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AGE 304

TECHNOLOGY OF BREEDING CROP

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Course code: AGE 304

Course title: Technology of Breeding Crop

Course credit load: 2 Units

Series 1: Concepts, Purposes, and Biological Variation in Crop Breeding

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Introduction

Crop breeding is the science and art of changing the genetic make-up of plants to produce varieties that better serve human needs. Every major food crop grown in Nigeria today is the product of centuries of deliberate or unconscious selection by farmers and, more recently, of systematic scientific breeding programmes. Understanding what crop breeding is, why it is practised, and where the raw material of breeding (biological variation) comes from is the essential starting point for any student of crop improvement.

This Series introduces the definition, history, and objectives of crop breeding, the purposes that drive breeding programmes, and the biological variation that makes breeding possible. We begin with the concept of crop breeding and the breeder's role, cover the main breeding objectives, and then examine the sources, types, and importance of variation, concluding with the conservation of genetic resources and the threat of genetic erosion. All subsequent Series build on the foundation established here.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 1.1** define crop breeding and explain how it differs from crop agronomy (Linked to Part 1.1),
- **SLO 1.2** describe the historical development of crop breeding from farmer selection to modern scientific breeding (Linked to Part 1.1),
- **SLO 1.3** state the main purposes of crop breeding programmes and explain the importance of each (Linked to Part 1.2),
- **SLO 1.4** identify and describe the major sources of genetic variation available to plant breeders (Linked to Part 1.3),
- **SLO 1.5** explain mutation and polyploidy as sources of variation and give examples relevant to Nigerian crops (Linked to Part 1.3),
- **SLO 1.6** distinguish between phenotypic and genotypic variation and explain why this distinction matters in breeding (Linked to Part 1.3),

- **SLO 1.7** describe how plant breeders exploit variation in a breeding programme (Linked to Part 1.4), and
- **SLO 1.8** explain the importance of genetic resource conservation and describe the consequences of genetic erosion (Linked to Part 1.4).

1.1 What is Crop Breeding?

1.1.1 Definition of crop breeding

Crop breeding is the purposeful manipulation of the genetic composition of plant populations to produce new varieties (cultivars) with improved characteristics that better meet human needs. It combines knowledge from genetics, agronomy, plant pathology, statistics, and molecular biology to develop plants that yield more, resist diseases and pests, tolerate environmental stresses, and produce better-quality products. Crop breeding differs from crop agronomy in that agronomy improves the environment around the plant (soil, water, nutrients) while breeding improves the plant itself at the genetic level.

A cultivar (variety) is a plant grouping that has been selected for particular characteristics and can be reproduced with those characteristics maintained. Breeding produces new cultivars through cycles of crossing, selection, and evaluation. The term "variety" is used informally; "cultivar" is the formal term in plant taxonomy. In Nigeria, the National Variety Release Committee (NVRC) under the Federal Ministry of Agriculture must approve new cultivars before they can be commercially released and distributed to farmers.

Fill in the blank: Crop breeding is the purposeful manipulation of the _____ composition of plant populations to produce new cultivars with improved characteristics.

1.1.2 Historical development of crop breeding

Crop breeding began approximately 10,000 years ago when early farmers in the Fertile Crescent, Mesoamerica, and sub-Saharan Africa began selecting and saving seed from the best plants in their fields. This unconscious selection gradually transformed wild plants into the domesticated

crops we know today: teosinte became maize, wild emmer became wheat, and wild cowpea became the cultivated cowpea dominant in Nigerian agriculture. Key features of domestication (larger seeds, non-shattering seed heads, synchronous maturity) are all the result of unconscious or deliberate selection.

Scientific crop breeding began with the rediscovery of Mendel's laws in 1900, which provided the theoretical basis for predicting the outcome of crosses. The 20th century saw the development of hybrid maize in the 1920s to 1940s (doubling yields in the United States), the Green Revolution in the 1960s to 1970s (semi-dwarf wheat and rice varieties that transformed food security in Asia), and more recently marker-assisted selection and genomic selection using molecular tools. In Nigeria, the International Institute of Tropical Agriculture (IITA) in Ibadan has been the leading centre for scientific breeding of tropical food crops since its establishment in 1967.

Fill in the blank: Scientific crop breeding began with the rediscovery of _____ laws in 1900, which provided the theoretical basis for predicting the outcome of crosses between parent plants.

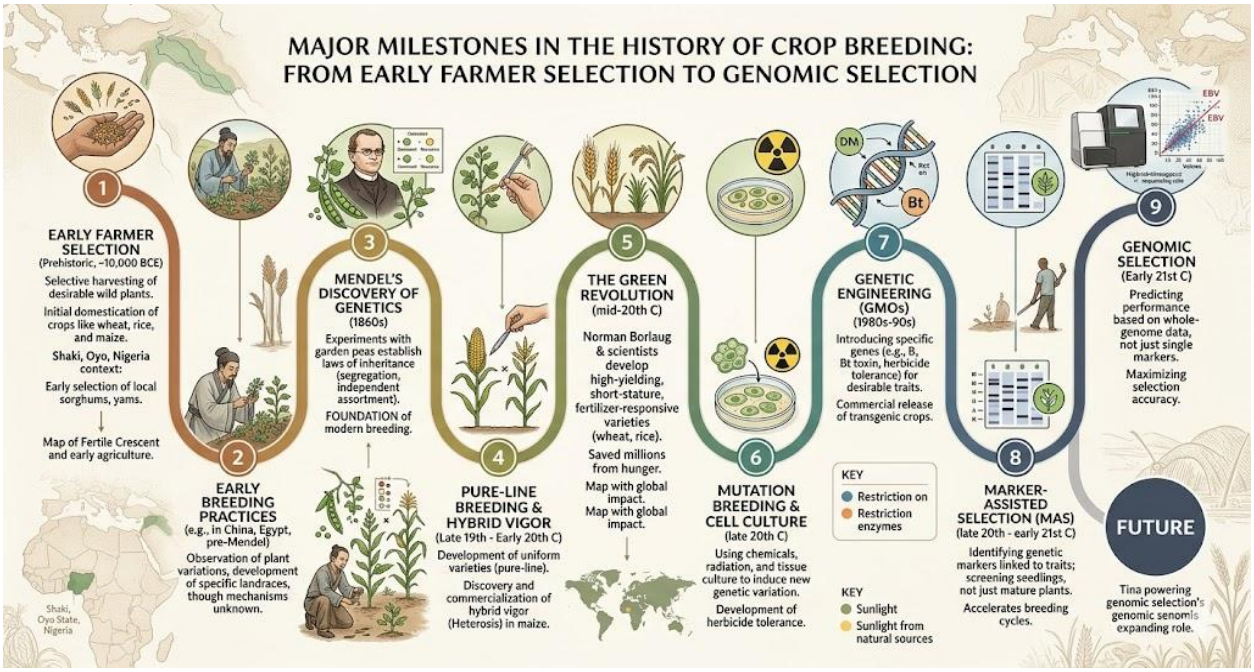

Figure 1.1: Timeline of the major milestones in the history of crop breeding

1.1.3 The role of the plant breeder

The plant breeder is a scientist who designs and manages the programme of crosses, selections, and evaluations that produces new cultivars. Key responsibilities include: defining the breeding objectives based on farmer and market needs; assembling the genetic base (collecting parent materials with the desired traits); making crosses to combine desired traits in one plant; selecting superior individuals or lines from the segregating offspring; evaluating selected lines in multi-location trials; and releasing superior lines as cultivars after meeting national variety release requirements.

The breeder must also understand the mating system of the target crop (self-pollinated or cross-pollinated) because it determines which breeding method is appropriate. Close collaboration with agronomists (for yield trial management), plant pathologists (for disease resistance screening), food technologists (for quality evaluation), and extension agents (for feedback on farmer needs) is essential. A breeding programme typically takes 8 to 15 years from the initial cross to the commercial release of a new cultivar, requiring sustained institutional support and funding.

Fill in the blank: A breeding programme typically takes _____ to 15 years from the initial cross to the commercial release of a new cultivar, requiring sustained institutional support and funding.

Pilot questions 1.1

1. Define crop breeding and explain how it differs from crop agronomy.
2. Define the term cultivar and explain the role of the NVRC in Nigeria.
3. Describe two key milestones in the historical development of crop breeding.
4. State four key responsibilities of a plant breeder.
5. Explain why a breeding programme takes 8 to 15 years to produce a new cultivar.

1.2 Purposes of Crop Breeding

1.2.1 Improving yield and yield stability

The primary purpose of most crop breeding programmes is to increase yield: the quantity of marketable product produced per unit area. Yield improvement directly addresses food security by enabling more food to be produced from the same land area. In Nigeria, the yield gap between actual farmer yields and the potential yields demonstrated in research station trials is very large for most food crops (for example, Nigerian farmers average 1 to 1.5 tonnes per hectare of maize against a research station potential of 5 to 8 tonnes per hectare). Breeding for higher yield potential is therefore a critical national priority.

Yield stability is equally important: a high-yielding variety that performs well in good seasons but collapses in drought or disease pressure is of limited value to smallholder farmers who cannot risk total crop failure. Breeders therefore select for broad adaptation (performance across many environments) or specific adaptation (high performance in a defined target environment). Yield stability is measured by evaluating varieties across multiple locations and seasons and using statistical tools such as stability analysis to identify varieties that maintain performance despite environmental variation.

Fill in the blank: Yield _____ is as important as high yield potential; it measures whether a variety maintains performance across multiple environments and seasons rather than only in favourable conditions.

1.2.2 Improving quality and resistance

Quality improvement covers nutritional quality (protein content and amino acid profile in cereals and legumes, oil content and fatty acid profile in oilseed crops, vitamin and mineral content), processing quality (milling recovery, cooking time, taste and texture), and market quality (grain size, colour, and appearance that determine market price). In Nigeria, breeding programmes have developed quality protein maize (QPM) with improved lysine and tryptophan content, high-iron and high-zinc cowpea varieties, and improved oil palm with higher oleic acid content.

Resistance breeding aims to develop cultivars that withstand or tolerate the major biotic stresses (diseases, pests, and parasitic weeds) and abiotic stresses (drought, flooding, heat, soil acidity, and low soil fertility) affecting the target crop in its production environment. In Nigeria, key disease targets include Striga resistance in sorghum and maize, Cassava mosaic disease resistance, late blight resistance in potato, and cercospora leaf spot resistance in groundnut. Resistance reduces the need for chemical inputs, lowers production costs, and is particularly important for resource-poor farmers who cannot afford pesticides.

Fill in the blank: Resistance breeding develops cultivars that withstand biotic stresses (diseases, pests, parasitic weeds) and abiotic stresses (drought, flooding, heat, soil _____, and low soil fertility).

Crop	Yield Objective	Quality Objective	Resistance Target
Maize	High grain yield, early maturity	Improved protein content (QPM), good kernel texture	Resistance to maize streak virus, drought tolerance
Rice	High paddy yield, short duration	Good milling quality, aroma, cooking quality	Resistance to blast disease, tolerance to iron toxicity
Cassava	High root yield, early bulking	High starch content, low cyanide levels	Resistance to cassava mosaic disease, mealybug, drought tolerance
Cowpea	High seed yield, short maturity	Good seed size, cooking quality	Resistance to Maruca pod borer, Striga, drought tolerance
Sorghum	High grain yield, adaptability to dry zones	Good malting quality, palatability	Resistance to anthracnose, drought tolerance

Table 1.1: Major breeding objectives for key Nigerian food crops

1.2.3 Adaptation to environmental conditions

Adaptation breeding develops cultivars suited to specific environmental conditions that limit production in a target region. Early maturity is among the most important adaptation traits for Nigerian farmers in the Sudan and Sahel zones where the growing season is short (90 to 120 days); short-season varieties of sorghum, millet, and cowpea allow farmers to complete their crop before the rains end. Drought tolerance is critical in drier zones; varieties with deep root

systems, efficient water use, and the ability to recover after temporary water stress are especially valuable.

Other important adaptation targets include tolerance to soil acidity and aluminium toxicity (important for the acid savanna soils of central Nigeria), waterlogging tolerance (for low-lying fadama areas and the Niger Delta), and high-temperature tolerance (increasingly important with climate change). Photoperiod sensitivity is also an adaptation trait: some varieties require specific day-length conditions to flower and are therefore restricted to a narrow range of latitudes or planting dates; photoperiod-insensitive varieties can be planted across a wider range of conditions and seasons.

Fill in the blank: Early _____ is a critical adaptation trait for farmers in the Sudan and Sahel zones of Nigeria where the growing season is only 90 to 120 days.

Pilot questions 1.2

1. Explain the difference between yield potential and yield stability in crop breeding.
2. Describe two quality improvement objectives in Nigerian crop breeding programmes and give one example of each.
3. Explain why resistance breeding is particularly important for resource-poor Nigerian smallholder farmers.
4. Define adaptation and explain why early maturity is a critical breeding objective in northern Nigeria.
5. Explain what photoperiod sensitivity is and why photoperiod-insensitive varieties are preferred in some breeding programmes.

1.3 Biological Variation in Crop Plants

1.3.1 Sources of genetic variation

Genetic variation is the raw material of plant breeding; without variation among individuals, there is nothing to select and no improvement is possible. The main sources of genetic variation available to breeders are: natural variation existing in wild relatives and traditional varieties (landraces), recombination of existing alleles through hybridisation (crossing), induced mutation, and polyploidy. Natural variation in gene banks (collections of diverse accessions) is the most important starting point because it provides the diversity generated by thousands of years of evolution and farmer selection across many environments.

Landrace varieties are traditional farmer varieties that have been selected over many generations for local adaptation and acceptable yield in specific farming systems. They contain valuable alleles for stress tolerance, pest resistance, and quality traits that may not be present in modern high-yielding varieties. Wild relatives of cultivated crops (the wild progenitors and species in the same genus or family) are another important source; they often carry resistance genes to diseases and pests that have been lost during domestication. Both landraces and wild relatives are collected and conserved in gene banks for use in breeding.

Fill in the blank: _____ varieties are traditional farmer varieties selected over many generations for local adaptation; they contain valuable alleles for stress tolerance that may be absent in modern high-yielding varieties.

