation exists within a population?

Dominance effects



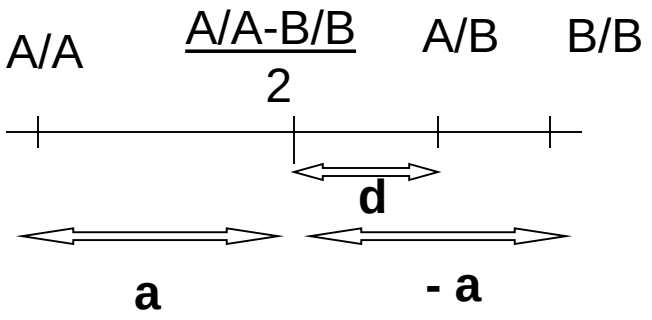
recessive

intermediate

dominant

overdominant

(modified after Tanksley 1993)



Degree of dominance d/a

>1	overdominant
=1	dominant
0<d/a<1	partially dominant
= 0	additive
= -1	recessive

DOMINANCE VERSUS ADDITIVE GENETIC VARIANCE

- Dominance variance is due to dominance deviations, which describe the extent to which heterozygotes are not exactly intermediate between the homozygotes.
- The additive genetic variance is responsible for the resemblance between parents and offspring.
- The additive genetic variance is the basis for the response to selection.

THE COMPONENTS OF PHENOTYPIC VARIANCE

$$V_P = V_A + V_D + V_I + V_E + V_{GxE}$$

V_A = additive genetic variance, V_D = dominance variance,

V_I = epistatic variance, V_E = environmental variance.

V_{GxE} = Genotype by environment interaction. If the same genotype results in a different phenotype in different environments, then this phenomenon will contribute to the phenotypic variance.

HERITABILITY

- The **heritability** (h^2) of a trait is a measure of the degree of resemblance between relatives.

$$h^2 = V_G / V_P = V_G / (V_G + V_E)$$

- Since heritability is a function of the environment (V_E), it is a *context dependent* measure.

It is influenced by both,

- The environment that organisms are raised in, and
- The environment that they are measured in.

Variation introduced due to genetic differences

Heritability

$$H^2 = \frac{\text{genetic variance}}{\text{genetic variance} + \text{environmental variance}}$$

$0 > H^2 > 1$

The variation of the trait is not “driven” by genetics

The variation of the trait is fully “driven” by genetics

The proportion of phenotypic variation that is genetic can be estimated by calculating "heritability"

- **Broad sense heritability – Measures the proportion of phenotypic variation that is genetic**

$$h_B^2 = V_G / (V_G + V_E) = V_G / V_P$$

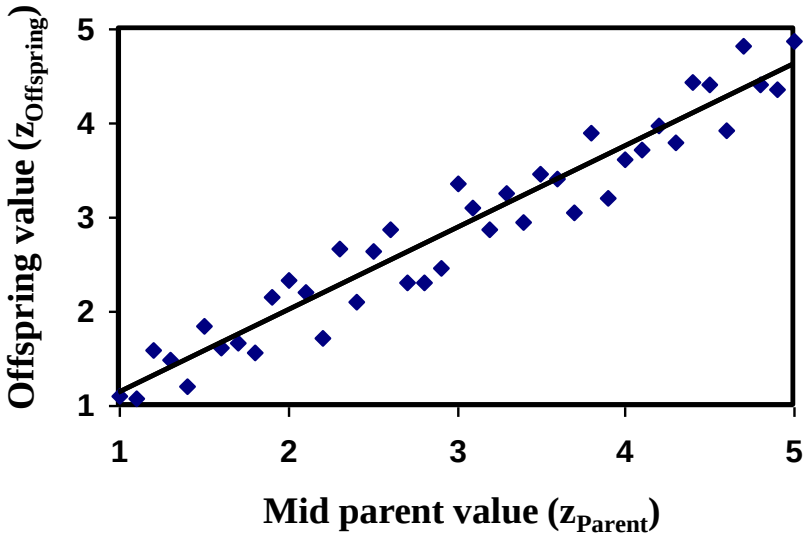
- **Narrow sense heritability – Measures the proportion of phenotypic variation attributable to the additive action of genes.**

$$h_N^2 = V_A / (V_A + V_I + V_D + V_E)$$

How can we measure narrow sense heritability?

