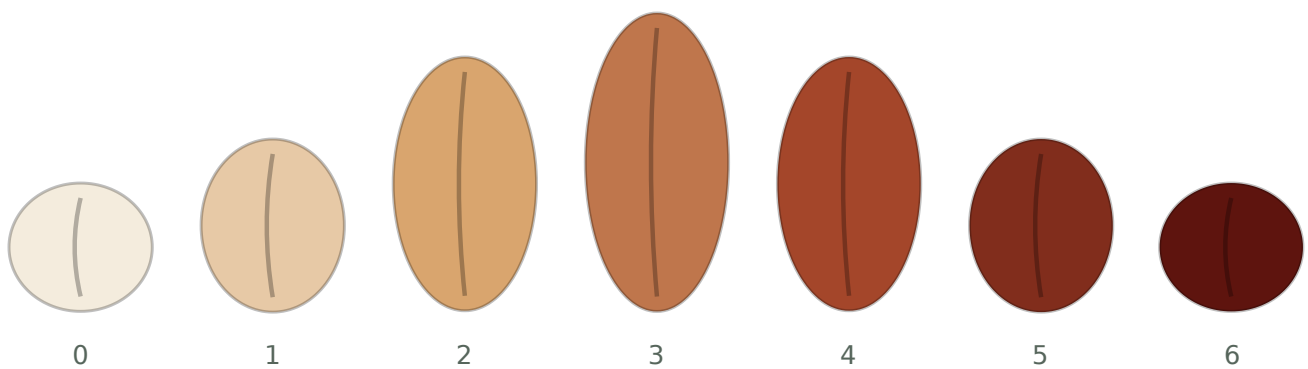


Polygenic inheritance

How many genes, each adding a small equal dose, turn Mendel's neat classes into the smooth bell curves of height, skin colour, grain colour and yield.



Seven kernel shades from a three-gene cross: 0 to 6 colour-adding alleles. Their F_2 frequencies follow 1 : 6 : 15 : 20 : 15 : 6 : 1.

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|--|---|
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1. The core idea

Polygenic inheritance (multiple-factor or quantitative inheritance) is the inheritance of a trait controlled by two or more genes whose alleles have small, *additive* and roughly equal effects. Each "effective" (contributing) allele adds

one unit of phenotype; each "non-effective" allele adds nothing. The phenotype depends only on *how many* effective alleles are present, not which gene they sit on.

Traits inherited this way are **quantitative traits**: they are measured (cm, kg, pigment units) rather than sorted into categories, and they show **continuous variation** in a population. The concept was established by **Nilsson-Ehle** (1909, wheat kernel colour) and **East** (1910–16, maize ear length and tobacco corolla length), and reconciled with Mendelism by **Fisher** (1918).

Five assumptions of the additive model. (1) Several independently assorting genes. (2) Each gene has two alleles, one effective and one not. (3) No dominance: effects are additive within a gene. (4) No epistasis: effects are additive between genes. (5) Every effective allele contributes the same amount.