1.3.2 Mutation and polyploidy as sources of variation

Mutation is a change in the DNA sequence of a gene that produces a new allele not previously present in the population. Natural mutation rates are very low (approximately one per gene per million gametes), but mutations are continuous and are the ultimate source of all genetic variation. Plant breeders can increase the mutation rate dramatically using mutagens: physical mutagens such as X-rays, gamma rays, and ultraviolet radiation, and chemical mutagens such as ethyl methane sulphonate (EMS) and colchicine. Mutation breeding has produced useful

varieties of barley, sorghum, groundnut, and cotton with improved disease resistance, altered plant architecture, or modified seed quality.

Polyploidy is the condition of having more than two complete sets of chromosomes per cell. It occurs naturally (autopolyploidy from chromosome doubling within a species, or allopolyploidy from hybridisation between species followed by chromosome doubling) and can be induced artificially using colchicine, which inhibits spindle formation during cell division, preventing chromosome separation. Many important crops are naturally polyploid: wheat (hexaploid, 6 sets), cotton (allotetraploid, 4 sets), sugarcane (octaploid, 8 sets), and banana (triploid, 3 sets). Polyploidy often produces larger plant parts (the gigas effect) and can restore fertility to interspecific hybrids.

Fill in the blank: _____ is the condition of having more than two complete sets of chromosomes per cell; it can be induced using colchicine and often produces larger plant parts through the gigas effect.

1.3.3 Phenotypic versus genotypic variation

Phenotypic variation is the observable difference among individuals in a population for a measurable trait (plant height, grain yield, leaf colour, disease score). It is the product of two components: genotypic variation (differences in the underlying DNA sequences and gene combinations) and environmental variation (differences in soil fertility, moisture, temperature, and other growing conditions experienced by individual plants). Only genotypic variation is heritable and transmissible to offspring; environmental variation is not passed on.

The distinction between genotypic and phenotypic variation is fundamental to plant breeding because selection is applied to the phenotype but its effect depends on the proportion of phenotypic variation that is genetic. A trait that is highly heritable (most of its phenotypic variation is genetic) responds rapidly to selection; a trait with low heritability (most variation is environmental) responds slowly and requires much larger population sizes and more generations of selection to achieve improvement. Heritability is covered in detail in Series 3; it is introduced here as the key concept linking genotypic and phenotypic variation.

Fill in the blank: Phenotypic variation has two components: _____ variation (heritable, DNA-based differences) and environmental variation (non-heritable differences due to growing conditions).

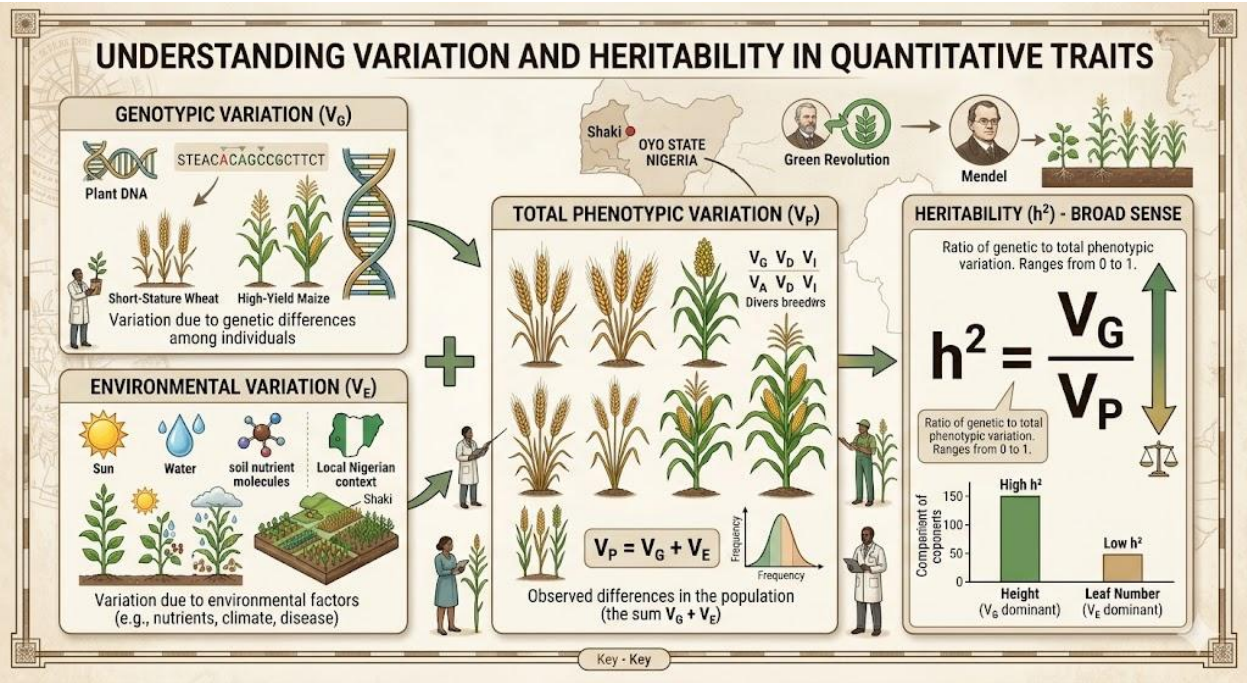

Figure 1.2: Diagram showing the components of phenotypic variation

Pilot questions 1.3

1. State four sources of genetic variation available to plant breeders.
2. Explain what a landrace variety is and state its importance as a source of genetic variation.
3. Define mutation and explain how plant breeders increase the mutation rate to create new variation.
4. Explain what polyploidy is and give two examples of naturally polyploid crop plants.
5. Distinguish between phenotypic and genotypic variation and explain why this distinction matters in selection.

1.4 Importance of Variation in Breeding Programmes

1.4.1 How breeders exploit variation

Plant breeders exploit genetic variation through selection: identifying and choosing individuals or populations with superior genotypes and using them as parents for the next generation. The effectiveness of selection depends on three factors: the amount of genetic variation present (more variation means more opportunity to select superior types), the heritability of the target trait (the higher the heritability, the more reliable the phenotypic values are as predictors of genetic merit), and the selection intensity (the more stringent the selection threshold, the larger the expected gain per generation, but at the cost of a smaller effective population size).

Hybridisation is the primary tool for combining variation from different sources. By crossing two parents with complementary desirable traits, the breeder creates a segregating population containing new combinations of alleles. From this population, individuals that combine the best traits of both parents (transgressive segregants) can be selected. The breeder then fixes the desired combinations through selfing (in self-pollinated crops) or maintains them in hybrid form (in cross-pollinated crops). This cycle of hybridisation and selection is the core activity of all conventional breeding programmes.

Fill in the blank: The effectiveness of selection depends on the amount of genetic variation present, the _____ of the target trait, and the selection intensity applied by the breeder.

1.4.2 Conservation of genetic resources

Genetic resources (the heritable materials of plants that have actual or potential value for food and agriculture) must be conserved because they are the source of the variation needed for future breeding. The main conservation strategies are: ex situ conservation (maintaining living plant materials outside their natural habitat in gene banks, seed banks, field collections, or in vitro tissue culture) and in situ conservation (maintaining species and varieties in their natural habitats or traditional farming systems). The International Plant Genetic Resources Institute (now Bioversity International) coordinates global gene bank networks.

In Nigeria, the National Centre for Genetic Resources and Biotechnology (NACGRAB) in Ibadan is the national gene bank institution, responsible for collecting, characterising, conserving, and distributing plant genetic resources. NACGRAB maintains collections of traditional varieties of cowpea, sorghum, millet, yam, and other Nigerian crops. The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA, 2004) governs the access to and benefit sharing of genetic resources among member countries, recognising that these resources are a global public good.

Fill in the blank: Ex situ conservation maintains plant materials _____ their natural habitat in gene banks, seed banks, field collections, or in vitro tissue culture.

1.4.3 Genetic erosion and its consequences

Genetic erosion is the loss of genetic diversity in crop species and their wild relatives, caused primarily by the replacement of diverse traditional varieties (landraces) with a small number of uniform modern varieties. When a landrace disappears from a farming system, the unique alleles it carries are lost permanently if no sample has been collected and stored in a gene bank. The consequences of genetic erosion are: reduced ability to respond to new diseases and pests (uniform crops are vulnerable to epidemics); loss of climate adaptation options (alleles for drought tolerance or heat resistance may be needed in future breeding programmes); and reduced raw material for breeding.

A dramatic historical example of genetic erosion's consequences is the Irish potato famine of 1845 to 1852, in which the entire Irish potato crop was destroyed by late blight (Phytophthora infestans) because Irish farmers grew only one or two genetically uniform varieties with no resistance to the pathogen. In Nigeria, the progressive adoption of uniform improved cassava varieties has reduced the diversity of traditional cassava varieties in many farming communities, raising concern about the long-term resilience of the crop. Preventing genetic erosion requires active collection and conservation programmes combined with policies that support the continued cultivation of traditional varieties.

Fill in the blank: Genetic _____ is the loss of genetic diversity caused primarily by the replacement of diverse traditional varieties with a small number of uniform modern cultivars.

Consequences	Strategies for Prevention
Loss of biodiversity	Establish gene banks and seed banks to conserve genetic material
Reduced adaptability to climate change	Promote on-farm conservation and use of diverse local breeds/crop varieties
Increased vulnerability to pests and diseases	Encourage integrated pest management and maintain genetic diversity in breeding programs
Decline in food security	Support community seed systems and farmer cooperatives to preserve traditional varieties
Loss of cultural heritage linked to indigenous breeds/crops	Document and promote indigenous knowledge and traditional farming practices
Reduced options for future breeding and improvement	Invest in research, extension services, and participatory breeding with farmers

Box 1.1: Consequences of genetic erosion and strategies for prevention

Pilot questions 1.4

1. Explain what selection is in plant breeding and state three factors that affect its effectiveness.
2. Explain what hybridisation achieves in a breeding programme and what transgressive segregation means.
3. Distinguish between ex situ and in situ conservation of genetic resources and give one example of each.
4. State the role of NACGRAB in Nigeria's genetic resource conservation programme.
5. Define genetic erosion and explain two consequences it has for crop breeding and food security.

Series Summary

This Series introduced the foundations of crop breeding. We defined crop breeding as the purposeful manipulation of plant genetic composition to produce improved cultivars, distinguished it from agronomy, traced its history from early farmer selection through Mendel's rediscovery in 1900, hybrid maize, the Green Revolution, and modern molecular tools, and described the plant breeder's role and the 8 to 15 year timeline from cross to cultivar release. We

then covered the main breeding purposes: yield and yield stability, quality improvement, resistance to biotic and abiotic stresses, and adaptation to environmental conditions.

We examined the sources of biological variation (natural variation in landraces and wild relatives, hybridisation recombination, mutation, and polyploidy), distinguished phenotypic from genotypic variation, and introduced heritability as the key concept linking the two. Finally, we covered how breeders exploit variation through selection and hybridisation, the importance of ex situ and in situ conservation of genetic resources by institutions such as NACGRAB in Nigeria, and the threat of genetic erosion. By completing this Series, you should be able to achieve all eight Series Learning Outcomes (SLO 1.1 to SLO 1.8).

Glossary of Terms

- **Allele:** one of two or more alternative forms of a gene at a given locus; different alleles produce different phenotypic effects for the same trait.
- **Broad adaptation:** the ability of a variety to perform well across a wide range of environments; desirable for varieties intended for large-scale distribution.
- **Colchicine:** a chemical mutagen derived from the autumn crocus plant that inhibits spindle formation during cell division, preventing chromosome separation and causing polyploidy.
- **Cultivar:** a plant grouping that has been selected for particular characteristics and can be reproduced with those characteristics maintained; the formal term for a plant variety.
- **Ex situ conservation:** the conservation of plant genetic resources outside their natural habitat in gene banks, seed banks, field collections, or in vitro tissue culture.
- **Genetic erosion:** the loss of genetic diversity in crop species caused primarily by the replacement of diverse traditional varieties with uniform modern cultivars.
- **Genetic variation:** heritable differences in DNA sequences among individuals in a population; the raw material of plant breeding and natural selection.

- **Genotypic variation:** variation among individuals due to differences in their underlying genetic composition (DNA sequences and gene combinations); the heritable component of phenotypic variation.
- **Gigas effect:** the tendency of polyploid plants to produce larger cells, organs, and plant parts than their diploid progenitors.
- **Green Revolution:** the period of the 1960s to 1970s marked by the development and widespread adoption of semi-dwarf, high-yielding wheat and rice varieties that dramatically increased food production in Asia and other regions.
- **Heritability:** the proportion of total phenotypic variation in a population that is attributable to genetic variation; ranges from 0 (all variation is environmental) to 1 (all variation is genetic).
- **Hybridisation:** the crossing of two genetically different parents to produce offspring (hybrids) with new combinations of alleles from both parents.
- **In situ conservation:** the conservation of plant genetic resources within their natural habitats or traditional farming systems.
- **Landrace:** a traditional farmer variety that has been selected over many generations for local adaptation, acceptable yield, and quality in specific farming systems; a major source of genetic diversity for breeding.
- **Mutagen:** a physical or chemical agent that increases the rate of mutation above the natural background level; used in mutation breeding to create new genetic variation.
- **Mutation:** a heritable change in the DNA sequence of a gene that produces a new allele not previously present in the population.
- **NACGRAB:** National Centre for Genetic Resources and Biotechnology; the Nigerian national gene bank institution responsible for collecting, conserving, and distributing plant genetic resources.
- **NVRC:** National Variety Release Committee; the Nigerian government body under the Federal Ministry of Agriculture that approves new crop cultivars for commercial release and distribution.
- **Phenotypic variation:** observable differences among individuals in a population for a measurable trait; the combined result of genotypic variation and environmental variation.

- **Photoperiod sensitivity:** the response of a plant's flowering time to day length; photoperiod-sensitive varieties flower only under specific day-length conditions, restricting their range of adaptation.
- **Polyploidy:** the condition of having more than two complete sets of chromosomes per cell; occurs naturally in many crop plants and can be induced artificially using colchicine.
- **Selection intensity:** the proportion of the population chosen as parents for the next generation; higher selection intensity (choosing fewer, better individuals) increases genetic gain per generation but reduces population size.
- **Transgressive segregation:** the appearance in a segregating population of individuals that exceed the performance of either parent for a quantitative trait, resulting from favourable recombination of alleles from both parents.
- **Wild relative:** a wild species that is the progenitor of or closely related to a cultivated crop; an important source of alleles for disease resistance and stress tolerance that may have been lost during domestication.
- **Yield gap:** the difference between the potential yield demonstrated in research trials and the actual yield achieved by farmers in their fields; a key indicator of the scope for agronomic and breeding improvement.