One possibility is a parent-offspring regression

- **The heritability is estimated by the slope of the linear regression**

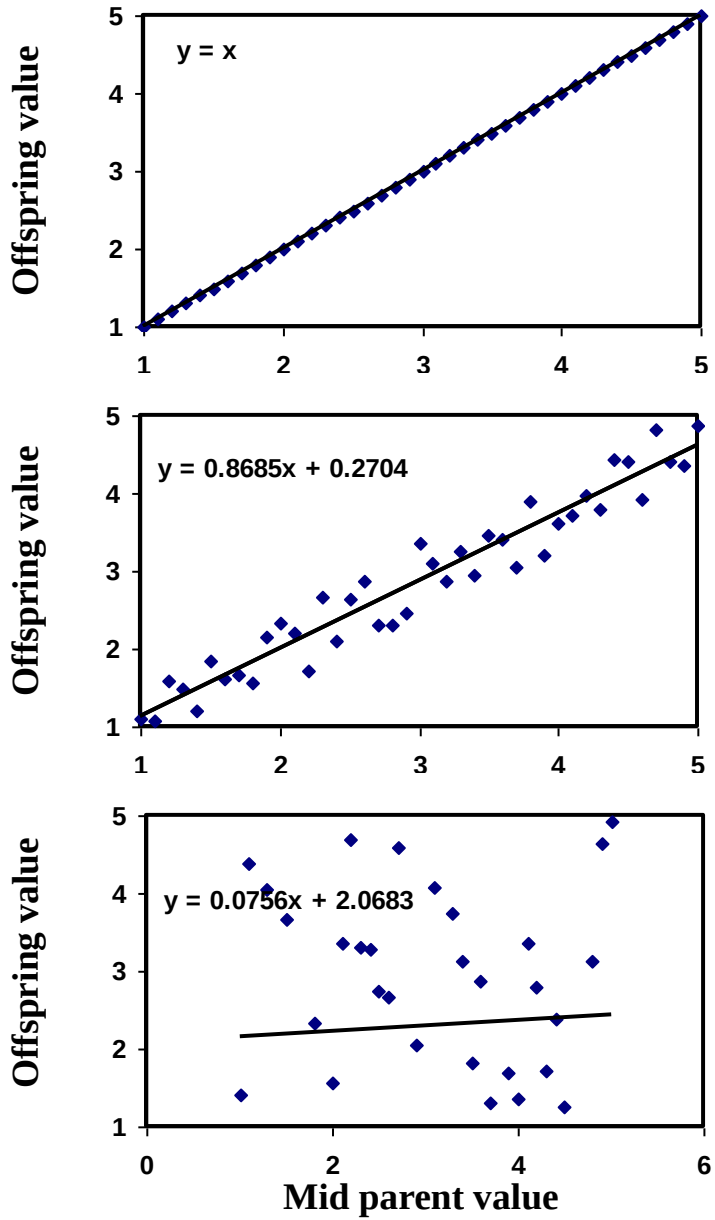


$$h^2 = \frac{Cov[z_{Parent}, z_{Offspring}]}{V[z_{Parent}]}$$

Where

$$Cov[z_{Parent}, z_{Offspring}] = \frac{\sum_{i=1}^{n}\left(z_{Parent,i} - \bar{z}_{Parent}\right)\left(z_{Offspring,i} - \bar{z}_{Offspring}\right)}{n}$$

One possibility is a parent-offspring regression



Perfectly heritable **– Slope is 1.0**

High heritability **– Slope is 0.8685**

Low heritability **– Slope is 0.0756**

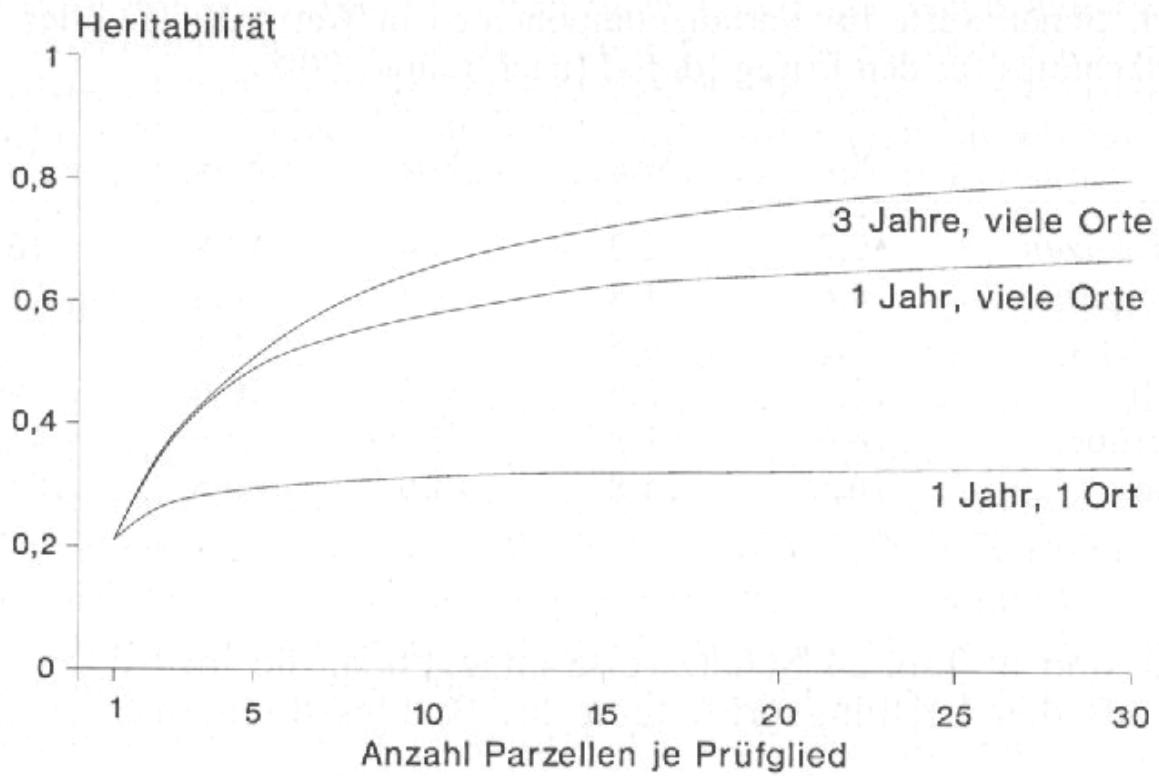
What determines heritability of a trait?