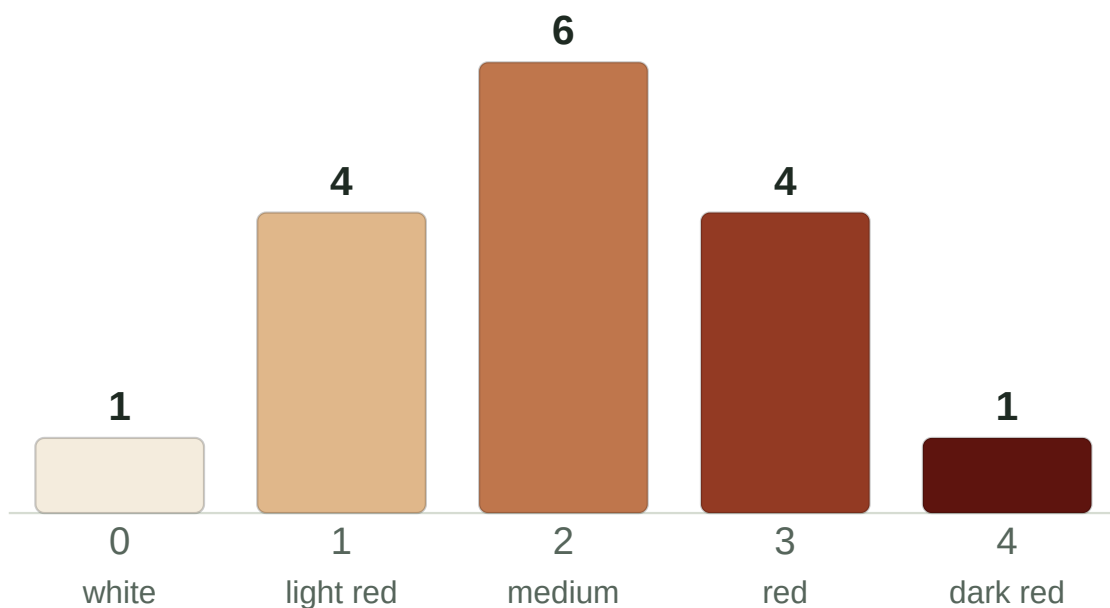
Feature	Qualitative (Mendelian)	Quantitative (polygenic)
Genes involved	One or few, major effect	Many (polygenes), each minor effect
Variation	Discontinuous, distinct classes	Continuous, graded classes
Allele interaction	Dominance common	Additive, cumulative
F ₁	Resembles dominant parent	Intermediate (mid-parent)
F ₂ ratio (2 genes)	9 : 3 : 3 : 1	1 : 4 : 6 : 4 : 1
Environment	Little effect	Strong effect; blurs classes
Analysis	Ratios, χ^2 test	Mean, variance, heritability
Examples	Pea seed shape, ABO blood group	Height, skin colour, IQ, yield, milk output

2. Nilsson-Ehle's wheat kernels

Nilsson-Ehle crossed a dark-red-kernelled wheat (**R₁R₁R₂R₂**) with a white one (**r₁r₁r₂r₂**). The F₁ (**R₁r₁R₂r₂**) was medium red, exactly halfway. Selfing the F₁ gave five colour classes in the ratio **1 : 4 : 6 : 4 : 1**. Below, A and B stand for R₁ and R₂; the number in each cell is the count of capital (colour-adding) alleles.

	AB	Ab	aB	ab
AB	4 AABB	3 AABb	3 AaBB	2 AaBb
Ab	3 AABb	2 AAbb	2 AaBb	1 Aabb
aB	3 AaBB	2 AaBb	2 aaBB	1 aaBb
ab	2 AaBb	1 Aabb	1 aaBb	0 aabb

F₂ Punnett square for AaBb × AaBb. Cells of the same shade share the same dose of colour alleles, however they are distributed across the two genes.



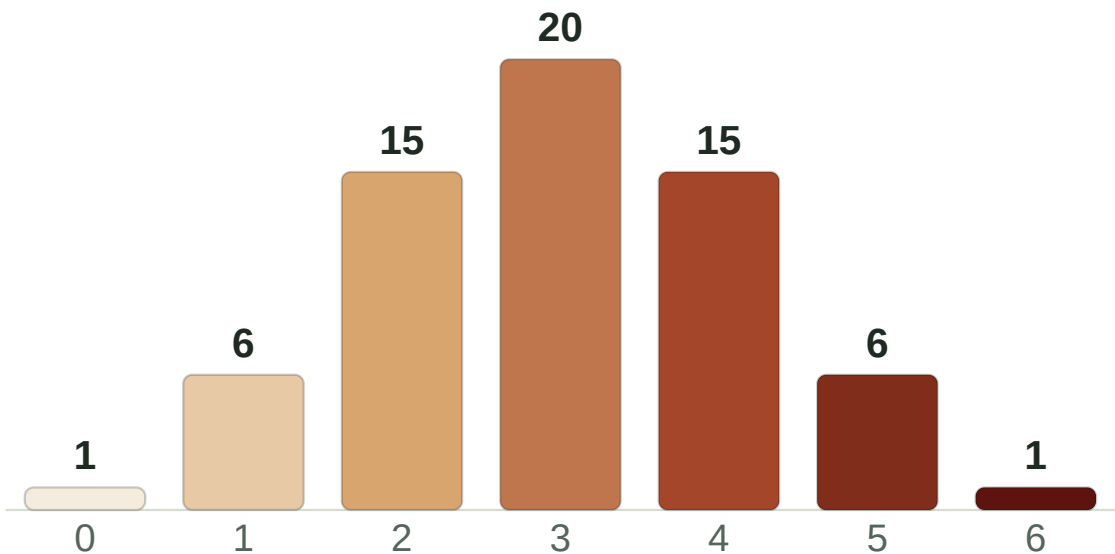
F₂ frequency by number of colour alleles (out of 16). Dark red 1, red 4, medium red 6, light red 4, white 1.