Concept Check Questions [Series 1]

Objective Questions

1. Crop breeding is the purposeful manipulation of the _____ composition of plant populations to produce cultivars with improved characteristics. (Linked to SLO 1.1)
2. Scientific crop breeding began with the rediscovery of _____ laws in 1900, which provided the theoretical basis for predicting the outcome of crosses. (Linked to SLO 1.2)
3. Yield _____ measures whether a variety maintains performance across multiple environments and seasons rather than only in favourable conditions. (Linked to SLO 1.3)

4. _____ varieties are traditional farmer varieties selected over many generations for local adaptation and contain valuable alleles that may be absent in modern cultivars. (Linked to SLO 1.4)
5. Genetic _____ is the loss of genetic diversity caused primarily by the replacement of diverse traditional varieties with uniform modern cultivars. (Linked to SLO 1.8)

Short-Answer Questions

6. State four main purposes of crop breeding programmes. (Linked to SLO 1.3)
7. State four sources of genetic variation available to plant breeders. (Linked to SLO 1.4)
8. Explain what polyploidy is and give two examples of naturally polyploid crop plants. (Linked to SLO 1.5)
9. Distinguish between phenotypic and genotypic variation and explain why the distinction matters in breeding. (Linked to SLO 1.6)
10. Distinguish between ex situ and in situ conservation and state the role of NACGRAB. (Linked to SLO 1.8)

Long-Answer Questions

11. Describe the definition, history, and objectives of crop breeding, explaining the role of the plant breeder and the timeline for cultivar development, with reference to Nigeria. (Linked to SLOs 1.1, 1.2, 1.3)
12. Describe the sources, types, and importance of biological variation in crop plants, explaining the distinction between phenotypic and genotypic variation and the significance of heritability in plant breeding. (Linked to SLOs 1.4, 1.5, 1.6)
13. Explain how plant breeders exploit genetic variation, the importance of genetic resource conservation, and the threat of genetic erosion to crop breeding and food security in Nigeria. (Linked to SLOs 1.7, 1.8)

Answers to Concept Check Questions [Series 1]

Objective Questions

1. Genetic.
2. Mendel's.
3. Stability.
4. Landrace.
5. Erosion.

Short-Answer Questions

6. Increasing yield (more product per unit area); improving yield stability (consistent performance across environments); improving quality (nutritional, processing, market quality); improving resistance to biotic stresses (diseases, pests, parasitic weeds); improving tolerance to abiotic stresses (drought, heat, soil acidity); and improving adaptation (early maturity, photoperiod insensitivity for specific environments).
7. Natural variation in landraces and wild relatives; recombination of alleles through hybridisation (crossing); induced mutation (using physical or chemical mutagens); and polyploidy (natural or induced chromosome doubling).
8. Polyploidy is the condition of having more than two complete sets of chromosomes per cell. Examples: wheat (hexaploid, 6 chromosome sets); cotton (allotetraploid, 4 sets); sugarcane (octaploid, 8 sets); banana (triploid, 3 sets).
9. Phenotypic variation is the observable difference among individuals for a measurable trait; it includes both genotypic variation (heritable, DNA-based differences) and environmental variation (non-heritable differences due to growing conditions). The distinction matters because selection is applied to the phenotype but improvement depends entirely on the genetic component; traits with high heritability (most variation is genetic) respond rapidly to selection, while those with low heritability respond slowly and require larger populations.
10. Ex situ conservation maintains plant materials outside their natural habitat in gene banks, seed banks, or field collections. In situ conservation maintains species in their natural habitats or traditional farming systems. NACGRAB (National Centre for Genetic Resources and Biotechnology) in Ibadan is the Nigerian national gene bank institution responsible for collecting, characterising, conserving, and distributing plant genetic resources including traditional varieties of cowpea, sorghum, millet, and yam.

Long-Answer Questions

11. Crop breeding: purposeful manipulation of plant genetic composition to produce improved cultivars; differs from agronomy (agronomy improves the environment; breeding improves the plant genetically). Cultivar: a plant grouping maintained with consistent characteristics; NVRC approves commercial release in Nigeria. History: farmer selection from 10,000 BP (domestication of teosinte to maize, wild cowpea to cultivated cowpea); Mendel's laws rediscovered 1900 (theoretical basis for crosses); hybrid maize 1920s to 1940s (doubled US yields); Green Revolution 1960s to 1970s (semi-dwarf wheat and rice); IITA established 1967 in Nigeria; marker-assisted selection 1990s to 2000s; genomic selection 2010s. Breeder's role: define objectives from farmer and market needs; assemble genetic base; make crosses; select from segregating populations; evaluate in multi-location trials; release cultivars. Timeline: 8 to 15 years from cross to commercial release. Purposes: yield potential, yield stability, quality improvement, resistance (biotic: diseases, pests, Striga; abiotic: drought, heat, soil acidity, waterlogging), adaptation (early maturity, photoperiod insensitivity).
12. Sources of genetic variation: natural variation in landraces and wild relatives (thousands of years of evolution and farmer selection); hybridisation recombination (new allele combinations from crosses); mutation (heritable DNA change; mutagens: gamma rays, EMS, colchicine; low natural rate increased by mutagens); polyploidy (more than two chromosome sets; natural in wheat hexaploid, cotton allotetraploid, banana triploid; induced by colchicine; gigas effect produces larger plant parts). Phenotypic vs genotypic variation: phenotypic = genotypic + environmental; only genotypic is heritable; heritability = genotypic variation / total phenotypic variation; ranges 0 to 1; high heritability = rapid response to selection; low heritability = slow response, needs large populations and many generations.
13. Exploiting variation: selection identifies superior genotypes from phenotypic performance; effectiveness depends on amount of genetic variation, heritability of trait, and selection intensity; hybridisation combines variation from different sources creating segregating populations; transgressive segregants combine best traits of both parents; breeders fix combinations through selfing (self-pollinated crops) or maintain in hybrid form (cross-pollinated crops). Conservation: genetic resources are essential raw material; ex situ (gene banks, seed banks, field collections, tissue culture) and in situ (natural habitats, traditional farming systems); NACGRAB collects and conserves Nigerian crop diversity; ITPGRFA (2004) governs international access and benefit

sharing. Genetic erosion: loss of diversity from replacement of landraces by uniform modern varieties; consequences: vulnerability to epidemic diseases (Irish potato famine example), loss of climate adaptation options (drought/heat alleles), reduced breeding raw material; in Nigeria, uniform improved cassava replacing diverse traditional varieties; prevention: active gene bank collection, in situ conservation, community seed banks, policies supporting landrace cultivation.

Answers to Pilot Questions [Series 1]

Part 1.1: What is Crop Breeding?

1. Crop breeding is the purposeful manipulation of the genetic composition of plant populations to produce new cultivars with improved characteristics that better meet human needs. It differs from crop agronomy in that agronomy improves the environment around the plant (soil preparation, fertilisation, irrigation, pest management) while crop breeding improves the plant itself by changing its genetic make-up to produce a genetically superior variety.
2. A cultivar is a plant grouping selected for particular characteristics that can be reproduced with those characteristics maintained; it is the formal term for what is informally called a variety. The National Variety Release Committee (NVRC) under the Federal Ministry of Agriculture is the Nigerian regulatory body that evaluates data from national performance trials, safety assessments, and distinctness, uniformity, and stability tests before approving a new cultivar for commercial release and distribution to farmers.
3. Any two: (1) Mendel's laws of inheritance were rediscovered in 1900, providing the theoretical basis for predicting the outcome of crosses and transforming crop improvement from an empirical art into a science. (2) The Green Revolution of the 1960s to 1970s involved the development of semi-dwarf, high-yielding, fertiliser-responsive wheat and rice varieties by CIMMYT and IRRI respectively, which dramatically increased food production in Asia and prevented widespread famine.
4. Any four: defining breeding objectives based on farmer and market needs; assembling the genetic base by collecting parent materials with desired traits; making crosses to combine desired traits in one plant; selecting superior individuals or lines from segregating offspring; evaluating selected lines in multi-location yield trials; submitting promising lines for national performance trials and variety release.

5. A breeding programme takes 8 to 15 years because each step requires multiple growing seasons: making the initial cross takes one season; developing homozygous lines through selfing takes 5 to 7 generations (each a season); yield trials at multiple locations require 3 to 5 seasons to generate statistically reliable performance data; regulatory review by the NVRC adds further time. Each step cannot be shortcut without risking release of an inferior cultivar.

Part 1.2: Purposes of Crop Breeding

1. Yield potential refers to the maximum yield a variety can achieve under optimal conditions (sufficient water, nutrients, and absence of pests and diseases); it is measured in controlled trials at research stations. Yield stability refers to the consistency of yield performance across different environments, seasons, and stress levels; a stable variety does not achieve the highest yield in any single environment but maintains acceptable yields across all environments. Smallholder farmers who cannot control their environment value stability; commercial farmers with full input access may prefer high potential even at the cost of stability.
2. Any two with examples: Nutritional quality improvement: quality protein maize (QPM) developed by IITA and CIMMYT with increased lysine and tryptophan content, addressing protein malnutrition in maize-dependent communities; high-iron and high-zinc cowpea varieties developed at IITA for Nigeria. Processing quality improvement: improved milling recovery in rice varieties so that a higher proportion of the paddy weight is converted to marketable white rice; reduced cooking time in cowpea varieties that saves fuel and water for Nigerian households.
3. Resource-poor smallholder farmers in Nigeria cannot afford or access chemical pesticides and fungicides for effective disease and pest control. A resistant variety provides built-in protection against the major pest or disease at no additional cost to the farmer, reducing yield losses without requiring cash input. Resistance also reduces the environmental and health risks associated with pesticide use. For farmers in remote areas where inputs are unavailable or unaffordable, a resistant variety may be the only viable way to manage biotic stress.
4. Adaptation in plant breeding refers to the ability of a variety to perform well (produce acceptable yield and quality) in a specific target environment. Early maturity is critical for northern Nigerian farmers in the Sudan and Sahel zones because the rainy season lasts only 90 to 120 days; a variety that requires 150 days to maturity will not complete its growth cycle before drought terminates. Early-maturing varieties of sorghum (75 to 90 days), millet (75 to 85 days), and cowpea (55 to 65 days) allow farmers to complete their crop within the available growing season.

5. Photoperiod sensitivity is the influence of day length on the timing of flowering in a plant. Photoperiod-sensitive varieties flower only under specific day-length conditions (for example, only when days are shorter than 12 hours); they can be planted only at specific times of year and in a narrow latitude range. Photoperiod-insensitive varieties flower independently of day length and can therefore be planted across a wider range of dates and latitudes, making them more widely adaptable. For breeders targeting large, diverse deployment areas in Nigeria, photoperiod insensitivity is preferred because it reduces the risk that a variety will fail to flower if planting is delayed.

Part 1.3: Biological Variation in Crop Plants

1. Natural variation in landraces and wild relatives; recombination of alleles through hybridisation; induced mutation using physical or chemical mutagens; and polyploidy (natural or induced chromosome doubling).
2. A landrace is a traditional farmer variety that has been selected over many generations for local adaptation, acceptable yield, and acceptable quality in a specific farming system. Its importance as a source of genetic variation lies in the unique combination of alleles it carries for stress tolerance, pest and disease resistance, and quality traits that were never exposed to modern plant breeding and therefore remain available in their original diversity. Many modern high-yielding varieties were developed by crossing landraces with each other or with improved materials, and future breeding for climate resilience will depend heavily on landrace alleles.
3. Mutation is a heritable change in the DNA sequence of a gene that produces a new allele not previously present in the population. The natural mutation rate (approximately one mutation per gene per million gametes) is very low. Breeders increase the mutation rate by treating seeds or pollen with mutagens: physical mutagens (X-rays, gamma rays from cobalt-60, ultraviolet radiation) damage or break DNA strands; chemical mutagens (ethyl methane sulphonate EMS, colchicine) alkylate DNA bases or inhibit chromosome separation. The treated material is then grown out and screened for useful new phenotypes that can be incorporated into breeding programmes.
4. Polyploidy is the condition of having more than two complete sets of chromosomes per cell. Naturally polyploid crop examples: hexaploid bread wheat (2n = 6x = 42 chromosomes; an allopolyploid derived from three different grass species); allotetraploid upland cotton (Gossypium

hirsutum, 2n = 4x = 52, derived from the hybridisation of two diploid cotton species with subsequent chromosome doubling).

5. Phenotypic variation is the observable difference among individuals in a population for a measurable trait; it is caused by both genetic and environmental factors. Genotypic variation is the heritable component of phenotypic variation attributable solely to differences in individuals' DNA sequences and gene combinations. The distinction matters in breeding because selection acts on the phenotype but improvement is transmitted only through the genetic component: if most phenotypic variation is environmental (low heritability), selecting high-performing individuals in one environment will not reliably produce high-performing offspring in other environments, making the selection inefficient.

Part 1.4: Importance of Variation in Breeding Programmes

1. Selection in plant breeding is the process of identifying and retaining individuals or families with superior phenotypic values for desired traits and using them as parents for the next generation. Three factors affecting its effectiveness: amount of genetic variation present (more variation provides more opportunity to identify superior genotypes); heritability of the target trait (higher heritability means the phenotype is a more reliable predictor of genotypic merit, so selected individuals are more likely to transmit their superiority to offspring); selection intensity (the more stringent the selection threshold, the greater the expected genetic gain per generation, but at the cost of reduced population size).
2. Hybridisation in plant breeding produces offspring with new combinations of alleles drawn from both parents, creating genetic variation that did not exist in either parent alone. Transgressive segregation occurs when some offspring in a segregating population exceed the performance of both parents for a quantitative trait; this happens when both parents carry some favourable alleles at different loci, and recombination brings all the favourable alleles together in a single individual. Transgressive segregants are among the most valuable outcomes of hybridisation because they allow breeders to achieve performance levels unattainable from either parent alone.
3. Ex situ conservation maintains plant genetic resources outside their natural habitat: examples include gene banks (such as the NACGRAB gene bank in Ibadan, which stores seeds of traditional Nigerian crop varieties at controlled temperature and humidity), field gene banks (living plant collections for vegetatively propagated crops such as yam and cassava), and in vitro collections (tissue culture of endangered or difficult-to-store materials). In situ conservation

maintains genetic diversity within natural ecosystems or traditional farming systems: examples include on-farm conservation (where farmers continue growing traditional varieties in their fields) and protected natural areas where wild relatives of crops are conserved.

