

# Quantitative genetics

A close-up photograph of a dragonfly perched on a green plant stem. The dragonfly has a dark blue-black thorax and head, and a long, segmented red abdomen. Its wings are transparent with a fine, dark network of veins. The background is a soft, out-of-focus brown.

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## Outline

- 1 Inheritance of traits
- 2 Johanssen's pureline theory
- 3 Polygenes in discontinuous traits
- 4 Heritability (Brown, Caligari, and Campos 2014)
- 5 Numerical problems
- 6 Bibliography

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## Background

- The character may be simply inherited or complex inherited with effect of many genes at different loci, each contributing a small effect to phenotypic expression of the character
  - 1 Qualitative characters
  - 2 Quantitative characters
- Study of inheritance of most characters/phenotypes can be classified into:
  - 1 Easily distinguished into discrete classes
    - ▶ barley plants may be
      - ★ black or white hulled
      - ★ two or six rowed
      - ★ rough or smooth awned
      - ★ rust resistant or rust susceptible

2 Cannot be easily classified into discrete classes - for grain yield  $kg\ ha^{-1}$

- ▶ thousand grain weight (gram),
- ▶ plant height (cm) variation may be differing by small units

## Quantitative inheritance

- Most of the important variation displayed by nearly all plant traits affecting growth, development and reproduction, is quantitative.
- Also called: *Continuous, Polygenic variation, Multiple gene controlled traits*
- Demonstrate same basic Mendelian properties for a gene, and also the Hardy-Weinberg equilibrium.
- Quantitative characters are governed by several genes; each gene has a small effect, which is usually cumulative.
- The environments considerably affect these characters.
- Quantitative characters often show continuous variation with normal distribution

## Qualitative inheritance

- Mendel purposed the law of inheritance based on his studies with qualitative characters.
- In the studies of qualitative inheritance, we study phenomena such as:
  - 1 Dominance,
  - 2 Segregation and independent assortment,
  - 3 Gene action and interactions (Epistasis, Masking gene action, Duplicate gene action, Complementary gene action, Additive gene action, Inhibiting gene action, Modifying gene action and Pleiotropy).
  - 4 Penetrance and expressivity
  - 5 Linkage

# Difference

**Table 1:** Difference between qualitative and quantitative traits

Character	Qualitative	Quantitative
Number of gene and loci controlling the character	Few, one (mongenic) or few major genes (oligogenic)	Many, polygenes (polygeneic)
Effect of individual gene	Large	Small
Follow mendel's law	Yes	Yes
Classification on few discrete classes that are easily distinguished	Yes	No
Measurement of the character	Observation	Measured in metric units
Frequency distribution	Discrete	Continuous and often normal
Effect of environment on expression of character	No or little affected	Largely affected
Examples	Disease resistance, Presence of awns, Seed color	Grain yield (kg/ha), Thousand kernel weight (gram)

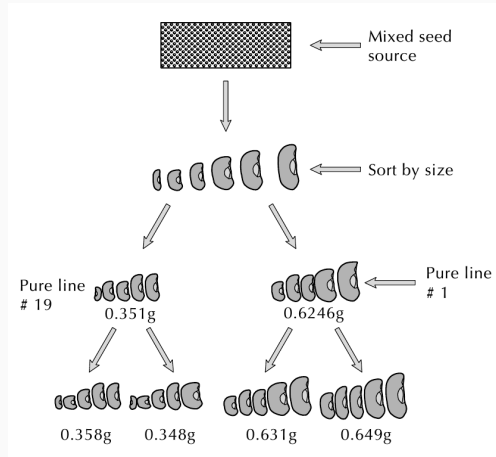


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## Pureline theory

- Johanssen demonstrated that a mixed population of self-pollinated species could be sorted out into genetically pure lines.
- These lines were subsequently non-responsive to selection within each of them.
- Lines that are genetically different may be successfully isolated from within a population of mixed genetic types.
- Any variation that occurs within a pure line is not heritable but due to environmental factors only. Consequently, as Johansen's bean study showed, further selection within the line is not effective.