Why 1 : 4 : 6 : 4 : 1? Four allele "slots" (two per gene), each filled by a colour allele with probability $\frac{1}{2}$. The number of colour alleles follows a binomial distribution, so the class sizes are the coefficients of $(\frac{1}{2} + \frac{1}{2})^4$, the fourth row of Pascal's triangle.

In some other wheat varieties Nilsson-Ehle found that only **1 in 64** F₂ plants were white. Since $(\frac{1}{4})^3 = 1/64$, three genes must be segregating there.

3. Three genes and human skin colour

Davenport (1913) modelled human skin colour with two genes; the modern textbook model uses three (A, B, C). Melanin production is additive: **AABBCC** is darkest, **aabbcc** lightest, and **AaBbCc** is intermediate. A marriage between two **AaBbCc** individuals can produce children spanning all seven shades.



Children of **AaBbCc** × **AaBbCc**, out of 64: 1 : 6 : 15 : 20 : 15 : 6 : 1. Only 1/64 are as dark as **AABBCC** and 1/64 as light as **aabbcc**.

Real skin colour involves many more loci (**MC1R**, **SLC24A5**, **SLC45A2**, **OCA2**, **TYR** and others) plus sun exposure, so the observed distribution is smooth rather than seven neat steps. The three-gene model is a teaching model, not a full description.