- Genetic architecture of a trait: mono-, oligo-, polygenic
- Environmental variation of a trait

Is heritability of a given trait in a given population fix?

$\mathbf{h^2_{(b.s.)} = V_G / V_P} = V_G / (V_G + V_{GE})$ Selection in 1 environment

$\mathbf{h^2 = V_G / V_P} = V_G / (V_G + V_{GE} /n)$ Selection in n environments



Becker (1993): Heritabilität of seed yield dependent of replication, year, and location

Inheritance of Quantitative traits

$$h^2 = \frac{V_G}{V_P}$$

A heritability of 40% for cold tolerance means that within that population, genetic differences among individuals are responsible of 40% of the variation.

Therefore, 60% is due to environmental causes.

However, that does not mean that the cold tolerance of a certain individual is due 40% to genetic causes and 60% to environmental causes.

h^2 is a property of the population and not of individuals

THE UNIVARIATE BREEDERS' EQUATION:

$$R = h^2 S$$

Response to Selection

Selection differential

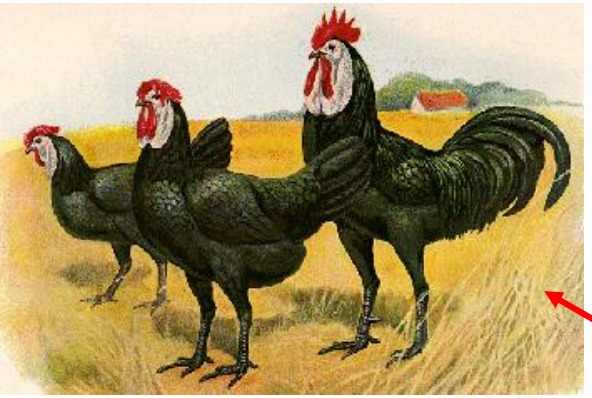
Heritability

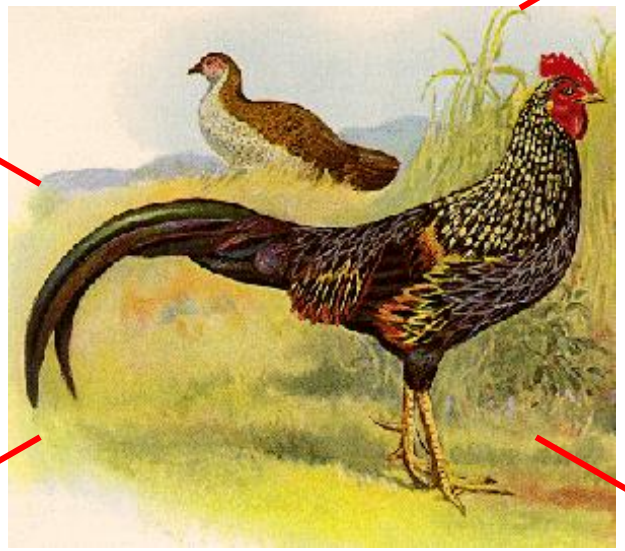
Where:

$$h^2 = \frac{V_A}{V_P}$$

(V_A: Additive Genetic Variance)

(V_P: Phenotypic Variance)





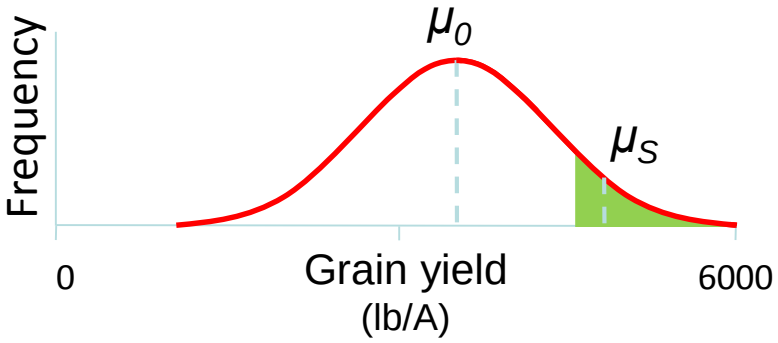
Inheritance of Quantitative traits

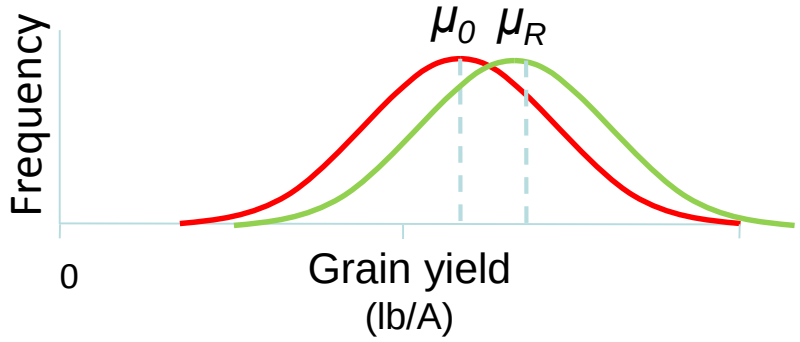
Heritability h^2 measures the proportion of phenotypic variation (variance) that is due to genetic causes

$$P = G + E; \qquad V_P = V_G + V_E \qquad h^2 = \frac{V_G}{V_P}$$

h^2 is very useful because it allows us to predict the response to artificial selection