4. NACGRAB (National Centre for Genetic Resources and Biotechnology), located in Ibadan, is Nigeria's national institution for plant genetic resource conservation. Its role is to collect germplasm of Nigerian crop varieties (particularly landraces and traditional varieties) from farming communities, characterise the collected accessions for agronomic and quality traits, conserve the accessions under long-term storage conditions, and distribute germplasm to breeders and researchers who need it for their breeding programmes. NACGRAB also maintains field collections for crops that cannot be stored as dry seeds.
5. Genetic erosion is the progressive loss of genetic diversity in crop species caused primarily by the replacement of diverse traditional varieties and landraces with a small number of genetically uniform modern cultivars. Two consequences: (1) Increased vulnerability to epidemic diseases and pests: genetically uniform crops grown over large areas are susceptible to devastating epidemics when a new pathogen race appears, because no individual in the population has resistance (the Irish potato famine of 1845 to 1852 is the classic example; in Nigeria, the rapid spread of cassava mosaic disease through uniform modern cassava varieties illustrates the same principle). (2) Permanent loss of alleles needed for future breeding: once a landrace is lost from farming and from gene banks, its unique alleles (including drought tolerance genes or resistance genes valuable under future climate change conditions) are lost permanently and cannot be recovered.

References and Attributions [Series 1]

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

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Series 2: Plant Cell Division, Fertilisation, and Genetic Principles

- **Part 2.1: The Plant Cell and Its Genetic Content**
    - Sub Part 2.1.1: Structure of the plant cell relevant to heredity
    - Sub Part 2.1.2: Chromosomes: structure and number
    - Sub Part 2.1.3: Genes, symbols, and terminology
- **Part 2.2: Mitosis: Somatic Cell Division**
    - Sub Part 2.2.1: Significance of mitosis in plant growth
    - Sub Part 2.2.2: Stages of mitosis
    - Sub Part 2.2.3: Mitosis and its relevance to plant breeding
- **Part 2.3: Meiosis: Gametogenesis**
    - Sub Part 2.3.1: Significance of meiosis in sexual reproduction
    - Sub Part 2.3.2: Stages of meiosis I and meiosis II
    - Sub Part 2.3.3: Crossing over, recombination, and genetic variation
- **Part 2.4: Fertilisation and the Genetic Basis of Inheritance**
    - Sub Part 2.4.1: Fertilisation in flowering plants
    - Sub Part 2.4.2: Double fertilisation and endosperm formation

- Sub Part 2.4.3: Genetic consequences of fertilisation for breeding

Introduction

All of crop breeding rests on the behaviour of chromosomes and genes during cell division and fertilisation. When a breeder makes a cross between two parent plants, the mechanism that combines and reshuffles parental genes in the offspring is meiosis, the process of gametogenesis. Understanding mitosis (ordinary cell division that maintains chromosome number), meiosis (reductive division that halves chromosome number and creates new gene combinations), and fertilisation (which restores the full chromosome number) is therefore essential background for understanding how breeding works at the cellular and molecular level.

This Series covers the plant cell and its genetic content, the process and significance of mitosis, the stages and outcomes of meiosis including crossing over and recombination, and the process of fertilisation in flowering plants including double fertilisation. We also introduce the key genetic terminology (gene, allele, locus, genotype, phenotype, dominance) that will be used throughout the course. All material in this Series provides the cellular and genetic foundation for the Mendelian genetics covered in Series 3.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 2.1** describe the structure of the plant cell nucleus and explain how genetic information is organised in chromosomes (Linked to Part 2.1),
- **SLO 2.2** define the key genetic terms: gene, allele, locus, genotype, phenotype, homozygous, heterozygous, dominant, recessive (Linked to Part 2.1),
- **SLO 2.3** describe the stages of mitosis and explain its significance for plant growth and breeding (Linked to Part 2.2),

- **SLO 2.4** describe the stages of meiosis I and meiosis II and explain how meiosis generates genetic variation (Linked to Part 2.3),
- **SLO 2.5** explain crossing over and recombination and state their importance for plant breeding (Linked to Part 2.3),
- **SLO 2.6** describe the process of fertilisation in flowering plants (Linked to Part 2.4),
- **SLO 2.7** explain double fertilisation and endosperm formation and state their significance for seed development (Linked to Part 2.4), and
- **SLO 2.8** explain the genetic consequences of fertilisation for plant breeding, including the restoration of ploidy and the creation of hybrid genotypes (Linked to Part 2.4).

2.1 The Plant Cell and Its Genetic Content

2.1.1 Structure of the plant cell relevant to heredity

The plant cell has three structures of particular importance for heredity: the nucleus, the chromosomes within it, and the DNA that makes up the chromosomes. The nucleus is a membrane-bound organelle that contains the cell's genetic information in the form of chromosomes. It is surrounded by the nuclear envelope, which has pores through which RNA molecules (transcribed from DNA) pass to the cytoplasm for translation into proteins. The nucleolus within the nucleus is the site of ribosomal RNA synthesis.

In addition to the nucleus, plant cells contain two other DNA-containing organelles: chloroplasts (which carry chloroplast DNA encoding photosynthetic proteins and some other functions) and mitochondria (which carry mitochondrial DNA encoding proteins of the electron transport chain). These organelles are inherited maternally in most plant species because the pollen grain (male gamete) contributes little or no cytoplasm to the zygote. Cytoplasmic (organellar) inheritance is important in plant breeding for traits such as cytoplasmic male sterility, which is used in the production of hybrid seed.

Fill in the blank: The _____ is the membrane-bound organelle containing the cell's chromosomes; plant cells also contain chloroplasts and mitochondria, which carry their own DNA and are inherited maternally.

2.1.2 Chromosomes: structure and number

A chromosome is a single linear molecule of DNA complexed with histone proteins into a compact structure called chromatin. During cell division the chromatin condenses into the visible structures we recognise as chromosomes. Each chromosome consists of two sister chromatids joined at the centromere; the centromere is the attachment site for spindle fibres during cell division. The ends of chromosomes are called telomeres, which protect the chromosomal DNA from degradation and prevent chromosome-to-chromosome fusions. Genes are arranged linearly along the chromosome; the specific position of a gene on a chromosome is called its locus.

The chromosome number (2n = the diploid number) is characteristic of each species. In crop plants: maize (Zea mays) 2n = 20; rice (Oryza sativa) 2n = 24; cowpea (Vigna unguiculata) 2n = 22; cassava (Manihot esculenta) 2n = 36; groundnut (Arachis hypogaea) 2n = 40; sorghum (Sorghum bicolor) 2n = 20; bread wheat (Triticum aestivum) 2n = 6x = 42. A haploid cell (gamete) contains one set of chromosomes (n); a diploid cell contains two sets (2n = two copies of each chromosome, one from each parent). The two copies of a chromosome are called homologous chromosomes (homologs).

Fill in the blank: The specific position of a gene on a chromosome is called its _____, and the two copies of each chromosome in a diploid cell (one from each parent) are called homologous chromosomes.

Crop	Chromosome Number
Maize (Zea mays)	2n = 20
Rice (Oryza sativa)	2n = 24
Cowpea (Vigna unguiculata)	2n = 22
Cassava (Manihot esculenta)	2n = 36
Groundnut (Arachis hypogaea)	2n = 40

Sorghum (Sorghum bicolor)	2n = 20
Wheat (Triticum aestivum)	2n = 42 (hexaploid)

Table 2.1: Chromosome numbers of major Nigerian food crops

2.1.3 Genes, symbols, and terminology

A gene is a segment of DNA that encodes a functional product (usually a protein) and influences one or more traits. Alleles are the alternative forms of a gene that can occupy the same locus; different alleles typically produce different phenotypic effects. In a diploid organism, each locus is represented twice (one allele on each homolog). If both alleles at a locus are identical, the individual is homozygous at that locus; if the two alleles differ, the individual is heterozygous. The genotype is the complete genetic constitution of an individual; the phenotype is its observable characteristics resulting from the interaction of genotype and environment.

In genetics notation, dominant alleles are written with capital letters and recessive alleles with lowercase letters. For example, for seed colour in peas: Y (dominant, yellow seed) and y (recessive, green seed). A homozygous dominant individual is YY; a homozygous recessive is yy; a heterozygous individual is Yy. Dominance describes the relationship between alleles at the same locus: a dominant allele produces its phenotypic effect when present in one copy (Yy looks yellow, the same as YY); a recessive allele produces its phenotype only when homozygous (yy, green). Codominance occurs when both alleles are expressed in the heterozygote.

Fill in the blank: A dominant allele produces its phenotypic effect in one copy (as in Yy), while a _____ allele produces its phenotype only when both copies at the locus are the same recessive allele (yy).

Pilot questions 2.1

1. Name three DNA-containing structures in a plant cell and explain why two of them are inherited maternally.
2. Define chromosome and name the three structural features of a chromosome important for cell division.

3. State the diploid chromosome number of maize, cowpea, and groundnut.
4. Define the following terms: gene, allele, locus, genotype, phenotype, homozygous, heterozygous.
5. Explain the difference between dominance and codominance, giving one example of each.

2.2 Mitosis: Somatic Cell Division

2.2.1 Significance of mitosis in plant growth

Mitosis is the type of cell division that produces two genetically identical daughter cells from a single parent cell, each with the same chromosome number as the parent (2n to 2n). It is the basis of all vegetative growth in plants: every time a shoot tip, root tip, or leaf primordium grows, it does so by mitosis. Mitosis is also the basis of asexual reproduction (vegetative propagation) by cuttings, tubers, and tillers, which is why vegetatively propagated plants are genetically identical to their parents. The genetic constancy maintained by mitosis is essential for producing uniform plant material in breeding experiments.

In plant breeding, mitosis is relevant to several specific contexts: the production of callus tissue and plant regeneration in tissue culture (used for rapid multiplication of selected genotypes); the creation of polyploids using colchicine (which blocks the mitotic spindle, causing chromosome doubling); and the understanding of somaclonal variation (random genetic changes that occur during tissue culture and can either generate useful new variation or introduce unwanted mutations into regenerated plants). Understanding mitosis is therefore not merely academic but has direct practical applications in modern plant breeding.

Fill in the blank: Mitosis produces two genetically _____ daughter cells from one parent cell, each with the same chromosome number; it is the basis of vegetative growth and asexual reproduction.

2.2.2 Stages of mitosis

Mitosis is preceded by interphase, during which DNA replication doubles the DNA content of the cell (producing two identical sister chromatids for each chromosome joined at the centromere) while the chromosome number remains the same. Mitosis itself is divided into four stages. Prophase: chromosomes condense and become visible; the nuclear envelope breaks down; the spindle apparatus (made of microtubules) begins to form from the centrioles (or in plants, from the spindle pole bodies). Metaphase: chromosomes align at the cell equator (metaphase plate); each chromosome is attached to spindle fibres from both poles via its centromere.

Anaphase: the centromeres split and sister chromatids are pulled to opposite poles of the cell by the shortening spindle fibres; each pole receives one complete set of chromosomes. Telophase: chromosomes arrive at the poles and decondense; a new nuclear envelope forms around each chromosome set; the spindle breaks down. Cytokinesis follows telophase: in plant cells, a cell plate forms at the cell equator (from Golgi vesicles) and grows outward to divide the cytoplasm, eventually becoming the new cell wall between the two daughter cells. The result is two cells each with the same chromosome number and genetic content as the parent cell.

Fill in the blank: In _____ of mitosis, chromosomes align at the cell equator with each centromere attached to spindle fibres from both poles; in anaphase, sister chromatids separate and are pulled to opposite poles.

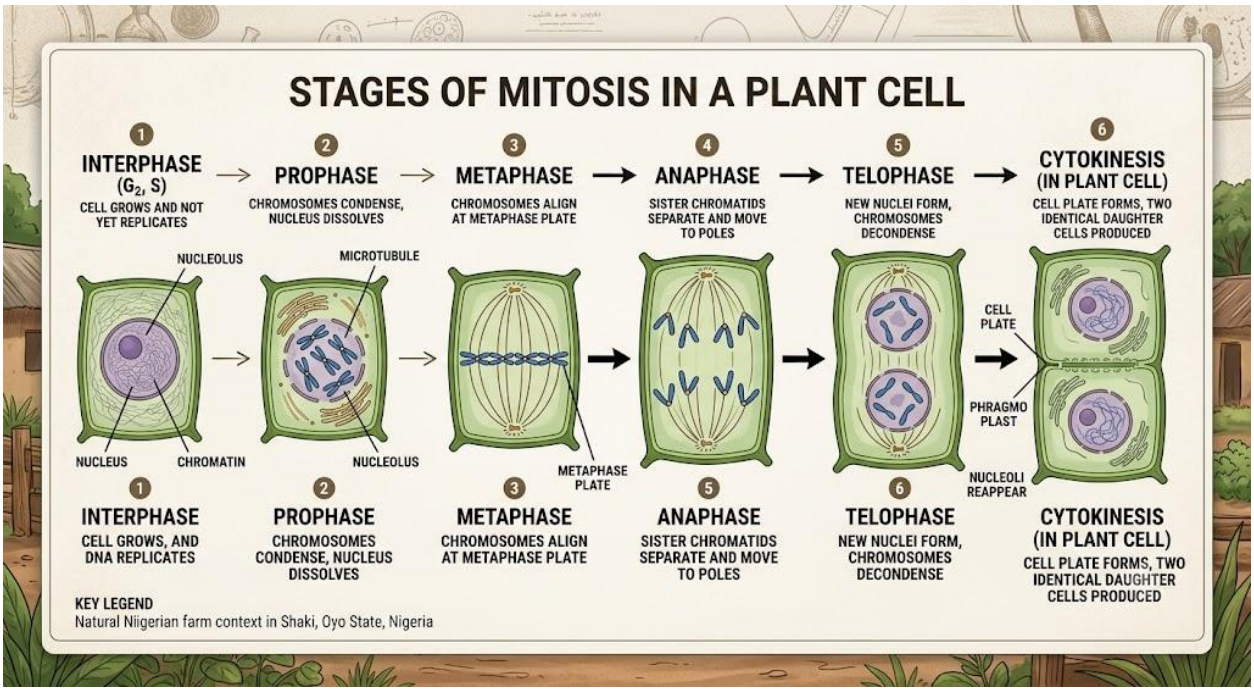

Figure 2.1: Diagram showing the stages of mitosis in a plant cell

2.2.3 Mitosis and its relevance to plant breeding

The genetic constancy of mitosis has important implications for plant breeding. When a breeder identifies a superior plant and propagates it vegetatively (by cuttings, grafts, or tissue culture), all copies are genetically identical to the original because vegetative propagation relies on mitosis. This is the basis of clonal varieties in cassava, yam, sugarcane, banana, and potato: the farmer plants a cutting or tuber that is genetically identical to the selected parent. Maintaining the identity of improved clonal material requires careful management to prevent outcrossing or contamination.