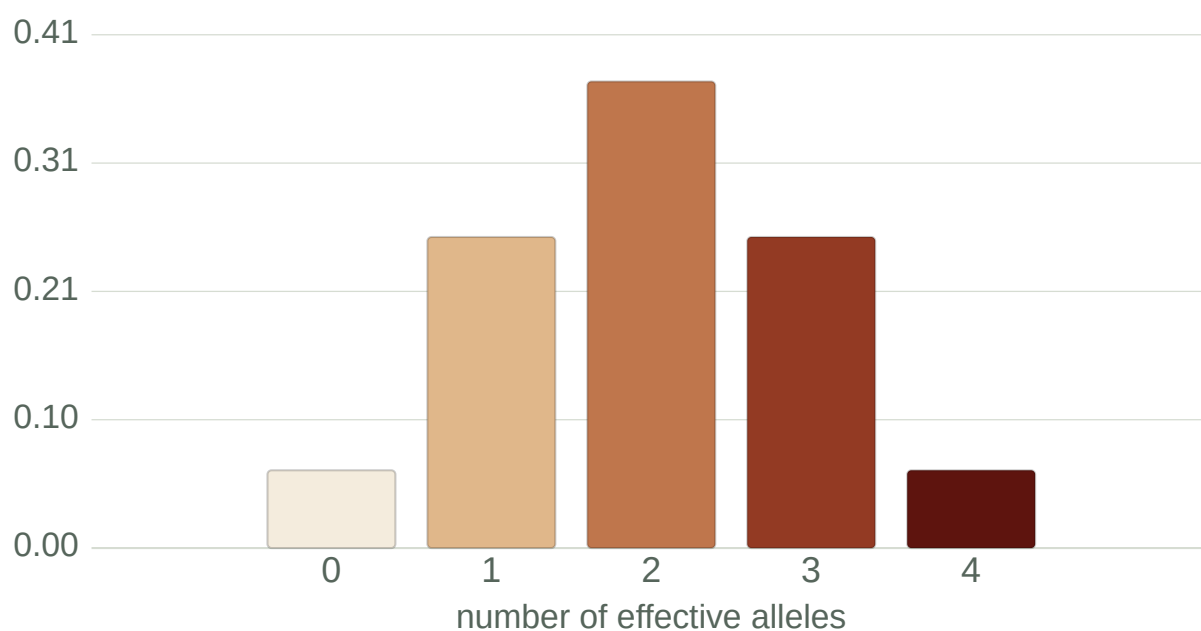
Other classic examples

Trait	Organism	Worker
Kernel colour	Wheat	Nilsson-Ehle (1909)
Ear length	Maize	East, Emerson & East (1913)
Corolla length	Nicotiana longiflora	East (1916)
Skin colour	Human	Davenport (1913)

Trait	Organism	Worker
Height, weight, IQ, blood pressure	Human	Galton; Fisher (1918)
Milk yield, egg production	Cattle, poultry	Animal breeding

4. From steps to a bell curve

Add genes and the classes multiply and narrow; add environmental noise and neighbouring classes overlap until no gaps remain. This is why a trait controlled by discrete Mendelian genes can look perfectly continuous. Move the sliders to see it happen.



Classes **5** Genotypes **9** Each extreme **1/16** Genetic variance **1.0** a^2

Bars: F_2 genotypic classes (fraction of plants). Line: what you would actually measure in the field once environmental variation smears each class.

Take-home. With n genes the F_2 distribution is binomial with $2n$ trials and $p = \frac{1}{2}$. As n grows it approaches a normal distribution with mean n and variance $n/2$ (in allele units). Environment adds its own variance on top.

5. Formula toolkit

For an F_2 from two pure-breeding extremes, with n additive genes (all heterozygous in F_1):

$$\text{Phenotypic classes} = 2n + 1$$

$$\text{Genotypes} = 3^n$$

$$\text{Fraction like either extreme parent} = \left(\frac{1}{4}\right)^n = \frac{1}{4^n}$$

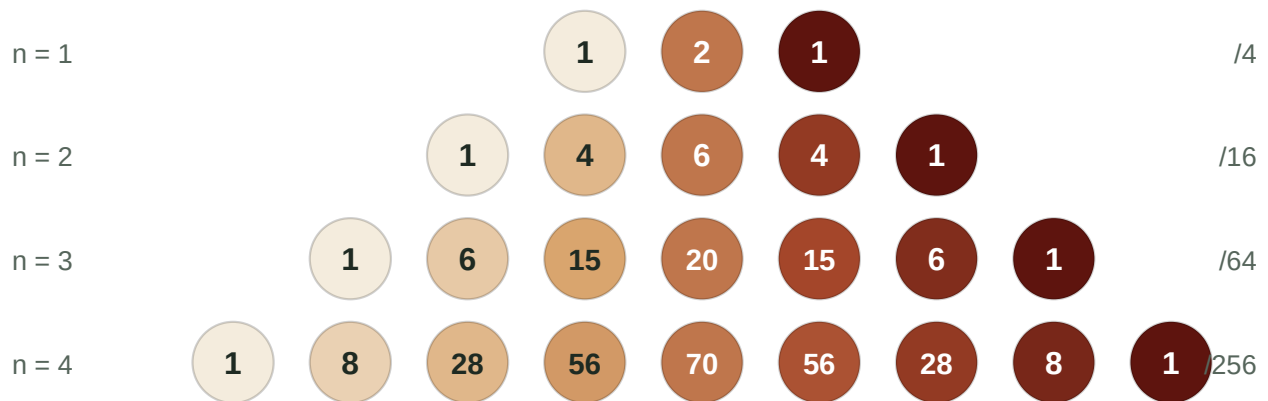
$$\text{Fraction with } k \text{ effective alleles} = \frac{{}^{2n}C_k}{4^n}$$

$$\text{Effect per allele } a = \frac{P_{\max} - P_{\min}}{2n}$$

$$\text{Phenotype} = P_{\min} + k \cdot a$$

$$\text{F}_1 \text{ mean} = \frac{\bar{P}_1 + \bar{P}_2}{2} \text{ (mid-parent)}$$

$$\text{Castle-Wright genes } n = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8 (V_{F2} - V_{F1})}$$



Pascal's triangle gives F_2 class frequencies directly. Use row $2n$: row 2 for one gene, row 4 for two, row 6 for three, row 8 for four.