In plant breeding, the starting point is a segregating population (with genetic variability). The best individuals are selected to be the progenitors of the next generation





Selection differential (S) = $\mu_S - \mu_0$

Response to selection (R) = $\mu_R - \mu_0$

Realized heritability:

$$h^2 = \frac{R}{S}$$

Is the ratio of the single-generation progress of selection to the selection differential of the parents. The higher h^2, the higher the progress of selection in each generation

COMPONENTS OF GENETIC VARIATION

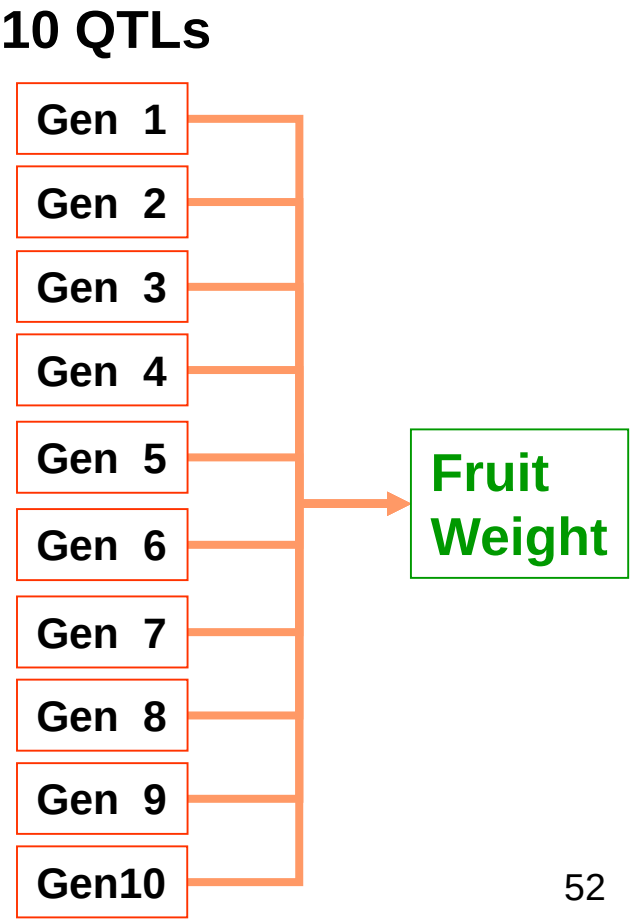
$$V_G = V_{L1} + V_{L2} + V_{L3} + \ldots.$$

- The total *genetic* variance for a character (V_G) is composed of the variance effects of all loci that contribute to the expression of a particular trait

A QTL *(Quantitative Trait Locus)* is a locus in the genome that together with other loci controls a quantitative trait

L. esculentum
< 1.000 g

L. pimpinellifolium
< 1 g



Frary et al. (2000)

Analysis of Quantitative traits

There are two main approaches for QTL analysis:

a) QTL analysis in mapping populations

b) Association mapping

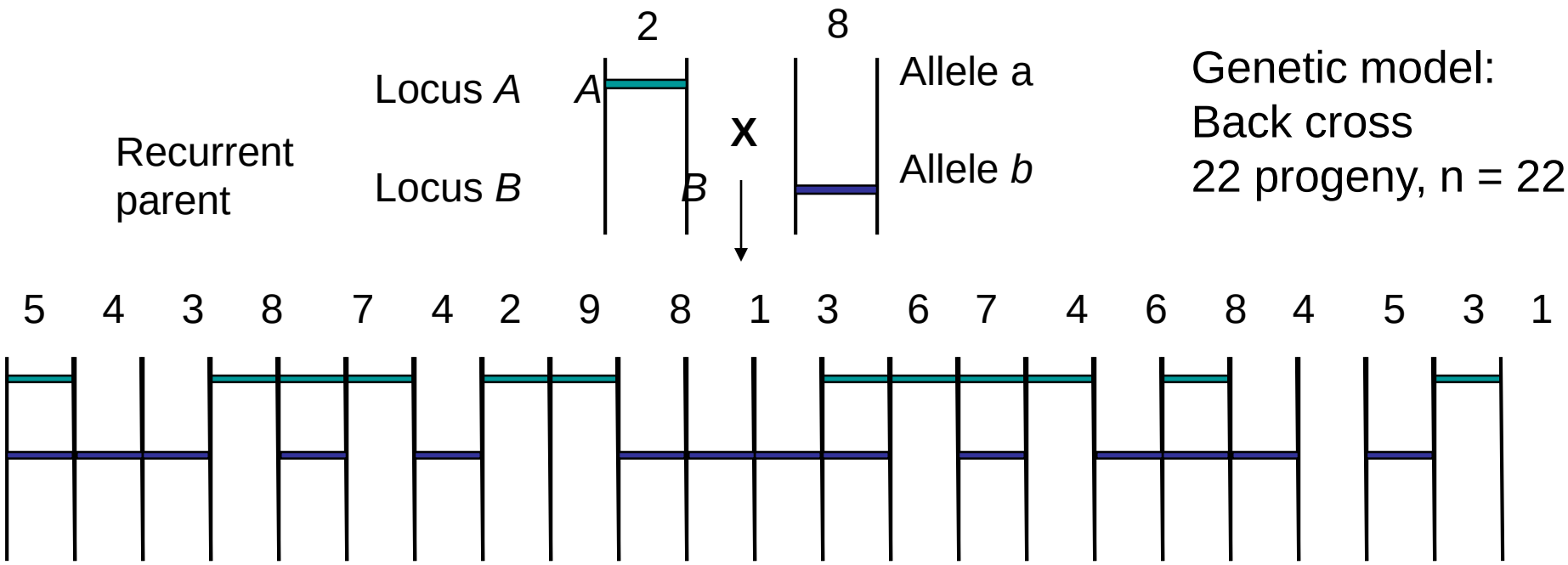
Both approaches share a set of common elements:

a) A population (array of individuals) that show variability for the trait of study
b) Phenotypic information: We need to design an experiment to estimate the phenotypic value of each individual
c) Genotypic information: A set of molecular markers that have been run in all the individuals of the population
d) A statistical method to estimate QTL position, effects and interactions

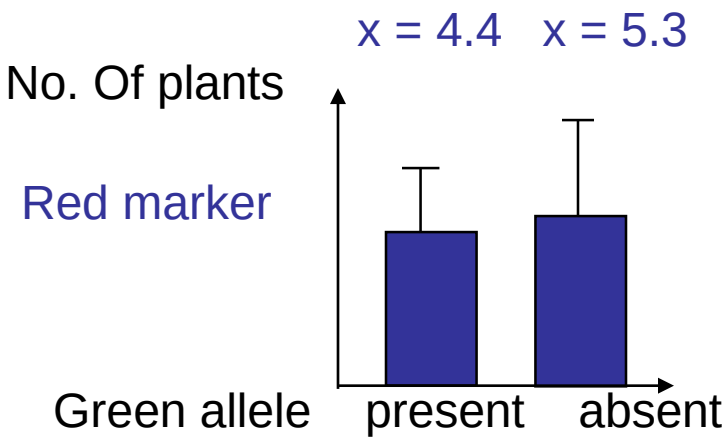
Analysis of Quantitative traits

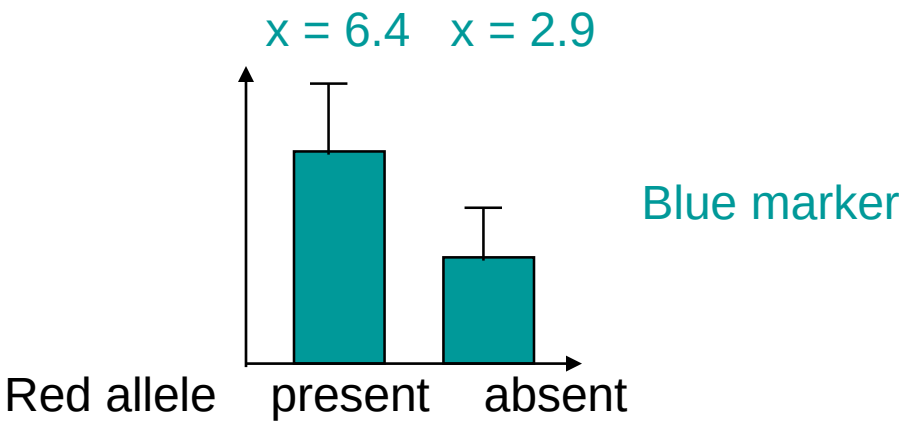
The basic QTL analysis method consists in walking trough the chromosomes performing statistical test at the positions of the markers in order to test whether there is a marker-trait association or not