Colchicine-induced chromosome doubling relies on disrupting mitosis: colchicine prevents spindle formation, so when chromosomes separate at anaphase the cell cannot divide, resulting in a cell with twice the normal chromosome number. When the colchicine is washed away and division resumes normally, the doubled cell produces daughter cells that are tetraploid. This technique is used to create fertile allopolyploids from sterile interspecific hybrids (restoring chromosome pairing) and to produce triploid watermelons (which are seedless because triploids

cannot complete meiosis normally). Colchicine treatment is a standard tool in the plant breeder's kit.

Fill in the blank: Colchicine disrupts _____ formation during mitosis, preventing cell division and resulting in a cell with twice the normal chromosome number (polyploidy).

Pilot questions 2.2

1. Explain the significance of mitosis for plant growth and asexual reproduction.
2. Describe what happens during interphase before mitosis begins.
3. Describe the events of prophase and metaphase of mitosis.
4. Describe the events of anaphase and telophase of mitosis, and explain what cytokinesis produces in plant cells.
5. Explain how colchicine uses the mechanism of mitosis to produce polyploid plants.

2.3 Meiosis: Gametogenesis

2.3.1 Significance of meiosis in sexual reproduction

Meiosis is the specialised cell division that produces gametes (pollen and egg cells in plants) with half the chromosome number of the parent (2n to n). It is the basis of sexual reproduction because it produces haploid cells that can fuse at fertilisation to restore the diploid number. Without meiosis, each fertilisation event would double the chromosome number, quickly leading to non-viable organisms. Meiosis consists of two successive divisions: meiosis I (the reductive division, which separates homologous chromosomes) and meiosis II (which separates sister chromatids, similar to mitosis).

Meiosis is the most important process in plant breeding because it generates the genetic variation that makes selection possible. Two mechanisms during meiosis I create new allele combinations: independent assortment (the random distribution of maternal and paternal homologs to the two poles, generating 2n different possible gametes for an organism with n chromosome pairs) and crossing over (the physical exchange of segments between homologous chromosomes, creating

recombinant chromosomes with new combinations of alleles). Together these mechanisms ensure that virtually every gamete is genetically unique.

Fill in the blank: Meiosis generates genetic variation through two mechanisms: independent _____ of homologous chromosomes and crossing over (exchange of segments between homologs) during meiosis I.

2.3.2 Stages of meiosis I and meiosis II

Meiosis I begins with prophase I, the longest and most complex stage. Homologous chromosomes pair up side by side in a process called synapsis, forming bivalents (tetrads of four chromatids). Crossing over occurs between non-sister chromatids of the homologs at points called chiasmata. Metaphase I: bivalents align at the cell equator with one homolog facing each pole (random orientation of each bivalent). Anaphase I: whole chromosomes (each consisting of two sister chromatids) are pulled to opposite poles; homologs separate but sister chromatids remain joined. Telophase I and cytokinesis I produce two haploid cells (each with n bivalent chromosomes, one from each homolog pair).

Meiosis II is similar to mitosis but acts on haploid cells. Prophase II: chromosomes condense (no new DNA replication). Metaphase II: chromosomes align at the equator. Anaphase II: centromeres split and sister chromatids are pulled to opposite poles. Telophase II and cytokinesis II produce four haploid cells (n chromosomes, each a single chromatid). In pollen development (microsporogenesis), the four haploid microspores develop into pollen grains. In egg development (megasporogenesis), three of the four megaspores typically degenerate and one develops into the embryo sac containing the egg cell.

Fill in the blank: In anaphase I of meiosis, whole _____ (each still consisting of two sister chromatids) are pulled to opposite poles; it is the separation of homologs, not sister chromatids, that makes meiosis I reductive.

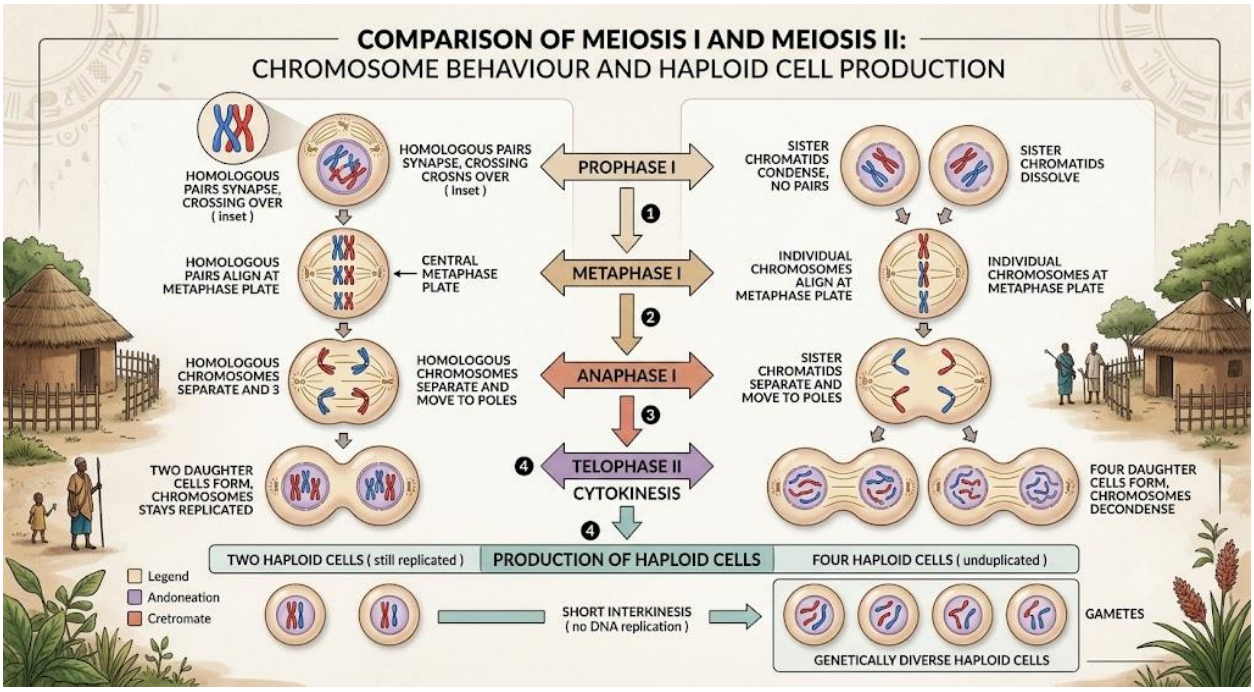

Figure 2.2: Diagram comparing the stages of meiosis I and meiosis II with chromosome behaviour

2.3.3 Crossing over, recombination, and genetic variation

Crossing over is the physical exchange of corresponding segments between non-sister chromatids of a homologous pair during prophase I of meiosis. It occurs at specific points called chiasmata, where the chromatids break and rejoin with the chromatid from the homolog. The result is recombinant chromosomes: chromosomes that carry alleles from both the maternal and paternal homologs on the same chromosome. Crossing over is detected genetically as the recombination frequency between two loci: if two genes are far apart on the same chromosome (or on different chromosomes), they recombine in 50 per cent of gametes (independent assortment); if they are close together, they recombine less frequently (they are linked).

Recombination is the breeder's most powerful tool for generating new combinations of desirable alleles from different parents. By making a cross between a high-yielding but disease-susceptible parent and a low-yielding but disease-resistant parent, the breeder creates a population in which crossing over during meiosis in F1 plants produces gametes that combine high-yield alleles from one parent with resistance alleles from the other. The frequency of such favourable recombinants

in the F2 population depends on how far apart the relevant genes are on the chromosome: genes on different chromosomes or far apart assort independently (50 per cent recombination); linked genes require more generations of selection to recover recombinants.

Fill in the blank: _____ over is the physical exchange of segments between non-sister chromatids of homologs during prophase I; it produces recombinant chromosomes carrying alleles from both parental homologs.

Pilot questions 2.3

1. Explain why meiosis is described as a reductive division and why this is necessary for sexual reproduction.
2. Explain the two mechanisms by which meiosis generates genetic variation.
3. Describe the events of prophase I of meiosis, naming the key processes that occur.
4. Distinguish between meiosis I and meiosis II in terms of what is separated at anaphase in each.
5. Explain crossing over and explain why it is important in plant breeding.

2.4 Fertilisation and the Genetic Basis of Inheritance

2.4.1 Fertilisation in flowering plants

Fertilisation in flowering plants begins with pollination: the transfer of pollen (containing the male gametophyte) from the anther to the stigma. Once on the stigma, compatible pollen germinates and grows a pollen tube through the style toward the ovule. The pollen tube carries two male nuclei (sperm nuclei): the tube nucleus guides the growth of the pollen tube and the two sperm nuclei are the actual male gametes. The pollen tube enters the ovule through the micropyle and delivers both sperm nuclei to the embryo sac (the female gametophyte).

The embryo sac in a mature ovule typically contains seven cells and eight nuclei: the egg cell (the female gamete, containing one n nucleus); two synergid cells flanking the egg cell (which guide the pollen tube); three antipodal cells at the opposite end (nutritive function); and the large

central cell containing two polar nuclei (which fuse or are fertilised separately to form the endosperm). In self-pollinated crops, pollen from the same plant fertilises its own eggs; in cross-pollinated crops, pollen from a different individual is required.

Fill in the blank: The pollen tube carries two _____ nuclei to the embryo sac; one fertilises the egg cell to produce the zygote and the other fuses with the polar nuclei to produce the endosperm.

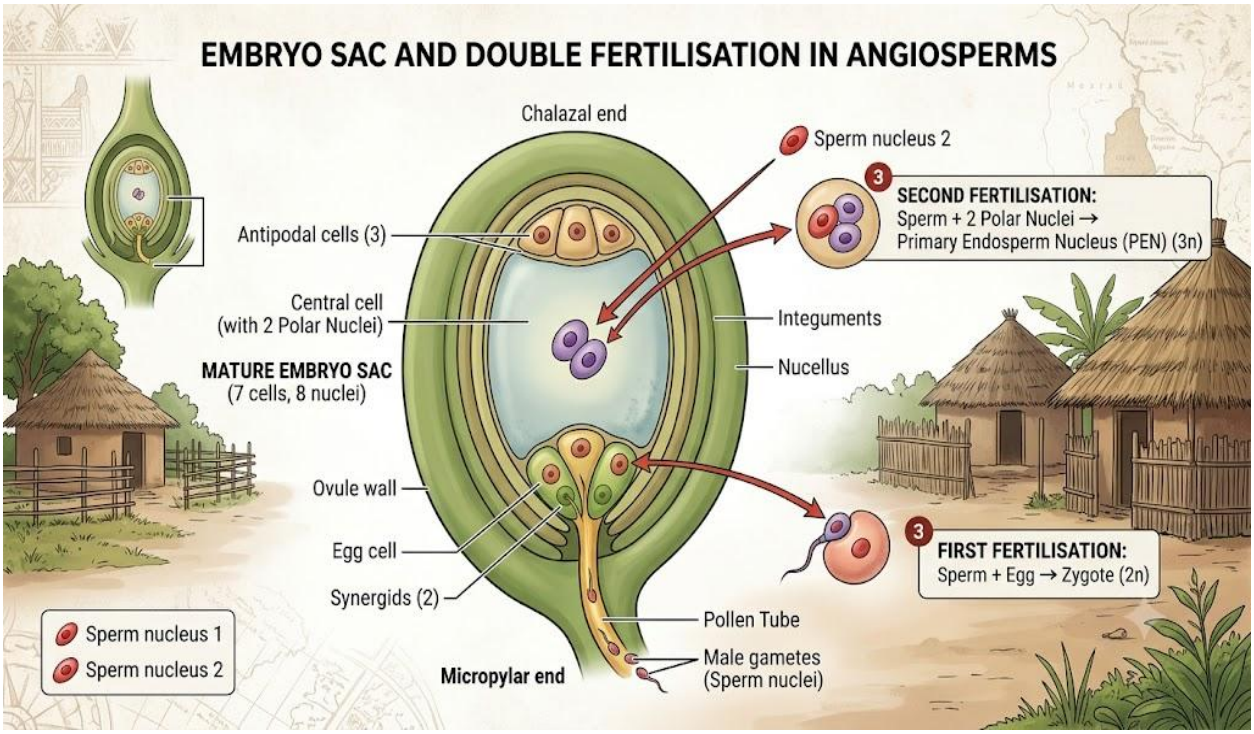

Figure 2.3: Diagram of the embryo sac and double fertilisation in a flowering plant

2.4.2 Double fertilisation and endosperm formation

Double fertilisation is a unique feature of flowering plants (angiosperms) in which both sperm nuclei delivered by the pollen tube participate in fertilisation. The first sperm nucleus fuses with the egg cell to produce the diploid zygote (n + n = 2n), which develops into the embryo. The second sperm nucleus fuses with the two polar nuclei of the central cell to produce the triploid primary endosperm nucleus (n + n + n = 3n), which divides to form the endosperm, the nutritive tissue that surrounds and nourishes the developing embryo in the seed.

The endosperm is agriculturally important because it is the main storage tissue in cereal grains: the starchy endosperm of maize, rice, sorghum, and wheat constitutes the bulk of the grain consumed by humans. The protein and starch composition of the endosperm is determined by genes expressed in the triploid (3n) endosperm tissue; because the endosperm receives two doses of the maternal genome and one of the paternal, maternal genes have a 2:1 dosage advantage in the endosperm. This has implications for quality breeding: the xenia effect occurs when pollen from a different genotype changes the endosperm composition of the current season's seed.

Fill in the blank: Double fertilisation produces a diploid _____ (2n, from egg + one sperm) that becomes the embryo, and a triploid primary endosperm nucleus (3n, from two polar nuclei + one sperm) that becomes the endosperm.