**Figure 1:** Johanssen's observation of Phaseolus bean shed light on Pureline theory

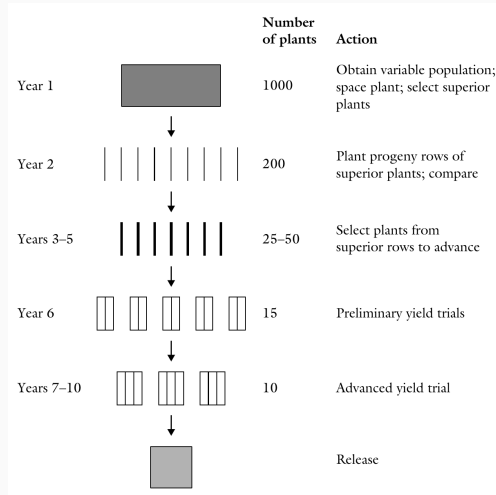
- Lines are used
  - ▶ as cultivars or as parents in hybrid production (inbred lines).
  - ▶ in the development of genetic stock (containing specific genes such as disease resistance, nutritional quality) and synthetic and multiline cultivars.
- Line cultivars have a very narrow genetic base and tend to be uniform in traits of interest (e.g., height, maturity).

## Application

- Cultivars for mechanized production that must meet a certain specification for uniform operation by farm machines (e.g., uniform maturity, uniform height for uniform location of economic part).
- Cultivars developed for a discriminating market that puts a premium on eye-appeal (e.g., uniform shape, size).
- Cultivars for the processing market (e.g., with demand for certain canning qualities, texture).
- Advancing "sports" that appear in a population (e.g., a mutant flower for ornamental use).
- Improving newly domesticated crops that have some variability.
- The pure-line selection method is also an integral part of other breeding methods such as the pedigree selection and bulk population selection.

## Overview

- The pure-line selection in breeding entails repeated cycles of selfing following the initial selection from a mixture of homozygous lines.
- Natural populations of self-pollinated species consist of mixtures of homozygous lines with transient heterozygosity originating from mutations and outcrossing.
- Steps:
  - ▶ Year 1: The first step is to obtain a variable base population (e.g., introductions, segregating populations from crosses, land race) and space plant it in the first year, select, and harvest desirable individuals.
  - ▶ Year 2: Grow progeny rows of selected plants. Rogue out any variants. Harvest selected progenies individually. These are experimental strains.
  - ▶ Year 3-6: Conduct preliminary yield trials of the experimental strains including appropriate check cultivars.
  - ▶ Year 7-10: Conduct advanced yield trials at multilocations. Release highest yielding line as new cultivar.



**Figure 2:** Generalized steps in breeding by pure-line selection

## Genetic issues

- Pure-line breeding produces cultivars with a narrow genetic base and, hence, that are less likely to produce stable yields over a wider range of environments. Such cultivars are more prone to being wiped out by pathogenic outbreaks.
- Pure-line cultivars depend primarily on phenotypic plasticity for production response and stability across environments.



## Advantages

- It is a rapid breeding method.
- The method is inexpensive to conduct. The base population can be a landrace. The population size selected is variable and can be small or large, depending on the objective.
- The cultivar developed by this method has great “eye appeal” (because of the high uniformity of, e.g., harvesting time, height, etc.).

## Disadvantages

- The purity of the cultivar may be altered through admixture, natural crossing with other cultivars, and mutations. Such off-type plants should be rogued out to maintain cultivar purity.
- The cultivar has a narrow genetic base and, hence, is susceptible to devastation from adverse environmental factors because of uniform response.
- A new genotype is not created. Rather, improvement is limited to the isolation of the most desirable or best genotype from a mixed population.
- The method promotes genetic erosion because most superior pure lines are identified and multiplied to the exclusion of other genetic variants.
- Progeny rows takes up more resources (time, space, funds).