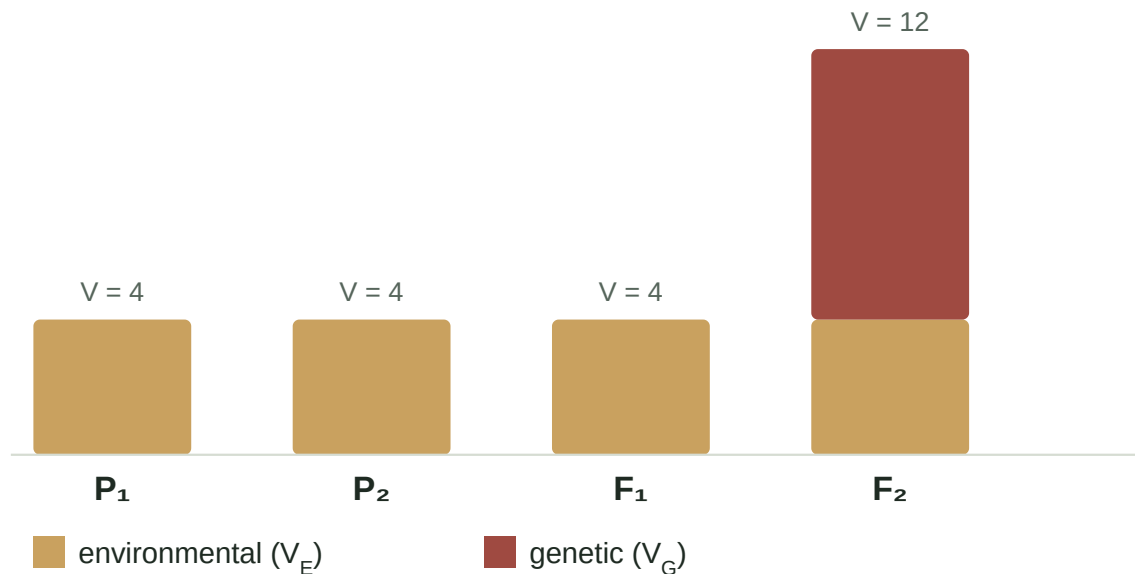
Shortcut for crosses that are not $F_1 \times F_1$

Treat each parent separately. A homozygous effective locus (AA) always passes one effective allele; a homozygous non-effective locus (aa) passes none; a heterozygous locus passes one with probability $\frac{1}{2}$. Add the fixed alleles from both parents, count the heterozygous loci across both parents (call it h), and the rest follows a binomial with h trials. Class frequencies are row h of Pascal's triangle, shifted by the fixed count. Numericals 4 and 9 use this.

Why the Castle-Wright formula works. With n genes each worth a per allele, the parental difference is $2na$ and the F_2 genetic variance is $n \cdot a^2/2$ (each locus contributes 0, a or $2a$ with probabilities $\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{4}$, giving variance $a^2/2$). Then $(2na)^2 \div (8 \cdot n \cdot a^2/2) = n$. The F_1 is genetically uniform, so V_{F_1} estimates environmental variance, and $V_{F_2} - V_{F_1}$ estimates genetic variance. The estimate is a *minimum*: unequal effects, linkage and dominance all make it too low.

6. Environment and heritability

Phenotypic variance splits into genetic and environmental parts: $V_P = V_G + V_E$, and genetic variance further into additive, dominance and epistatic parts: $V_G = V_A + V_D + V_I$.



Parents and F₁ are genetically uniform, so all their variation is environmental. F₂ adds segregating genetic variation on top.

Broad-sense heritability $H^2 = V_G / V_P$

Narrow-sense heritability $h^2 = V_A / V_P$

Response to selection $R = h^2 \cdot S$

S is the selection differential (mean of selected parents minus population mean) and R is the gain in the next generation. Narrow-sense h^2 matters to breeders because only additive effects are reliably passed from parent to offspring.