2.4.3 Genetic consequences of fertilisation for breeding

Fertilisation combines one haploid gamete from the male parent with one from the female parent to restore the diploid number. If two parents with different genotypes are crossed, the zygote formed is heterozygous at every locus where the parents differed. This first-generation hybrid (F1) is genetically uniform (all F1 plants from the same cross are identical) and expresses the dominant allele at each heterozygous locus. When F1 plants are selfed or intercrossed to produce F2, meiosis generates gametes with all possible combinations of the parental alleles, and F2 plants segregate into different genotypic and phenotypic classes according to Mendelian ratios covered in Series 3.

The xenia effect and metaxenia are practical consequences of double fertilisation for seed production. Xenia: the immediate effect of pollen genotype on the endosperm phenotype in the current seed (for example, when yellow-endosperm maize pollen fertilises white-endosperm maize, some kernels on the ear are yellow due to the triploid endosperm expressing the dominant yellow allele from the pollen). Metaxenia: the effect of pollen on the maternal pericarp or fruit tissue of the current season's fruit (rarer, seen in date palm). Breeders working with seed quality traits must account for xenia when evaluating endosperm quality in crossing nurseries.

Fill in the blank: The _____ effect is the direct influence of the pollen genotype on the endosperm phenotype of the current season's seed, caused by the triploid nature of the endosperm which expresses alleles from both parents.

Pilot questions 2.4

1. Describe the journey of the pollen tube from the stigma to the embryo sac.
2. Name the seven cells of the mature embryo sac and state the function of each type.
3. Explain double fertilisation and state what each fusion event produces.
4. Explain why the endosperm is triploid and state its agricultural importance.
5. Define the xenia effect and explain why it matters for maize quality breeding.

Series Summary

This Series provided the cellular and genetic foundation for crop breeding. We described the plant cell nucleus, chromosomes (structure, centromere, telomere, locus), and the chromosome numbers of key Nigerian crops. We introduced the core genetic terminology: gene, allele, locus, genotype, phenotype, homozygous, heterozygous, dominant, recessive, and codominant. We then covered mitosis (the four stages producing two identical daughter cells, relevant for vegetative propagation and polyploid induction by colchicine) and meiosis (two divisions producing four haploid cells with new allele combinations through independent assortment and crossing over during prophase I).

We examined fertilisation in flowering plants (pollen tube delivery of two sperm nuclei to the embryo sac), double fertilisation (one sperm fertilising the egg to produce the diploid zygote; the other fusing with the polar nuclei to produce the triploid endosperm), and the genetic consequences for breeding (F1 uniformity and dominance expression, F2 segregation following Mendel's laws, and the xenia effect on endosperm quality). By completing this Series, you should be able to achieve all eight Series Learning Outcomes (SLO 2.1 to SLO 2.8).

Glossary of Terms

- **Allele:** one of two or more alternative forms of a gene at a given locus; different alleles produce different phenotypic effects.
- **Anaphase:** the stage of mitosis (or meiosis II) in which centromeres split and sister chromatids are pulled to opposite poles by the spindle.
- **Anaphase I:** the stage of meiosis I in which whole chromosomes (each consisting of two sister chromatids) are pulled to opposite poles; homologous chromosomes separate.
- **Bivalent (tetrad):** the paired structure formed by two homologous chromosomes (four chromatids total) during prophase I of meiosis.
- **Centromere:** the constriction on a chromosome that is the attachment site for spindle fibres during cell division; joined sister chromatids are held together at the centromere.
- **Chiasma (plural chiasmata):** the visible point of crossing over between non-sister chromatids of a homologous pair during prophase I of meiosis.
- **Codominance:** the situation in which both alleles at a heterozygous locus are fully expressed in the phenotype of the heterozygote.
- **Crossing over:** the physical exchange of corresponding segments between non-sister chromatids of homologous chromosomes during prophase I; produces recombinant chromosomes.
- **Cytokinesis:** the division of the cytoplasm following nuclear division; in plant cells, a cell plate forms from Golgi vesicles to produce the new cell wall.
- **Diploid (2n):** a cell or organism with two complete sets of chromosomes, one set inherited from each parent.
- **Dominant:** an allele that produces its phenotypic effect in a single copy (when heterozygous); the phenotype of a dominant allele is the same in both Aa and AA.

- **Double fertilisation:** the unique angiosperm process in which one sperm fuses with the egg (to form the 2n zygote) and the second sperm fuses with the two polar nuclei (to form the 3n endosperm nucleus).
- **Embryo sac:** the female gametophyte of a flowering plant, typically containing seven cells (egg cell, two synergids, three antipodals, and central cell with two polar nuclei).
- **Endosperm:** the triploid (3n) nutritive tissue in the seed of a flowering plant, formed from the fusion of the second sperm with the two polar nuclei; the main storage tissue of cereal grains.
- **Gene:** a segment of DNA encoding a functional product (usually a protein) that influences one or more heritable traits.
- **Genotype:** the complete genetic constitution of an individual; the combination of alleles present at all loci.
- **Haploid (n):** a cell or organism with one complete set of chromosomes; gametes (pollen and egg cells) are haploid.
- **Heterozygous:** having two different alleles at a given locus (for example, Aa).
- **Homologous chromosomes:** the pair of chromosomes in a diploid cell that are similar in size, shape, and gene content, one inherited from each parent.
- **Homozygous:** having two identical alleles at a given locus (for example, AA or aa).
- **Independent assortment:** the random and independent segregation of non-homologous chromosome pairs to the two poles during meiosis I; one of the two mechanisms generating genetic variation in meiosis.
- **Locus (plural loci):** the specific physical position of a gene on a chromosome.
- **Meiosis:** a specialised two-division cell cycle producing four haploid cells from one diploid cell; the basis of gametogenesis and sexual reproduction.
- **Metaphase:** the stage of mitosis (or meiosis II) in which chromosomes align at the cell equator (metaphase plate).

- **Metaphase I:** the stage of meiosis I in which bivalents align at the cell equator with one homolog oriented toward each pole; the point of independent assortment.
- **Mitosis:** the type of cell division producing two genetically identical daughter cells from one parent cell, maintaining the chromosome number (2n to 2n).
- **Phenotype:** the observable characteristics of an individual resulting from the interaction of its genotype with the environment.
- **Polar nuclei:** the two nuclei of the central cell in the embryo sac; they fuse with the second sperm nucleus to form the triploid primary endosperm nucleus.
- **Prophase I:** the longest stage of meiosis I, during which homologs synapse to form bivalents and crossing over occurs at chiasmata.
- **Recessive:** an allele that produces its phenotypic effect only when homozygous (aa); its phenotype is masked by the dominant allele when heterozygous (Aa).
- **Recombination:** the production of new combinations of alleles in gametes by crossing over and independent assortment during meiosis; the primary source of variation for plant breeding.
- **Somaclonal variation:** random genetic or epigenetic changes occurring in plant cells during tissue culture and regeneration; can generate useful new variation or introduce unwanted mutations.
- **Synapsis:** the precise pairing of homologous chromosomes along their entire length during prophase I of meiosis; the prerequisite for crossing over.
- **Telomere:** the repetitive DNA sequence at each end of a chromosome that protects against degradation and chromosome-to-chromosome fusions.
- **Xenia:** the direct effect of the pollen genotype on the phenotype of the endosperm in the current season's seed; caused by the expression of pollen-derived alleles in the triploid endosperm.

- **Zygote:** the diploid cell formed by fusion of egg cell and sperm nucleus at fertilisation; the first cell of a new plant individual.

Concept Check Questions [Series 2]

Objective Questions

1. The specific position of a gene on a chromosome is called its _____. (Linked to SLO 2.1)
2. An individual with two different alleles at a locus (Aa) is described as _____ at that locus. (Linked to SLO 2.2)
3. Mitosis produces two genetically _____ daughter cells, each with the same chromosome number as the parent. (Linked to SLO 2.3)
4. The physical exchange of segments between non-sister chromatids of homologs during prophase I is called _____ over. (Linked to SLO 2.5)
5. Double fertilisation produces a diploid _____ (from egg + one sperm) and a triploid endosperm nucleus (from polar nuclei + one sperm). (Linked to SLO 2.7)

Short-Answer Questions

6. State the diploid chromosome numbers of maize, cowpea, and groundnut. (Linked to SLO 2.1)
7. Describe the events of metaphase and anaphase of mitosis. (Linked to SLO 2.3)
8. Explain the two mechanisms by which meiosis generates genetic variation. (Linked to SLO 2.4)
9. Describe the events of anaphase I of meiosis and explain why it is described as reductive. (Linked to SLO 2.4)
10. Explain double fertilisation and state the significance of the endosperm for crop production. (Linked to SLO 2.7)

Long-Answer Questions

11. Describe the structure of plant chromosomes, explain the key genetic terminology (gene, allele, locus, genotype, phenotype, dominance, recessiveness), and compare the processes and outcomes of mitosis and meiosis. (Linked to SLOs 2.1, 2.2, 2.3, 2.4)
12. Describe meiosis I and meiosis II in detail, explain crossing over and recombination, and evaluate the importance of meiosis and recombination for plant breeding. (Linked to SLOs 2.4, 2.5)
13. Describe fertilisation and double fertilisation in flowering plants, explain the genetic consequences for breeding including F1 uniformity, F2 segregation, and the xenia effect. (Linked to SLOs 2.6, 2.7, 2.8)

Answers to Concept Check Questions [Series 2]

Objective Questions

1. Locus.
2. Heterozygous.
3. Identical.
4. Crossing.
5. Zygote.

Short-Answer Questions

6. Maize (Zea mays): 2n = 20; cowpea (Vigna unguiculata): 2n = 22; groundnut (Arachis hypogaea): 2n = 40.
7. Metaphase of mitosis: chromosomes align at the cell equator (metaphase plate), each chromosome attached to spindle fibres from both poles via its centromere. Anaphase of

mitosis: centromeres split and sister chromatids are pulled to opposite poles by the shortening spindle fibres; each pole receives one complete set of chromosomes.

8. Independent assortment: during metaphase I, each bivalent aligns with its two homologs randomly oriented toward either pole; the orientation of one bivalent is independent of another, producing 2n different possible combinations of maternal and paternal chromosomes in gametes (where n is the haploid chromosome number). Crossing over: during prophase I, non-sister chromatids of homologs exchange corresponding segments at chiasmata, producing recombinant chromosomes with new combinations of alleles from both parental homologs.
9. During anaphase I, whole chromosomes (each consisting of two sister chromatids still joined at the centromere) are pulled to opposite poles by the spindle fibres; the centromeres do not split. It is reductive because homologous chromosomes are separated: each pole receives one chromosome from each homologous pair, halving the chromosome number from 2n to n. This is unlike anaphase of mitosis (or anaphase II of meiosis) where the centromeres split and sister chromatids separate.
10. Double fertilisation: one sperm nucleus from the pollen tube fuses with the egg cell to produce the diploid (2n) zygote, which develops into the embryo; the second sperm nucleus fuses with the two polar nuclei of the central cell to produce the triploid (3n) primary endosperm nucleus, which divides to form the endosperm. The endosperm is agriculturally important because it is the main starch and protein storage tissue of cereal grains (maize, rice, sorghum, wheat), constituting the bulk of grain consumed by humans.

Long-Answer Questions

11. Chromosome structure: linear DNA + histone proteins forming chromatin; two sister chromatids joined at centromere; telomeres at ends; genes arranged linearly at loci. Chromosome numbers: maize 2n=20, rice 2n=24, cowpea 2n=22, cassava 2n=36, groundnut 2n=40, sorghum 2n=20, bread wheat 2n=42. Terminology: gene (DNA segment encoding a protein, influencing a trait); allele (alternative form of a gene at a locus); locus (specific chromosome position of a gene); genotype (complete genetic

constitution); phenotype (observable characteristics from genotype x environment); homozygous (identical alleles at a locus, AA or aa); heterozygous (different alleles, Aa); dominant (allele expressed in one copy); recessive (allele expressed only when homozygous); codominant (both alleles expressed in heterozygote). Mitosis: interphase (DNA replication, 2n chromosomes become 4 chromatids); prophase (condensation, nuclear envelope breakdown, spindle formation); metaphase (alignment at equator); anaphase (centromere split, chromatids to poles); telophase (nuclear envelope reforms); cytokinesis (cell plate in plants); result: two identical 2n cells. Meiosis: two divisions, four haploid cells; meiosis I reductive (homologs separate); meiosis II like mitosis (sister chromatids separate); result: four genetically unique n cells.

12. Meiosis I: Prophase I (synapsis of homologs into bivalents/tetrads, crossing over at chiasmata, chiasma = visible point of exchange); Metaphase I (bivalents at equator, random orientation; basis of independent assortment); Anaphase I (whole chromosomes separated, each with two chromatids; centromeres do not split; reductive); Telophase I + cytokinesis I (two haploid cells, each with n bivalent chromosomes). Meiosis II: Prophase II (chromosomes condense); Metaphase II (chromosomes at equator); Anaphase II (centromeres split, sister chromatids separate); Telophase II + cytokinesis II (four haploid cells, each with n single chromatids). Crossing over: physical exchange of segments between non-sister chromatids at chiasmata during prophase I; produces recombinant chromosomes with alleles from both parents. Importance in breeding: when two parents with complementary traits are crossed, crossing over in F1 meiosis combines high-yield alleles from one parent with resistance alleles from the other in a single gamete; F2 segregants include plants combining the best traits of both parents (transgressive segregants); frequency of favourable recombinants depends on distance between loci (linked genes recombine less frequently).
13. Fertilisation: pollen germinates on stigma, pollen tube grows through style to ovule micropyle delivering two sperm nuclei. Embryo sac: egg cell, two synergids (guide pollen tube), three antipodals (nutritive), central cell with two polar nuclei; seven cells, eight nuclei. Double fertilisation: sperm 1 + egg = diploid zygote (develops into embryo); sperm 2 + two polar nuclei = triploid (3n) endosperm nucleus (develops into endosperm, main grain storage tissue). Genetic consequences: F1 uniformity (all F1 plants from same

cross are genetically identical, heterozygous at every locus where parents differed, express dominant allele at each locus); F2 segregation (F1 selfing produces gametes with all allele combinations by meiosis; F2 segregates in Mendelian ratios, covered in Series 3); xenia effect (pollen genotype directly affects endosperm phenotype in current season; triploid endosperm expresses two maternal doses and one paternal dose; yellow maize pollen on white maize ear gives yellow kernels on same ear; breeder must account for xenia in quality evaluation in crossing nurseries); metaxenia (rarer, pollen affects maternal pericarp, e.g. date palm).