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- Polygenes are genes with effects that are too small to be individually distinguished. They are sometimes called **minor genes**
- Most of the important variation displayed by nearly all plant traits affecting growth, development and reproduction, is quantitative (continuous or polygenic variation; controlled by many genes).
- Polygenes demonstrate the same properties in terms of dominance, epistasis, and linkage as classical Mendelian genes.

- In many cases discontinuous or stepwise distinction between phenotypes inevitably accompany measurements for a particular characteristic.
- For example, the number of vertebrae in some species of chordates may differ between individuals, but the difference is generally classified on the basis of whole numbers of vertebrae, or, as in resistance to disease, the character is expressed in an “all or none” fashion.
- Such characters may nevertheless be influenced by numerous polygenes.

- Polygenes and their expression of discontinuous characters comes about through the establishment of “thresholds.” Expression of particular phenotypes of polygenic genotypes occur only when the genotypes have values above this threshold.
- Thus, although there is superficial discontinuous phenotypic distribution, there underlies a continuous polygenic distribution.
- Wright first demonstrated the **relationship between two scales** in crosses between strains of guinea pigs, that differed from each other in the **number of toes on the hind leg**.

- One strain (number 2) had the normal three toes on hind leg, and the other (D) was polydactylous, with four toes.
- Their  $F_1$  offspring were 3 toed, as expected.
- In  $F_2$ , however, ratio of Three toed: Four toed  $\simeq 3 : 1$  (188:45 individuals).
- It seems as if these crosses were segregating for only a single gene difference in the  $F_2$ . This was further corroborated by the testcross results.
- In the testcross however, one gene hypothesis was evidently disproved with the observation that three-toed parental type was not heterozygous.
- On the contrary, wright found that backcrossing these three-toed “heterozygotes” to the four-toed stock resulted in 77 percent four-toed to 23 percent three-toed offspring.

- With support of other evidence, wright proposed that polydactyly is affected by four pair of polygens (8 alleles).
- Individuals which had about five or more polydactylous alleles out of eight had exceeded the “threshold” and appeared as four toed.
- Initial four toed stock was therefore entirely of this type.
- Since parental three-toed stock had its polygenic distribution centered far below the threshold,  $F_1$  hybrids were mostly three toed.