Transgressive segregation. When the parents are not the extremes (e.g. AAbb × aaBB, both medium), recombination in F₂ can produce AABB and aabb offspring that lie outside the range of both parents. Breeders exploit this to get lines better than either parent.

7. Solved numericals

Numerical 1 — wheat kernels

Dark red ($R_1R_1R_2R_2$) $\times$ white ($r_1r_1r_2r_2$) wheat. What fraction of the F_2 is medium red, and what fraction has at least three colour alleles?

▼ Show solution

$n = 2$, so $2n = 4$ slots; use row 4: 1 : 4 : 6 : 4 : 1 (out of 16).

Medium red = 2 colour alleles = $6/16 = \mathbf{3/8}$.

At least 3 alleles = $(4 + 1)/16 = \mathbf{5/16}$.

Numerical 2 — plant height

Height is controlled by three additive genes. $AABBCC$ plants are 100 cm, $aabbcc$ plants 40 cm. Find the F_1 height, the fraction of F_2 that is 80 cm, and the fraction taller than 80 cm.

▼ Show solution

$a = (100 - 40)/6 = 10$ cm per effective allele. F_1 $AaBbCc$ has 3 $\rightarrow 40 + 30 = \mathbf{70}$ cm.

80 cm needs $k = 4$. Fraction = ${}^6C_4/64 = \mathbf{15/64}$.

Taller than 80 cm: $k = 5$ or $6 \rightarrow (6 + 1)/64 = \mathbf{7/64}$.

Numerical 3 — counting genes from the extremes

In an F_2 of 1024 plants, 4 are as short as the short parent. How many genes control height? How many phenotypic classes and genotypes are expected?

▼ Show solution

Fraction = $4/1024 = 1/256 = (1/4)^n \rightarrow 4^n = 256 \rightarrow \mathbf{n = 4}$.

Classes = $2(4) + 1 = \mathbf{9}$. Genotypes = $3^4 = \mathbf{81}$.

Numerical 4 — a non-F₁ cross

Using the height system of Numerical 2 (base 40 cm, 10 cm per allele), cross $AaBbCc \times AABbcc$. Give the range of offspring heights and the probability of a 70 cm plant.

▼ Show solution

Parent 1 ($AaBbCc$): 3 heterozygous loci, 0 fixed. Parent 2 ($AABbcc$): AA gives 1 fixed allele; Bb is 1 heterozygous locus; cc gives 0.

Fixed = 1; heterozygous loci $h = 3 + 1 = 4$. Offspring alleles $k = 1 + \text{Bin}(4, \frac{1}{2})$, so k runs 1 to 5 in ratio 1 : 4 : 6 : 4 : 1.

Range: $40 + 10 = 50 \text{ cm}$ to $40 + 50 = 90 \text{ cm}$.

70 cm $\rightarrow k = 3 \rightarrow$ binomial part = 2 $\rightarrow 6/16 = 3/8$.

Numerical 5 — skin colour in a family

Two parents of genotype $AaBbCc$ (three-gene model). What is the probability that a child is (a) as dark as possible, (b) the same shade as the parents, (c) lighter than the parents?

▼ Show solution

Row 6: 1 : 6 : 15 : 20 : 15 : 6 : 1 over 64. Parents have $k = 3$.

(a) $k = 6$: **1/64**. (b) $k = 3$: $20/64 = 5/16$. (c) $k = 0, 1, 2$: $(1 + 6 + 15)/64 = 22/64 = 11/32$.

Numerical 6 — Castle-Wright estimate

Two inbred maize lines have mean ear lengths 10 cm and 22 cm. Variance of $F_1 = 2.0 \text{ cm}^2$, variance of $F_2 = 6.5 \text{ cm}^2$. Estimate the minimum number of genes.

▼ Show solution

$n = (22 - 10)^2 / [8 \times (6.5 - 2.0)] = 144 / 36 = 4 \text{ genes}$.

This is a minimum because the formula assumes equal, additive, unlinked genes.