Answers to Pilot Questions [Series 2]

Part 2.1: The Plant Cell and Its Genetic Content

1. Three DNA-containing structures: nucleus (contains chromosomes, the primary repository of the plant's genetic information); chloroplasts (contain chloroplast DNA encoding photosynthetic proteins); mitochondria (contain mitochondrial DNA encoding electron transport chain proteins). Chloroplasts and mitochondria are inherited maternally in most plant species because the pollen grain (male gamete) contributes almost no cytoplasm to the zygote at fertilisation; the cytoplasm of the zygote comes almost entirely from the egg cell and therefore contains only the maternal organelles.
2. A chromosome is a single linear DNA molecule complexed with histone proteins into chromatin that condenses into a visible structure during cell division. Three structural features important for cell division: centromere (the constriction where spindle fibres attach, holding sister chromatids together until anaphase); telomeres (repetitive sequences at the chromosome ends that protect against degradation and prevent fusion with other chromosomes); and the two sister chromatids (the two identical copies of the chromosome produced by DNA replication, held together at the centromere until they are separated at anaphase).
3. Maize (Zea mays): 2n = 20; cowpea (Vigna unguiculata): 2n = 22; groundnut (Arachis hypogaea): 2n = 40.

4. Gene: a segment of DNA that encodes a functional product (usually a protein) and influences one or more heritable traits. Allele: one of two or more alternative forms of a gene occupying the same locus; different alleles typically produce different phenotypic effects. Locus: the specific physical position of a gene on a chromosome. Genotype: the complete genetic constitution of an individual, including the combination of alleles at every locus. Phenotype: the observable characteristics of an individual resulting from the interaction of its genotype with the environment. Homozygous: having two identical alleles at a given locus (AA or aa). Heterozygous: having two different alleles at a given locus (Aa).
5. Dominance occurs when one allele (the dominant) completely masks the phenotypic effect of the other allele (the recessive) at a heterozygous locus; the heterozygote (Aa) shows the same phenotype as the dominant homozygote (AA). Example: in peas, yellow seed colour (Y) is dominant over green (y); plants with genotype Yy have yellow seeds, identical to YY plants. Codominance occurs when both alleles at a heterozygous locus are fully and independently expressed, so the heterozygote shows a phenotype that includes characteristics of both homozygotes. Example: in ABO blood groups, the IA and IB alleles are codominant; a person with genotype IAIB has both A and B antigens on their red blood cells (blood type AB).

Part 2.2: Mitosis: Somatic Cell Division

1. Mitosis is significant for plant growth because every cell added to a growing root tip, shoot tip, leaf, or other organ is produced by mitosis, which maintains the chromosome number and genetic constitution from one cell generation to the next. It is the basis of asexual reproduction because vegetative propagation (cuttings, tubers, tillers, runners, grafts) all rely on mitosis to produce new cells; all cells and therefore all offspring are genetically identical to the parent plant. This is why cassava stem cuttings, yam setts, and banana suckers produce plants identical to the parent.
2. Interphase is the phase between cell divisions, often called the resting phase, though the cell is metabolically very active. It consists of G1 phase (cell grows, produces proteins

and organelles), S phase (DNA replication: each chromosome is copied to produce two identical sister chromatids joined at the centromere, so the DNA content doubles while the chromosome number remains 2n), and G2 phase (cell continues to grow and prepares for division by synthesising proteins needed for spindle formation and chromosome condensation). At the end of interphase the cell is ready for mitosis.

3. Prophase of mitosis: chromosomes condense from the diffuse chromatin state and become visible as distinct rod-shaped structures; the nuclear envelope breaks down; the spindle apparatus begins to assemble from the centrioles (in animals) or from the polar caps of microtubules (in plants, which lack centrioles); spindle fibres extend toward the chromosomes. Metaphase of mitosis: all condensed chromosomes move to and align along the cell equator (the metaphase plate) such that each chromosome is attached to spindle fibres from both poles via its centromere; this alignment is the point at which chromosome number can be counted most reliably.
4. Anaphase of mitosis: the centromeres of each chromosome split simultaneously; the two sister chromatids of each chromosome are now separate and are pulled to opposite poles by the shortening spindle fibres; each pole receives one complete set of chromosomes. Telophase of mitosis: the chromosomes arrive at the poles and begin to decondense; a new nuclear envelope reforms around each chromosome set at each pole; the spindle apparatus breaks down; two nuclei are now present in one cell. Cytokinesis in plant cells: Golgi vesicles transport cell wall components (cellulose, hemicellulose, pectin) to the cell equator, where they fuse to form the cell plate, which grows outward from the centre until it fuses with the existing cell wall, dividing the cell into two daughter cells each with one nucleus.
5. Colchicine blocks spindle formation during mitosis by binding to tubulin and preventing it from polymerising into the microtubule fibres that make up the spindle. Without a functional spindle, the chromosomes cannot be pulled to the poles at anaphase. However, DNA replication and chromosome condensation proceed normally; when colchicine is removed, a new spindle can form and cell division resumes, but the cell now has twice the normal number of chromosomes (because both sets of sister chromatids remain in one cell rather than being separated into two). The daughter cells are therefore tetraploid (4n) instead of diploid (2n).

Part 2.3: Meiosis: Gametogenesis

1. Meiosis is described as a reductive division because it reduces the chromosome number from diploid (2n) to haploid (n). This is necessary for sexual reproduction because at fertilisation the gametes from two parents fuse; if gametes were diploid, each fusion event would double the chromosome number, and after many generations the chromosome number would reach an unviable level. By producing haploid gametes, meiosis ensures that fertilisation restores the species-characteristic diploid number rather than doubling it.
2. Two mechanisms: (1) Independent assortment: during metaphase I, each bivalent (pair of homologous chromosomes) aligns at the cell equator with either the maternal or paternal homolog facing either pole, randomly and independently of all other bivalents. An organism with n pairs of chromosomes can produce 2n different gamete types by independent assortment alone (for example, maize with n=10 can produce 2^10 = 1,024 different gamete types from independent assortment). (2) Crossing over: during prophase I, non-sister chromatids of homologous chromosomes exchange corresponding segments at chiasmata, creating recombinant chromosomes with alleles from both parental homologs; this multiplies the number of unique gamete types far beyond what independent assortment alone can generate.
3. During prophase I, which is the longest and most complex stage of meiosis: homologous chromosomes find each other and undergo synapsis (precise pairing along their entire length) to form bivalents (also called tetrads because each consists of four chromatids); the synaptonemal complex holds the homologs together; crossing over occurs at points called chiasmata where non-sister chromatids break and rejoin with the chromatid from the other homolog, exchanging corresponding segments; the nuclear envelope begins to break down; the spindle apparatus forms. Chiasmata are visible throughout much of prophase I and hold the bivalent together until anaphase I.
4. In anaphase I of meiosis, whole chromosomes (each still consisting of two sister chromatids joined at the centromere) are pulled to opposite poles; the centromeres do not split; what separates is the homologous chromosomes within each bivalent. In anaphase

II of meiosis (and in anaphase of mitosis), the centromeres split and sister chromatids separate and are pulled to opposite poles. Meiosis I is therefore the reductive division (chromosome number halved) and meiosis II is the equational division (chromatids separate; chromosome number unchanged at n).

5. Crossing over is the physical exchange of corresponding DNA segments between non-sister chromatids of a homologous pair of chromosomes during prophase I of meiosis. It produces recombinant chromosomes, that is, chromosomes that carry alleles from both the maternal and paternal homolog on the same chromosome. It is important in plant breeding because when a breeder crosses two parents with different desirable alleles (for example, parent A has high-yield alleles but no resistance; parent B has resistance alleles but low yield), crossing over in the F1 hybrids creates gametes that combine high-yield alleles from parent A with resistance alleles from parent B on the same chromosome; offspring from these gametes are transgressive segregants that exceed both parents, which is the goal of most crossing programmes.

Part 2.4: Fertilisation and the Genetic Basis of Inheritance

1. After pollen lands on a compatible stigma, the pollen grain germinates and grows a pollen tube. The tube grows through the style by enzymatic digestion of the transmitting tissue, guided by chemical signals produced by the synergid cells of the embryo sac. The pollen tube enters the ovule through the micropyle (a small opening in the integuments), grows through the nucellus, and enters the embryo sac through the micropylar synergid. It then ruptures to discharge its contents: the tube nucleus (which has guided the tube growth) and two sperm nuclei (the actual male gametes) directly into the embryo sac.
2. The mature embryo sac contains seven cells: the egg cell (female gamete, haploid n, fuses with one sperm to form the zygote); two synergid cells flanking the egg cell (guide the pollen tube into the embryo sac, degenerate after fertilisation); three antipodal cells at the chalazal end opposite the egg (nutritive function during early embryo development, degenerate after fertilisation); and the central cell (the large cell occupying most of the

embryo sac volume, contains two polar nuclei that fuse with the second sperm to form the triploid endosperm nucleus).

3. Double fertilisation is the process unique to angiosperms (flowering plants) in which both sperm nuclei delivered by the pollen tube participate in separate fertilisation events. First fusion: one sperm nucleus fuses with the egg cell nucleus; the result is a diploid zygote (n + n = 2n) that develops by mitosis into the embryo. Second fusion: the second sperm nucleus fuses with the two polar nuclei of the central cell; the result is the triploid (3n) primary endosperm nucleus (n + n + n = 3n) that divides to form the endosperm, the nutritive tissue of the seed.
4. The endosperm is triploid (3n) because it is formed by the fusion of two haploid (n) polar nuclei (from the mother plant) with one haploid (n) sperm nucleus from the pollen: n + n + n = 3n. Its agricultural importance: the endosperm is the primary storage tissue of cereal grains, storing starch (in the starchy endosperm), proteins (glutelins, prolamins forming the protein matrix), and lipids; it constitutes the bulk of the grain weight in maize, rice, sorghum, wheat, and barley and is therefore the primary source of calories in the human diets of most Nigerian and global populations. Endosperm quality traits (protein content, starch type, vitamin content) are primary targets of quality breeding programmes.
5. The xenia effect is the direct influence of the pollen genotype on the phenotype of the endosperm in the current season's seed (not in the next generation, but in the seed currently developing on the plant receiving the pollen). It occurs because the endosperm is triploid, containing two sets of chromosomes from the mother and one from the pollen; if the pollen carries a dominant allele for an endosperm trait, that allele is expressed immediately in the current seed's endosperm. In maize quality breeding it matters because: if a white-endosperm (recessive) female plant is cross-pollinated by yellow-endosperm (dominant) pollen, some or all of the kernels on that ear will be yellow (xenia effect) due to the dominant yellow allele from the pollen being expressed in the triploid endosperm; the breeder evaluating white endosperm quality must self-pollinate or use white-endosperm pollen to avoid contamination of the quality phenotype in the evaluation ear.

References and Attributions [Series 2]

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Table 2.1: Chromosome numbers of Nigerian food crops Attribution: AI generated. Suggested OER search string: "chromosome numbers Nigerian food crops maize cowpea cassava sorghum OER table".
- Figure 2.1: Stages of mitosis in a plant cell Attribution: AI generated. Suggested OER search string: "mitosis stages plant cell prophase metaphase anaphase telophase OER diagram".
- Figure 2.2: Meiosis I and meiosis II stages Attribution: AI generated. Suggested OER search string: "meiosis stages I II prophase metaphase anaphase telophase crossing over OER diagram".
- Figure 2.3: Double fertilisation in a flowering plant Attribution: AI generated. Suggested OER search string: "double fertilisation embryo sac egg polar nuclei endosperm flowering plant OER".

Course code: AGE 304

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Series 3: Mendelian Laws, Traits, and Statistical Applications in Breeding

- **Part 3.1: Mendel's Experiments and Laws of Inheritance**
  - Sub Part 3.1.1: Mendel's experimental design and choice of pea
  - Sub Part 3.1.2: The Law of Segregation
  - Sub Part 3.1.3: The Law of Independent Assortment
- **Part 3.2: Monohybrid and Dihybrid Crosses**
  - Sub Part 3.2.1: Monohybrid crosses and the Punnett square
  - Sub Part 3.2.2: Dihybrid crosses and expected ratios
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- **Part 3.3: Qualitative and Quantitative Traits**
  - Sub Part 3.3.1: Qualitative traits and their inheritance
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- **Part 3.4: Chi-Square Analysis and Selection Response**
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- Sub Part 3.4.3: Selection response and the breeder's equation

Introduction

Gregor Mendel's experiments with garden peas, published in 1866 and rediscovered in 1900, established the foundational principles of heredity that underpin all of modern plant breeding. His two laws, the Law of Segregation and the Law of Independent Assortment, predict how alleles and chromosome pairs are transmitted from parents to offspring and set the mathematical framework within which breeders work. Understanding these laws, and the statistical tools used to test them, is essential for every crop improvement scientist.

This Series covers Mendel's experimental design and his two laws, the prediction of offspring ratios in mono- and dihybrid crosses using the Punnett square, modifications of Mendelian ratios, the distinction between qualitative and quantitative traits, heritability and its estimation, the chi-square test for testing observed against expected ratios, and the breeder's equation for predicting selection response. The quantitative and statistical content of this Series directly supports the practical breeding activities described in Series 4 and 5.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 3.1** describe Mendel's experimental design and explain why the garden pea was an ideal experimental organism (Linked to Part 3.1),
- **SLO 3.2** state and explain Mendel's Law of Segregation and Law of Independent Assortment (Linked to Part 3.1),
- **SLO 3.3** construct Punnett squares for monohybrid and dihybrid crosses and predict offspring phenotypic and genotypic ratios (Linked to Part 3.2),

- **SLO 3.4** explain modifications of Mendelian ratios including incomplete dominance, codominance, and epistasis (Linked to Part 3.2),
- **SLO 3.5** distinguish between qualitative and quantitative traits and explain polygenic inheritance (Linked to Part 3.3),
- **SLO 3.6** define heritability, distinguish between broad-sense and narrow-sense heritability, and explain how heritability is estimated (Linked to Part 3.3),
- **SLO 3.7** apply the chi-square test to determine whether observed offspring ratios fit expected Mendelian ratios (Linked to Part 3.4), and
- **SLO 3.8** explain the breeder's equation and calculate the expected selection response for a quantitative trait (Linked to Part 3.4).