## Polygenes in discontinuous traits

Gamete types	abcd	abcD	abCd	abCD	aBcd	aBcD	aBCd	aBCD	Abcd	AbcD	AbCd	AbCD	ABcd	ABcD	ABCd	ABCD
abcd	aabbcddd	aabbccdD	aabbcCdd	aabbcCdD	aabBccdd	aabBccdD	aabBcCdd	aabBcCdD	aAbbccdd	aAbbccdD	aAbbcCdd	aAbbcCdD	aAbBccdd	aAbBccdD	aAbBcCdd	aAbBcCdD
abcD	aabbcddd	aabbccDD	aabbcCdD	aabbcCDD	aabBccDd	aabBccDD	aabBcCdD	aabBcCDD	aAbbccdD	aAbbccDD	aAbbcCdD	aAbbcCDD	aAbBccdD	aAbBccDD	aAbBcCdD	aAbBcCDD
abCd	aabbcCdd	aabbcCdD	aabbCCdd	aabbCCDd	aabBcCdd	aabBcCdD	aabBCCdd	aabBCCDd	aAbbcCdd	aAbbcCdD	aAbbCCdd	aAbbCCDd	aAbBcCdd	aAbBcCdD	aAbBCCdd	aAbBCCDd
abCD	aabbcCdD	aabbcCDD	aabbCCDd	aabbCCDD	aabBcCdD	aabBcCDD	aabBCCDd	aabBCCDD	aAbbcCdD	aAbbcCDD	aAbbCCDd	aAbbCCDD	aAbBcCdD	aAbBcCDD	aAbBCCDd	aAbBCCDD
aBcd	aabBccdd	aabBccdD	aabBcCdd	aabBcCdD	aabBccdd	aabBccdD	aaBBcCdd	aaBBcCdD	aAbBccdd	aAbBccdD	aAbBcCdd	aAbBcCdD	aABBccdd	aABBccdD	aABBcCdd	aABBcCdD
aBcD	aabBccdd	aabBccDD	aabBcCdD	aabBcCDD	aaBBccdd	aaBBccDD	aaBBcCdD	aaBBcCDD	aAbBccdD	aAbBccDD	aAbBcCdD	aAbBcCDD	aABBccdd	aABBccDD	aABBcCdD	aABBcCDD
aBCd	aabBcCdd	aabBcCdD	aabBCCdd	aabBCCDd	aaBBcCdd	aaBBcCdD	aaBBCCdd	aaBBCCDd	aAbBcCdd	aAbBcCdD	aAbBCCdd	aAbBCCDd	aABBcCdd	aABBcCdD	aABBCCdd	aABBCCDd
aBCD	aabBcCdD	aabBcCDD	aabBCCDd	aabBCCDD	aaBBcCdD	aaBBcCDD	aaBBCCDd	aaBBCCDD	aAbBcCdD	aAbBcCDD	aAbBCCDd	aAbBCCDD	aABBcCdD	aABBcCDD	aABBCCDd	aABBCCDD
Abcd	aAbbccdd	aAbbccdD	aAbbcCdd	aAbbcCdD	aAbBccdd	aAbBccdD	aAbBcCdd	aAbBcCdD	AAbbccdd	AAbbccdD	AAbbcCdd	AAbbcCdD	AABbccdd	AABbccdD	AABbcCdd	AABbcCdD
AbcD	aAbbccdD	aAbbccDD	aAbbcCdD	aAbbcCDD	aAbBccdD	aAbBccDD	aAbBcCdD	aAbBcCDD	AAbbccdD	AAbbccDD	AAbbcCdD	AAbbcCDD	AABbccdD	AABbccDD	AABbcCdD	AABbcCDD
AbCd	aAbbcCdd	aAbbcCdD	aAbbCCdd	aAbbCCDd	aAbBcCdd	aAbBcCdD	aAbBCCdd	aAbBCCDd	AAbbcCdd	AAbbcCdD	AAbbCCdd	AAbbCCDd	AABbcCdd	AABbcCdD	AABBCCdd	AABBCCDd
AbCD	aAbbcCdD	aAbbcCDD	aAbbCCDd	aAbbCCDD	aAbBcCdD	aAbBcCDD	aAbBCCDd	aAbBCCDD	AAbbcCdD	AAbbcCDD	AAbbCCDd	AAbbCCDD	AABbcCdD	AABbcCDD	AABBCCDd	AABBCCDD
ABcd	aAbBccdd	aAbBccdD	aAbBcCdd	aAbBcCdD	aABBccdd	aABBccdD	aABBcCdd	aABBcCdD	AAbBccdd	AAbBccdD	AAbBcCdd	AAbBcCdD	AABBccdd	AABBccdD	AABBcCdd	AABBcCdD
ABcD	aAbBccdd	aAbBccDD	aAbBcCdD	aAbBcCDD	aABBccdd	aABBccDD	aABBcCdD	aABBcCDD	AAbBccdD	AAbBccDD	AAbBcCdD	AAbBcCDD	AABBccdd	AABBccDD	AABBcCdD	AABBcCDD
ABCd	aAbBcCdd	aAbBcCdD	aAbBCCdd	aAbBCCDd	aABBcCdd	aABBcCdD	aABBCCdd	aABBCCDd	AAbBcCdd	AAbBcCdD	aAbBCCdd	aAbBCCDd	AABBcCdd	AABBcCdD	aABBCCdd	aABBCCDd
ABCD	aAbBcCdD	aAbBcCDD	aAbBCCDd	aAbBCCDD	aABBcCdD	aABBcCDD	aABBCCDd	aABBCCDD	AAbBcCdD	AAbBcCDD	aAbBCCDd	aAbBCCDD	AABBcCdD	AABBcCDD	aABBCCDd	aABBCCDD

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## Genetics of heritability

- Dominance model of quantitative inheritance dictates that total genetic variance will contain dominance genetic variance (denoted by  $V_D$ ) and additive genetic variance (denoted by  $V_A$ ).
- Dominance genetic variance is variation caused by heterozygotes loci in the individuals in the population, whereas additive genetic variance is the variation existing between homozygous loci in the segregating population.