Numerical 7 — broad-sense heritability

Variance in $F_1 = 4 \text{ units}^2$, variance in $F_2 = 12 \text{ units}^2$. Estimate V_E , V_G and H^2 .

▼ Show solution

F_1 is genetically uniform, so $V_E = V_{F_1} = \mathbf{4}$.

$V_G = 12 - 4 = \mathbf{8}$. $H^2 = 8/12 = \mathbf{0.67}$ (67% of F_2 variation is genetic).

Numerical 8 — from phenotypic classes

An F_2 shows 11 distinct phenotypic classes. How many gene pairs are involved, and what fraction of the F_2 resembles one extreme parent?

▼ Show solution

$2n + 1 = 11 \rightarrow \mathbf{n = 5}$. Fraction = $(1/4)^5 = \mathbf{1/1024}$.

Numerical 9 — fruit weight

Fruit weight: $aabbcc = 150 \text{ g}$, $AABBCC = 270 \text{ g}$, additive. Cross $AABbCc \times aabbCc$. What fraction of offspring weighs 190 g?

▼ Show solution

$a = (270 - 150)/6 = 20 \text{ g}$. $190 \text{ g} \rightarrow k = (190 - 150)/20 = 2$.

Parent 1: AA gives 1 fixed; Bb and Cc are 2 heterozygous loci. Parent 2: aa and bb give 0; Cc is 1 heterozygous locus.

$k = 1 + \text{Bin}(3, 1/2)$. Need binomial part = 1 $\rightarrow {}^3C_1/8 = \mathbf{3/8}$.

Numerical 10 — genetic variance from the model

Three additive genes, each effective allele adding 10 cm. Find the F_2 genetic variance and verify it with Castle–Wright.

▼ Show solution

Per locus, values 0, a, 2a with probabilities $\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{4}$: mean a, variance $a^2/2 = 50 \text{ cm}^2$.

Three independent loci: $V_G = 3 \times 50 = \mathbf{150 \text{ cm}^2}$.

Check: parental difference = $2na = 60 \text{ cm}$. $n = 60^2 / (8 \times 150) = 3600/1200 = 3 \checkmark$.

8. End-semester questions

Short answer (2 marks each)

1. Define polygenic inheritance and give two examples from humans.
2. Why is the F_1 of a polygenic cross intermediate between the parents?
3. State the F_2 phenotypic ratio for a three-gene additive trait.
4. What is transgressive segregation?
5. Distinguish broad-sense from narrow-sense heritability.
6. Why is the variance of F_1 used as an estimate of environmental variance?

Long answer (5 or 10 marks)

1. Describe Nilsson-Ehle's experiment on wheat kernel colour with a checkerboard, and explain how it supports the multiple-factor hypothesis. (10)
2. Compare qualitative and quantitative inheritance under at least six heads. (5)
3. Explain how a small number of Mendelian genes plus environmental variation produce a continuous normal distribution. Illustrate with a diagram. (10)
4. Derive the Castle–Wright formula and state its limitations. (5)
5. Explain the inheritance of human skin colour using the three-gene model. What proportion of children of two AaBbCc parents will be darker than both parents? (5)

9. Case-study MCQs

Tap "Show answer" under each to check yourself.

1 A breeder crosses pure squash lines averaging 1.2 kg and 3.6 kg. The F_1 averages 2.4 kg. Of 2048 F_2 plants, 8 weigh about 1.2 kg. How many genes control fruit weight?

- A. 3
- B. 4
- C. 5
- D. 8

▼ Show answer

B. 4

$8/2048 = 1/256 = (1/4)^4$, so $n = 4$.

2 In the same squash system, how much does each effective allele add?

- A. 0.15 kg
- B. 0.24 kg
- C. 0.30 kg
- D. 0.60 kg

▼ Show answer

C. 0.30 kg

$(3.6 - 1.2) / (2 \times 4) = 2.4/8 = 0.30$ kg.

3 An F_2 grown in a growth chamber falls into seven sharp classes, but the same seed grown in an open field shows a smooth unimodal curve. The best explanation is:

- A. Field conditions cause new mutations
- B. Environmental variance blurs the boundaries between genotypic classes
- C. Dominance is expressed only in the field
- D. Linkage breaks down in the field

▼ **Show answer**

B. Environmental variance blurs the boundaries between genotypic classes

Genotypes are unchanged; environmental noise widens each class until neighbours overlap.