Genetic linkage between DNA-based markers and a quantitative trait

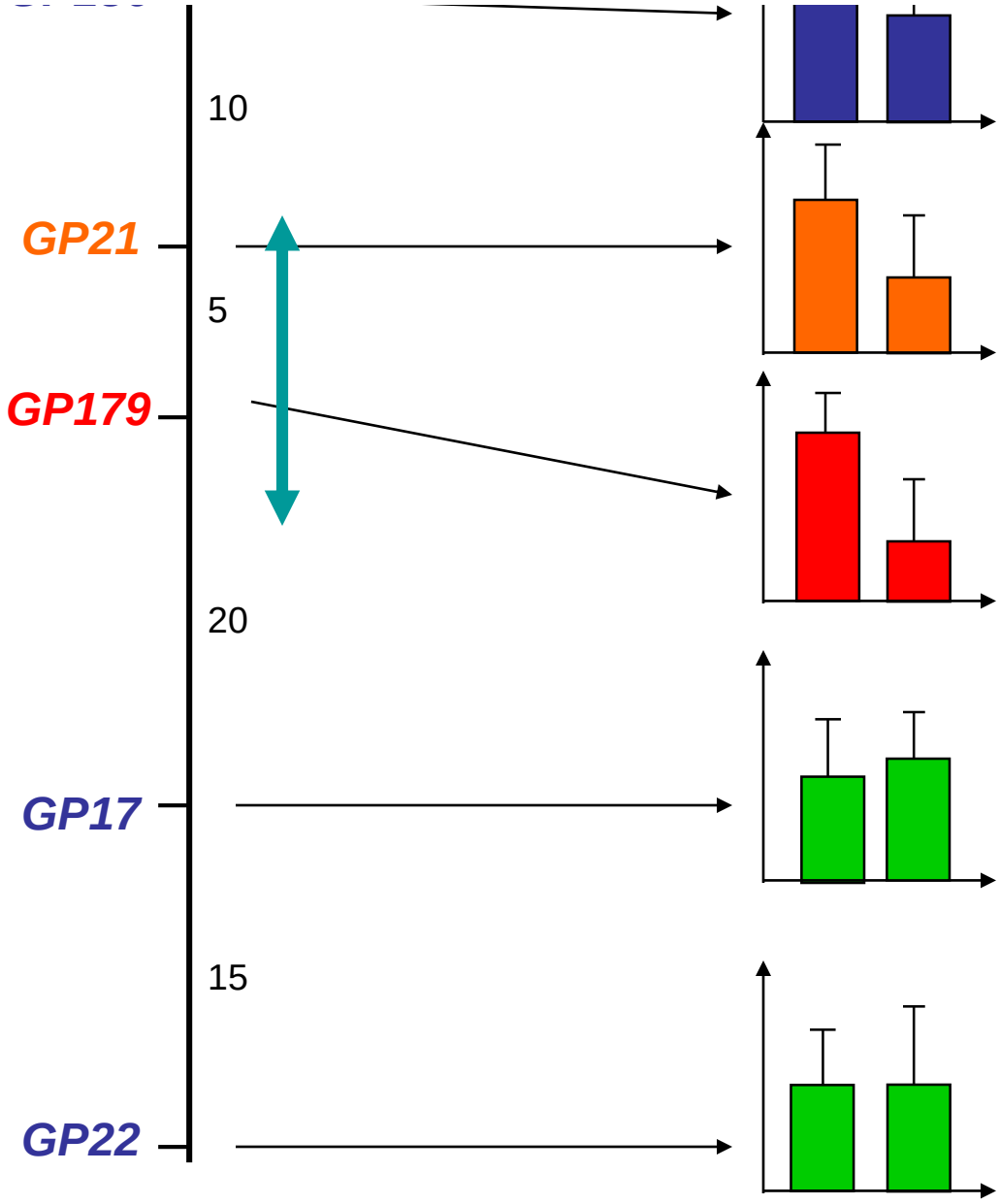


Phenotypic values: scores from 1 to 9: 1 = very susceptible, 9 = highly resistant



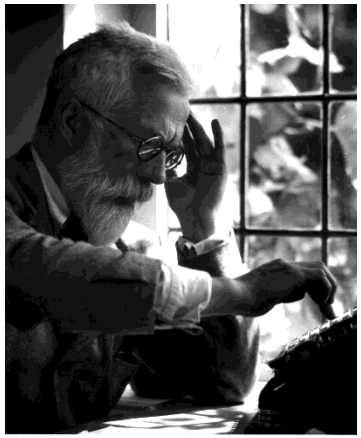


Test: ist der Mittelwert aller Linien mit Elternallel a unterschiedlich vom Mittelwert aller Linien mit Elternallel b am Markerlocus x



QTL =
Quantitative Trait Locus

Definitions



Remember: RA Fischer, 1919- Evolutionary Biology

- ANOVA: analysis of variation or of a statistical variance in order to determine the contributions of given factors or variables to the variance.
- Remember: Variance: the square of the standard deviation

One-Way ANOVA- x-factorial ANOVA

- One factor (manipulated variable) – several factors
- One response variable
- Two or more groups to compare per factor

For instance, ANOVA Could be Used to:

- Compare biomass of different genotypes measured in different environments or experiments

- Quantify the contribution of genetic and environmental (experimental) variation to total phenotypic variation.

$$Y = G + E + G+E$$

How ANOVA works (outline)

ANOVA measures two sources of variation in the data and compares their relative sizes

- variation BETWEEN groups
  - for each data value look at the difference between its group mean and the overall mean

$$\left(\overline{x}_i - \overline{x}\right)^2$$

- variation WITHIN groups
  - for each data value we look at the difference between that value and the mean of its group

$$\left(x_{ij} - \overline{x}_i\right)^2$$

How ANOVA works (outline)

The ANOVA F-statistic is a ratio of the Between Group Variaton divided by the Within Group Variation:

$$F = \frac{Between}{Within} = \frac{MSG}{MSE}$$

A large F is evidence *against* H_0, since it indicates that there is more difference between groups than within groups.