## Broad sense heritability

- The total genetic variance divided by the total phenotypic variance is Broad-sense heritability ( $h_b^2$ ).
- This estimation uses the total genetic variance in an additive-dominance model, while the total phenotypic variance is obtained by adding environmental variance to this genetic variance.

$$h_b^2 = \frac{V_A + V_D}{V_A + V_D + V_E} \quad (i)$$

- Dominant genetic variance will be dependent upon the degree of heterozygosity in the population and will differ between filial generations.

## Narrow sense heritability

- A more useful form of heritability for plant breeders, therefore, is *narrow-sense heritability* ( $h_n^2$ ), which is:

$$h_n^2 = \frac{V_A}{V_A + V_D + V_E} \quad (\text{ii})$$

## Dominance and additive effects

- Reason for why lack of resemblance between parents and their offspring should be attributable to dominance but not additive components
  - ▶ Dominance effects are a feature of particular genotypes; but genotypes are 'made' and 'unmade' between generations as a result of genetic segregation during the production of gametes.
  - ▶ Thus, the mean dominance effect in the offspring of a particular cross can be different from that of the parents, even when there is no selection.
- However, additive genetic variance is constant between filial generations, and so narrow-sense heritability of recombinant inbred lines can be estimated from early-generation segregating families.

## Variance partitioning of filial generation

- In the first filial generation ( $F_1$ ), after hybridization between two homozygous parents, there is not genetic variance between individuals of a progeny (they will be genetically alike) and all the variation observed between  $F_1$  plants will be entirely environmental.
- In the generation following ( $F_2$  and forth) there are both genetic and environmental components of phenotypic variance.
- The genetic variance of the  $F_2$  generation is:

$$\sigma_{F_2}^2 = \frac{1}{2}V_A + \frac{1}{4}V_D + \sigma_E^2$$

- Thus broad sense heritability of the  $F_2$  generation is:

$$h_b^2 = \frac{\frac{1}{2}V_A + \frac{1}{4}V_D}{\frac{1}{2}V_A + \frac{1}{4}V_D + \sigma_E^2} \quad \text{(iii)}$$

In simple terms, to estimate the  $h_b^2$  of  $F_2$  family (or any other segregating family), only following estimates are required:

- 1 Total phenotypic variance (Obtained from measurement on plants within  $F_2$  families)
- 2 Environmental variance (Obtained from measurement on  $F_1$  families)



## Problem

Consider a field experiment with an inbreeding species such as wheat or barley. Parent 1 included 20 plants, Parent 2 included 20 plants and  $F_2$  family derived from selfing of  $F_1$  generation, which was obtained by intercrossing the two parents (i.e. Parent 1 x Parent 2), consisted of 100 individuals. These 140 plants were completely randomized within the experiment, and at harvest the weight of seeds from each plant was recorded. The variances in seed weight of the two parents were  $\sigma_{\bar{P}_1}^2 = 16.8 \text{ kg}^2$  and  $\sigma_{\bar{P}_2}^2 = 18.4 \text{ kg}^2$ . The phenotypic variance (which included both genetic and environmental variation) of the  $F_2$  was  $\sigma_{\bar{F}_2}^2 = 56.9 \text{ kg}^2$ . The total phenotypic variance of the  $F_2$  generation is represented by denominator term of  $h_b^2$  is estimated to be  $56.9 \text{ kg}^2$ .