4 Two parents are both AaBbCc for skin colour (three additive genes). The probability that their first child is darker than both parents is:

- A. 1/64
- B. 5/16
- C. 11/32
- D. 1/2

▼ **Show answer**

C. 11/32

Darker means $k = 4, 5$ or 6 : $(15 + 6 + 1)/64 = 22/64 = 11/32$.

5 Two medium-height inbred lines, AAbb and aaBB, are crossed. Some F_2 plants are taller than either parent. This is:

- A. Heterosis in F_1
- B. Transgressive segregation from recombination
- C. Incomplete penetrance
- D. Maternal inheritance

▼ **Show answer**

B. Transgressive segregation from recombination

Recombination produces AABB (and aabb), which lie outside the parental range.

6 The variance of F_1 equals that of the parents, but the F_2 variance is three times as large. What fraction of F_2 variance is genetic?

- A. $1/3$
- B. $1/2$
- C. $2/3$
- D. $3/4$

▼ Show answer

C. $2/3$

$V_E = V_{F1} = V$; $V_{F2} = 3V$; $V_G = 2V$; $H^2 = 2V/3V = 2/3$.

7 Which F_2 observation best distinguishes a polygenic trait from a single gene with incomplete dominance?

- A. F_1 is intermediate
- B. F_2 is more variable than F_1
- C. Only $1/64$ of F_2 resemble each parent instead of $1/4$
- D. F_2 mean equals F_1 mean

▼ Show answer

C. Only $1/64$ of F_2 resemble each parent instead of $1/4$

All other options hold for both models; the rarity of parental types reveals several genes.

8 Inbred lines have means 12 and 28 units. $V_{F1} = 3$ and $V_{F2} = 7$. The Castle–Wright estimate of gene number is:

- A. 2
- B. 4
- C. 8
- D. 16

▼ Show answer

C. 8

$(28 - 12)^2 / (8 \times 4) = 256/32 = 8$.

9 In a three-gene additive height system ($aabbcc = 40$ cm, 10 cm per allele), which genotype has the same height as $AaBbcc$?

- A. $AaBbCc$
- B. $AAbbcc$
- C. $AABbcc$
- D. $aabbCc$

▼ Show answer

B. $AAbbcc$

$AaBbcc$ has 2 effective alleles (60 cm); $AAbbcc$ also has 2.

10 Narrow-sense heritability of height in a population is 0.8. The correct interpretation is:

- A. 80% of each person's height is due to genes
- B. 80% of the variation in height among individuals in that population is additive genetic
- C. Height cannot be changed by nutrition
- D. 80% of offspring will match their parents' height

▼ Show answer

B. 80% of the variation in height among individuals in that population is additive genetic

Heritability describes variance in a particular population and environment, not individuals.

10. One-page revision

Model	Many genes, 2 alleles each, additive, equal, no dominance, no epistasis
F_1	Intermediate, uniform (all heterozygous)
F_2 classes	$2n + 1$, frequencies from row $2n$ of Pascal's triangle
Extreme parent in F_2	$(\frac{1}{4})^n$
Genotypes	3^n

Per-allele effect	$(\text{max} - \text{min}) / 2n$
1 gene / 2 / 3 / 4	1:2:1 · 1:4:6:4:1 · 1:6:15:20:15:6:1 · 1:8:28:56:70:56:28:8:1
Variance	$V_P = V_G + V_E$; $V_E \approx V_{F1}$; $V_G \approx V_{F2} - V_{F1}$
Castle-Wright	$n = (\bar{P}_1 - \bar{P}_2)^2 / 8(V_{F2} - V_{F1})$, a minimum estimate
Heritability	$H^2 = V_G/V_P$; $h^2 = V_A/V_P$; $R = h^2S$
Key workers	Nilsson-Ehle (wheat), East (maize, tobacco), Davenport (skin), Fisher (1918 synthesis)

Polygenic inheritance · study notes with diagrams, numericals and exam questions.