Usefulness

- Similar to t-test
- More versatile than t-test
- Compare one parameter (response variable) between two or more groups

Why Not Just Use t-tests?

- Tedious when many groups are present
- Using all data increases stability
- Large number of comparisons→ some may appear significant by chance

Notation

- k = # of groups
- n = # observations in each group
- x_{ij} = one observation in group i
- $\bar{\bar{x}}$ = mean over all groups
- $\bar{x}_i$ = mean for group i
- SS = Sum of Squares
- MS = Mean of Squares
- λ = Between MS/Within MS

FYI this is how SS Values are calculated

- Total SS $= \sum_{i=1}^{k} \sum_{j=1}^{ni} (x_{ij} - \bar{x})^2 = SS_{tot}$

- Within SS $= \sum_{i=1}^{k} \sum_{j=1}^{ni} (x_{ij} - \bar{x}_i)^2 = SS_w$

- Between SS $= \sum_{i=1}^{k} \sum_{j=1}^{ni} (\bar{x}_i - \bar{x})^2 = SS_{bet}$

$SS_{tot} = SS_w + SS_{bet}$

Calculating MS Values

- MS = SS/df
- For between groups, df = k-1
- For within groups, df= n-k

F-Ratio = MS_{Bet}/MS_w

- If:
  - The ratio of Between-Groups MS: Within-Groups MS is LARGE→ reject H_0→ there *is* a difference between groups
  - The ratio of Between-Groups MS: Within-Groups MS is SMALL→do not reject H_0→ there is *no* difference between groups

$$Y = G + E + G*E + e$$

F-Ratio = MSg/MSe

What ANOVA Cannot Do

- Tell which groups are different
  - Post-hoc test of mean differences required
- Compare multiple parameters for multiple groups (so it cannot be used for multiple response variables)

R^2 Statistic

R^2 gives the percent of variance due to between group variation

$$R^2 = \frac{SS[Between]}{SS[Total]} = \frac{SSG}{SST}$$

Genotype Environment Interaction in *Potentilla* (Clausen et al. 1940)

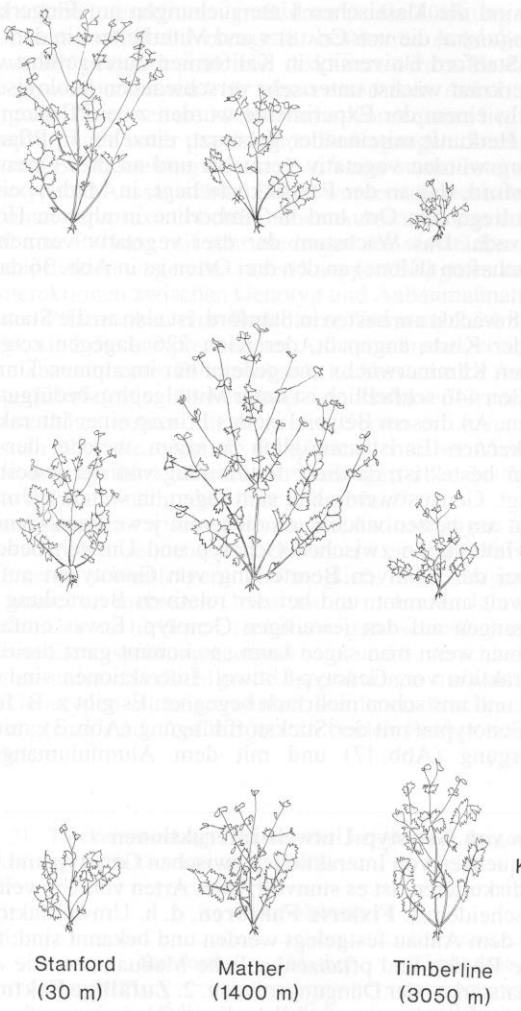


Abb. 36. Genotyp-Umwelt-Interaktionen bei *Potentilla* (modifiziert nach CLAUSEN et al. 1940).

Heritability and Variance

What is the contribution of genetic and environmental variance to the total phenotypic variance?

What is the extent of genotype x environment interactions?

What is the heritability of a trait, how to calculate it?

What is the contribution of a marker locus to the variation of a trait- single marker QTL analysis?