But the problem is what is the value of environmental component of the phenotypic variance  $\sigma_E^2$ ?

## Solution

It now follows that the  $h_b^2$ , from given inform is:

$$h_b^2 = \frac{56.9 - \sigma_E^2}{56.9}$$

Since, both parents are homozygous inbreds, any variance displayed by either must be attributable exclusively to the environment. The best estimate of the  $\sigma_E^2$  is therefore:

$$\begin{aligned}\sigma_E^2 &= \frac{\sigma_{\bar{P}_1}^2 + \sigma_{\bar{P}_2}^2}{2} \\ &= \frac{16.8 + 18.4}{2} = 17.6 \text{ kg}^2\end{aligned}$$

And, therefore,

$$h_b^2 = \frac{56.9 - 17.6}{56.9} = 0.691$$

Thus 69.1% of the phenotypic variance of the  $F_2$  generation is estimated to be genetic in origin.

## Partitioning environmental variance

The other generation in which the phenotypic variance is also entirely attributable to environmental effects is the  $F_1$ . On the other hand, if the phenotypic variances of all these three generations were available, the environmental component of the phenotypic variance of the  $F_2$  generation could be estimated as follows (in a simplified way):

$$\sigma_E = \frac{\sigma_{\bar{P}_1}^2 + 2\sigma_{\bar{F}_1}^2 + \sigma_{\bar{P}_2}^2}{4} \quad (\text{iv})$$

## Partitioning genetic variance

The ratio of additive genetic variance to total phenotypic variance is called the narrow-sense heritability.

$$h_n^2 = \frac{\frac{1}{2}V_A}{\frac{1}{2}V_A + \frac{1}{4}V_D + \sigma_E^2} \quad (v)$$

In order to estimate  $h_n^2$ , it is therefore necessary to partition the genetic variance into its two components ( $V_A$  and  $V_D$ ). This is done by considering the phenotypic variance of the two backcross families ( $\sigma_{\bar{B}_1}^2$  and  $\sigma_{\bar{B}_2}^2$ ).

The expected variances of  $\sigma_{\bar{B}_1}^2$  and  $\sigma_{\bar{B}_2}^2$  are:

$$\sigma_{\bar{B}_1}^2 = \frac{1}{4}V_A + \frac{1}{4}V_D - \frac{1}{2} \left[ \sum(a) \times \sum(d) \right] + \sigma_E^2$$

$$\sigma_{\bar{B}_2}^2 = \frac{1}{4}V_A + \frac{1}{4}V_D + \frac{1}{2} \left[ \sum(a) \times \sum(d) \right] + \sigma_E^2$$

Note the sign before expression  $\frac{1}{2} [\sum(a) \times \sum(d)]$ . Adding together the equations,

$$\sigma_{\bar{B}_1}^2 + \sigma_{\bar{B}_2}^2 = \frac{1}{2}V_A + \frac{1}{2}V_D + 2\sigma_E^2 \quad (\text{vi})$$

From the relationship we addressed earlier of  $\sigma_{\bar{F}_2}^2$  in terms of variance components, provided that numerical values for  $\sigma_{\bar{B}_1}^2$  and  $\sigma_{\bar{B}_2}^2$  can be estimated, we have sufficient information to calculate both  $V_A$  and  $V_D$ , and hence the  $h_n^2$ .

$$\begin{aligned}\sigma_{\bar{B}_1}^2 + \sigma_{\bar{B}_2}^2 - \sigma_{\bar{F}_2}^2 &= \frac{1}{2}V_A + \frac{1}{2}V_D + 2\sigma_E^2 - \left(\frac{1}{2}V_A + \frac{1}{4}V_D + \sigma_E^2\right) \\ &= \frac{1}{4}V_D + \sigma_E^2\end{aligned}$$

Therefore,

$$V_D = 4 \left( \sigma_{\bar{B}_1}^2 + \sigma_{\bar{B}_2}^2 - \sigma_{\bar{F}_2}^2 - \sigma_E^2 \right) \quad (\text{vii})$$

## Problem

A properly designed glasshouse experiment was carried out using the garden pea. Progeny from the  $F_1$ ,  $F_2$  and both backcross families ( $B_1$  and  $B_2$ ) were arranged as single plants in a completely randomized block design, and plant height recorded after flowering. The following variances were calculated from the recorded data:

$$\begin{aligned}\sigma_{B_1}^2 &= 285 \text{ cm}^2; & \sigma_{B_2}^2 &= 251 \text{ cm}^2; \\ \sigma_{F_2}^2 &= 358 \text{ cm}^2; & \sigma_E^2 &= 155 \text{ cm}^2\end{aligned}$$

Calculate  $h_b^2$  and  $h_n^2$ .



## Solution

- Variance based approaches - ratio of variance estimates:

$$h_{bs}^2 = \frac{V_G}{V_P}$$

$$h_{ns}^2 = \frac{V_A}{V_P}$$

- Mean based approaches:

- ▶ realized heritability:  $h^2 = \frac{R}{S}$
- ▶ Six generation mean analysis method

## Parent offspring regression

- This method is based on how much does the resemblance parents and offspring exist.
- If there is perfect resemblance between parents and offspring, then,  $b = 1$  and there is perfect heritable genetic effect.
- On contrary if there is no resemblance between parents and offspring  $b = 0$ , and there is no heritable effect but variation is only due to environment.
- Therefore, narrow sense heritability (  $h_{ns}$  )

$$b = h_{ns}^2 = \frac{V_A}{V_P}$$

- If only one parent is known (animal experiments or polycrosses)

$$b = \frac{1}{2} \cdot \frac{V_A}{V_P}$$

$$h_{ns}^2 = 2b$$

$b$  = slope of parent offspring regression line

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- 1 Two pure lines of rice are crossed. In the  $F_1$  the variance in spike length is 1.5. The  $F_1$  is selfed. In the  $F_2$  the variance in spike length is 4.5. Estimate broad sense heritability of spike length in rice
- 2 The phenotypic variance of yield in maize  $200 \text{ kg}^2$  per acre. The variance within an inbred line is 80. The regression of offspring phenotype on mid parent values is 0.32. Find additive variance, genetic variance, environmental variance, narrow sense heritability and broad sense heritability.

- 3 Estimate heritability through parent offspring regression method from the following available data.

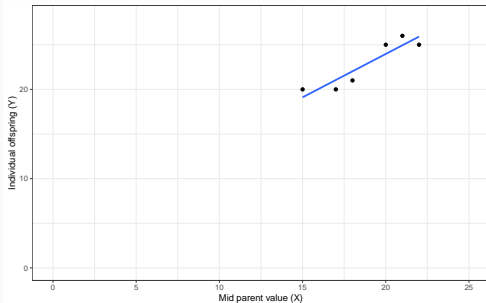
Mid parent value (X)	Individual offspring (Y)
20	25
18	21
15	20
17	20
21	26
22	25

- 4 Suppose 2 inbred lines A and B are crossed to produce hybrid. The genotype of A is AAbbccDDEEFF and the genotype of B is aaBBCCddeeFF. A, B, C, D, E and F are the dominant genes. If dominant homozygote contributes  $2 \text{ ton ha}^{-1}$ , recessive homozygote contributes  $1 \text{ ton ha}^{-1}$  and heterozygote contributes  $2.5 \text{ ton ha}^{-1}$ , Find the grain yields of Parent A, Parent B and  $F_1$  hybrid on the basis of dominance and over-dominance hypothesis.

## Solution

### Question 3

term	estimate	std.error	statistic	p.value
(Intercept)	4.54	3.93	1.2	0.31
'Mid parent value (X)'	0.97	0.21	4.7	0.01





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## References

Brown, Jack, Peter Caligari, and Hugo Campos. 2014. *Plant Breeding*. Wiley Blackwell.