Calculation of Variance components: effects of genotype and environment on biomass of potentilla

Means

Genotype	locations			Genotypic mean
	Stanfort	Mather	Timberline	
468	5.9	3.6	0.4	
446	5.5	9.5	2.7	
226	0.6	2.8	3.2	
Location mean				

Genotype environment interaction

Genotype	locations			Genotypic mean
	Stanfort	Mather	Timberline	
468				
446				
226				
Location mean				

Variance analysis

Variance factor	DF	SQ	MQ	Variance component
Genotype	g-1			
Location	l-1			
G*L	(g-1)*(l-1)			
Total	n-1			

Estimation of variance components

1) ***GO-Interaktion:*** $I = x_{ij} + \bar{x}_{ij} - \bar{x}_{i.} - \bar{x}_{.j}$

individual value: x_{ij}

total mean: $\bar{x}_{ij} = \sum_{i=1}^{g} \sum_{j=1}^{o} x_{ij} / n$

genotypic mean: $\bar{x}_{i.} = \sum_{j=1}^{o} x_{ij} / g$

environmental mean: $\bar{x}_{.j} = \sum_{i=1}^{g} x_{ij} / e$

***) g = number of genotypes, e = number of environments, n = g x e**

factor	DF
Genotype	g-1
Environment	e-1
GE	(g-1) (e-1)

Calculation of variance = mean square (MQ):

MQ = SQ/ DF

sums of squares (SQ):

$SQ = \Sigma x^2 - [(\Sigma x)^2 / n] = \Sigma(x - \bar{x})^2$

$SQ_{Total} = \Sigma x_{ij}^2 - [(\Sigma x_{ij})^2 / n]$

$SQ_{Geno} = [(\Sigma x_{i.}^2) / g] - [(\Sigma x_{ij})^2 / n]$

$SQ_E = [(\Sigma x_{.j}^2) / e] - [(\Sigma x_{ij})^2 / n]$

$SQ_{Ge} = SQ_{Total} - SQ_{Geno} - SQ_E$

$MQ = SQ / DF$

$MQ_{Geno} = SQ_{Geno} / (g-1)$

$MQ_E = SQ_E / (e-1)$

$MQ_{GE} = SQ_{GE} / [(g-1)(e-1)]$

$V_{Geno} = (MQ_{Geno} - MQ_{GE}) / e$

$V_E = (MQ_E - MQ_{GE}) / g$

$V_{GE} = MQ_{GE}$

Genotype Environment Interaction in *Potentilla* (Clausen et al. 1940)

Tab. 21. Trockenmasse (g/Pflanze) der in Abb. 36 dargestellten Pflanzen (modifiziert nach CLAUSEN et al. 1940).

Klon	Anbauort			Klonmittel
	Stanford	Mather	Timberline	
468	5,9	3,6	0,4	3,3
446	5,5	9,5	2,7	5,9
226	0,6	2,8	3,2	2,2
Ortsmittel	4,0	5,3	2,1	3,8

Tab. 22. Genotyp-Umwelt-Interaktionen, errechnet aus den Daten in Tab. 21.

Klon	Anbauort			Mittel
	Stanford	Mather	Timberline	
468	2,4	−1,2	−1,2	0
446	−0,6	2,1	−1,5	0
226	−1,8	−0,9	2,7	0
Mittel	0	0	0	0

Tab. 23. Varianzanalyse der Werte aus Tab. 21.

Varianzursache	FG	SQ	MQ	Varianzkomponente
Klon	2	21,66	10,83	$V_G = 1,36$
Ort	2	15,54	7,77	$V_E = 0,34$
Klon × Ort	4	27,00	6,75	$V_{GE} = 6,75$

Becker, 1993

Heritability

Phenotypic value

$P = G + E + GE$

G = Genotypic Value
E = Environment
GE = Interaction between genotype and environment

Phenotypic variance

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

Broad sense heritability

$\mathbf{h^2 = V_G / V_P} = V_G / (V_G + VE + V_{GE})$ Selection 1 environment

$\mathbf{h^2_{(b.S.)} = V_G / V_P} = V_G / (V_G + VE + V_{GE} / n)$ Selection n environments

For the calculation of h^2 only variance components with the factor genotype are considered ($V_G + V_{GE}$).

Example Potentilla:

$h^2 = 1{,}36 / (1{,}36 + 6{,}75) = 0{,}17$ Selection 1 environment
$h^2 = 1{,}36 / (1{,}36 + 6{,}75 / 3) = 0{,}38$ Selection 3 environments

Calculations

$Sq_{total} = 5.9^2 + 3.6^2+0.4^2 +....-(5.9+3.6+0.4+...)^2/9$

$= 194.16 - 1169.64/9$

$= 64.2$

$SQ_G = ((5.9+3.6+0.4)^2 +(5.5+9.5+2.7)^2 +(0.6+2.8+3.2)^2)/3-(5.9+3.6+0.4+...)^2/9$

$= (98.01+313.29+43.56)/3 – 1169.64/9$

$= 21.66$

$SQ_E = ((5.9+5.5+0.6)^2 +(3.6+9.5+2.8)^2 +(0.4+2.7+3.2)^2)/3-(5.9+3.6+0.4+...)^2/9$

$= (144+249.64+39.69)/3 – 1169.64/9$

$= 15.54$

$SQ_{E*G} = 64.2-21.66 -15.54$

Decomposition of phenotypic variance

Example: Flowering time measured under short and long days in ca. 400 diverse genotypes

Genotype	Environment	Time to flowering	Marker 1	Marker 2
1	LD	55	1	2
2	LD	69	2	1
3	.....	45	1	2

Analyse for genetic and environmental variation (photoperiod) - ANOVA

Flowering time = G + E +G*E

Association analysis: are marker 1 or 2 associated with flowering time – ANOVA
Flowering time = E + M1+M2+E*M1+ E*M2 (+M1*M2)