3.1 Mendel's Experiments and Laws of Inheritance

3.1.1 Mendel's experimental design and choice of pea

Gregor Mendel (1822-1884) conducted his famous hybridisation experiments with the garden pea (Pisum sativum) between 1856 and 1863 at the monastery in Brno (now Czech Republic). His success depended on several features that made the garden pea an ideal experimental organism: it naturally self-pollinates (so true-breeding lines are easily maintained), crosses can be made by hand-pollination, the generation time is short (one season), large numbers of offspring can be produced, and several traits show clear-cut alternative forms (tall vs dwarf plant height, yellow vs green seed colour, smooth vs wrinkled seed texture, and four others).

Mendel's key methodological innovations were: starting with true-breeding parent lines (homozygous for each trait), making reciprocal crosses (testing whether the result was the same regardless of which parent was male or female), counting large numbers of offspring (providing statistical power), and following individual traits across multiple generations (P, F1, F2, and backcross). He studied seven pairs of contrasting traits, each controlled by a single gene on a different chromosome, which is why his data supported independent assortment. A lesser methodological genius would have chosen linked genes and obtained confusing results.

Fill in the blank: Mendel chose the garden pea for his experiments because it naturally _____ pollinates, making it easy to maintain true-breeding lines, and because several traits show clear-cut alternative forms.

3.1.2 The Law of Segregation

The Law of Segregation states that the two alleles of a gene in an individual separate (segregate) from each other during gamete formation, so that each gamete carries only one allele for each gene. When tall (TT) pea plants were crossed with dwarf (tt) plants, all F1 offspring were tall (Tt), showing that T is dominant over t. When F1 plants were selfed to produce F2, Mendel observed approximately three tall plants for every one dwarf plant (a 3:1 ratio). He interpreted this as evidence that the two alleles (T and t) in the F1 heterozygote (Tt) segregate equally into gametes (50 per cent T gametes and 50 per cent t gametes), and that random fusion of gametes at fertilisation produces the 3:1 ratio.

The cellular basis of the Law of Segregation is the separation of homologous chromosomes during anaphase I of meiosis (covered in Series 2). Since the two alleles of a gene occupy the same locus on the two homologs, and homologs separate to opposite poles at anaphase I, each gamete receives exactly one allele. The Law of Segregation applies universally to all diploid organisms and all genes, regardless of whether the trait is qualitative or quantitative. It is the most fundamental principle of Mendelian genetics and the basis of all breeding calculations involving allele frequencies.

Fill in the blank: The Law of _____ states that the two alleles of a gene separate from each other during gamete formation so that each gamete carries only one allele; its cellular basis is the separation of homologs at anaphase I of meiosis.

3.1.3 The Law of Independent Assortment

The Law of Independent Assortment states that alleles of different genes assort independently of one another during gamete formation, provided the genes are on different (non-homologous) chromosomes. Mendel demonstrated this by crossing plants that differed in two traits simultaneously (a dihybrid cross): yellow smooth (YYRR) crossed with green wrinkled (yyrr)

gave all yellow smooth F1 (YyRr), and selfing F1 produced F2 offspring in the ratio 9 yellow smooth : 3 yellow wrinkled : 3 green smooth : 1 green wrinkled. This 9:3:3:1 ratio is the expected outcome when two independently assorting genes each show 3:1 segregation.

The cellular basis of independent assortment is the random orientation of bivalents at metaphase I of meiosis: each bivalent aligns independently, so the distribution of alleles at one locus is unaffected by alleles at a different locus on a non-homologous chromosome. Independent assortment is limited to genes on different chromosomes; genes on the same chromosome are linked and do not assort independently (though crossing over creates some recombinants). Linkage and the recombination frequency between linked genes were studied by Morgan and colleagues after Mendel, and form the basis of genetic mapping.

Fill in the blank: The Law of Independent _____ states that alleles of different genes on non-homologous chromosomes assort independently during meiosis; its cellular basis is the random orientation of bivalents at metaphase I.

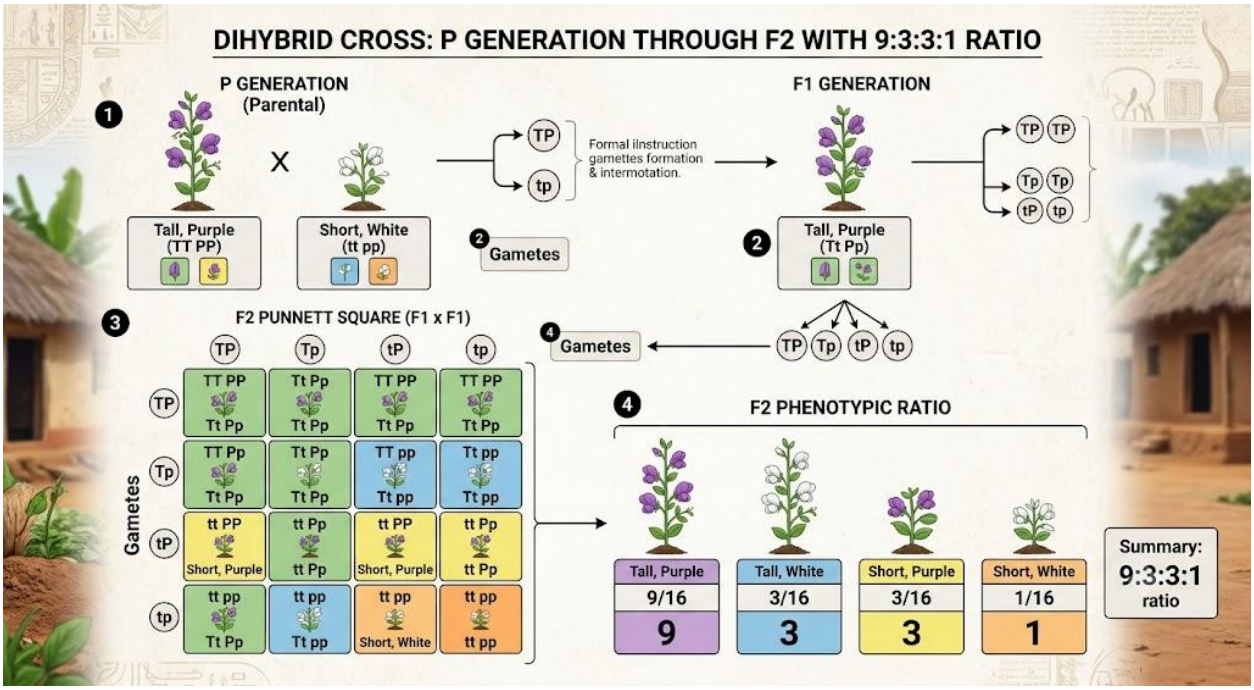

Figure 3.1: Diagram of a dihybrid cross showing P, F1, and F2 generations with expected ratios

Pilot questions 3.1

1. State four features of the garden pea that made it ideal for Mendel's experiments.
2. State Mendel's Law of Segregation and explain its cellular basis.
3. Explain what Mendel observed in his monohybrid cross and how he interpreted the 3:1 F2 ratio.
4. State Mendel's Law of Independent Assortment and explain its cellular basis.
5. Explain why the Law of Independent Assortment does not apply to genes on the same chromosome.

3.2 Monohybrid and Dihybrid Crosses

3.2.1 Monohybrid crosses and the Punnett square

A monohybrid cross involves parents that differ in a single gene. The Punnett square is a grid method for systematically listing all possible gamete combinations to predict the genotypic and phenotypic ratios of offspring. For a cross between two F1 heterozygotes (Aa x Aa): list the gametes of one parent along the top (A, a) and the other parent down the side (A, a); fill each cell with the gamete combination from the corresponding column and row; the four cells give genotypes AA, Aa, Aa, aa in a 1:2:1 ratio (genotypic ratio) and, if A is dominant, a 3:1 phenotypic ratio (3 A_ : 1 aa).

A testcross is used to determine the unknown genotype of an individual with the dominant phenotype: the individual is crossed with a homozygous recessive (aa). If the individual is AA, all offspring show the dominant phenotype (Aa); if the individual is Aa, offspring are 1 Aa (dominant) : 1 aa (recessive). The backcross is a cross of an F1 hybrid back to one of the parent genotypes; it is widely used in breeding to recover the genotype of an elite recurrent parent while introgressing a specific trait from a donor parent. In backcross breeding, the proportion of recurrent parent genome is restored by approximately 50 per cent with each generation of backcrossing.

Fill in the blank: A _____ cross involves crossing a dominant-phenotype individual of unknown genotype with a homozygous recessive to determine whether the individual is AA or Aa.

3.2.2 Dihybrid crosses and expected ratios

A dihybrid cross involves parents differing in two genes. If both genes show complete dominance and are on different chromosomes (independent assortment), the F2 from selfed F1 dihybrids (AaBb x AaBb) produces the 9:3:3:1 phenotypic ratio: 9 A_B_ (dominant for both traits) : 3 A_bb (dominant for first, recessive for second) : 3 aaB_ (recessive for first, dominant for second) : 1 aabb (recessive for both). The corresponding F2 genotypic ratio contains nine distinct genotypes (1 AABB : 2 AABb : 2 AaBB : 4 AaBb : 1 AAbb : 2 Aabb : 1 aaBB : 2 aaBb : 1 aabb).

The gametes produced by an F1 dihybrid (AaBb) are AB, Ab, aB, and ab, each in equal frequency (1/4). The probability of any F2 genotype can be calculated by multiplying the frequency of the two gametes that combine to produce it. For example, the frequency of AABB = 1/4 (AB gametes) x 1/4 (AB gametes) = 1/16; the frequency of AaBb = 2 (because it can be formed by AB x ab or Ab x aB) x 1/4 x 1/4 = 2/16. The sum of all genotype frequencies must equal 1 (16/16). Students should practise deriving these ratios before tackling chi-square analysis in Part 3.4.

Fill in the blank: The F2 of a dihybrid cross between two heterozygotes (AaBb x AaBb) produces a phenotypic ratio of 9 A_B_ : 3 A_bb : 3 aaB_ : 1 aabb when the two genes are on different chromosomes and show complete _____.

3.2.3 Modifications of Mendelian ratios

The 3:1 and 9:3:3:1 ratios assume complete dominance. When dominance is incomplete, the heterozygote shows an intermediate phenotype (for example, red x white flowers give pink F1; F2 gives 1 red : 2 pink : 1 white, a 1:2:1 phenotypic ratio). When codominance occurs, both alleles are expressed fully in the heterozygote (no blending); the F2 ratio is also 1:2:1 but with three distinct phenotypes. Epistasis occurs when alleles at one locus mask or modify the

phenotypic expression of alleles at a different locus, producing modified dihybrid ratios such as 9:7, 12:3:1, 15:1, or 9:3:4 depending on the type of epistatic interaction.

In crop breeding, epistasis is important because the phenotypic value of a genotype depends not only on its alleles at individual loci but also on how those alleles interact with alleles at other loci. This gene-by-gene interaction (epistasis) contributes to the non-additive genetic variance that does not respond to simple selection but can be captured in hybrid combinations. Understanding epistasis helps the breeder choose between selection methods: additive variance responds to recurrent selection; epistatic (dominance and interaction) variance is best exploited in F1 hybrid varieties. The distinction between additive and non-additive variance is developed further in the heritability section.

Fill in the blank: _____ occurs when alleles at one locus mask or modify the expression of alleles at a different locus, producing modified dihybrid F2 ratios such as 9:7, 12:3:1, or 15:1.

Pilot questions 3.2

1. Construct a Punnett square for the cross Aa x Aa and state the genotypic and phenotypic ratios.
2. Explain what a testcross is and how it is used to determine an unknown genotype.
3. State the expected F2 phenotypic ratio for a dihybrid cross (AaBb x AaBb) assuming complete dominance and independent assortment.
4. Explain incomplete dominance and give the expected F2 ratio when it applies.
5. Define epistasis and explain its importance for choosing a breeding method.

3.3 Qualitative and Quantitative Traits

3.3.1 Qualitative traits and their inheritance

Qualitative traits are controlled by one or a few genes with large individual effects and show discrete, non-overlapping phenotypic classes. Examples in crop plants include seed colour (yellow vs green in peas), disease reaction (resistant vs susceptible to a specific pathogen race),

grain texture (waxy vs non-waxy endosperm in maize), and presence or absence of pubescence (hairiness) on leaves or pods. The phenotypic classes of a qualitative trait can be clearly distinguished by visual inspection without measurement; individual plants can be unambiguously classified into one category or another. Environmental variation has little effect on the expression of qualitative traits.

Qualitative traits are the simplest to work with in breeding because their inheritance follows predictable Mendelian ratios, the genes can be tracked through generations using the phenotype, and selection for them is straightforward (select the resistant plant, reject the susceptible one). In Nigeria, qualitative disease resistance traits have been used to develop Striga-resistant maize and sorghum, late blight-resistant cassava, and blackeye cowpea varieties with smooth seed coat (preferred in northern Nigerian markets). Molecular markers linked to qualitative resistance genes allow marker-assisted selection (MAS) to accelerate introgression of resistance alleles into elite backgrounds.

Fill in the blank: _____ traits are controlled by one or a few genes with large effects, show discrete non-overlapping phenotypic classes, and are little influenced by the environment; they follow predictable Mendelian ratios.

3.3.2 Quantitative traits and polygenic inheritance

Quantitative traits are controlled by many genes (polygenes), each with a small individual effect, and they show continuous variation in a population rather than discrete classes. Examples include grain yield, plant height, days to flowering, drought tolerance, and protein content; these traits cannot be classified as simply "high" or "low" but are measured on a continuous scale. The continuous distribution of quantitative traits in a population typically approximates a normal (bell-shaped) distribution, arising from the combined effects of many genes and environmental variation. The number of polygenes controlling a trait can be estimated from the degree of transgressive segregation in an F2 population.

The phenotypic value (P) of an individual for a quantitative trait can be partitioned as $P = G + E$, where G is the genotypic value (the contribution of the genotype) and E is the environmental deviation. The genotypic value is further partitioned as $G = A + D + I$, where A is the additive

genetic value (the sum of average effects of individual alleles, the component that responds to selection and can be passed to offspring), D is the dominance deviation (allele interaction within a locus), and I is the epistatic deviation (interaction between loci). Additive genetic variance (VA) is the breeder's primary target because it determines the response to selection; non-additive variance (VD + VI) contributes to heterosis exploited in hybrid varieties.

Fill in the blank: The phenotypic value of a quantitative trait is partitioned as P = G + E; the genotypic value G is further partitioned as A + D + I, where _____ is the additive genetic value that responds to selection.

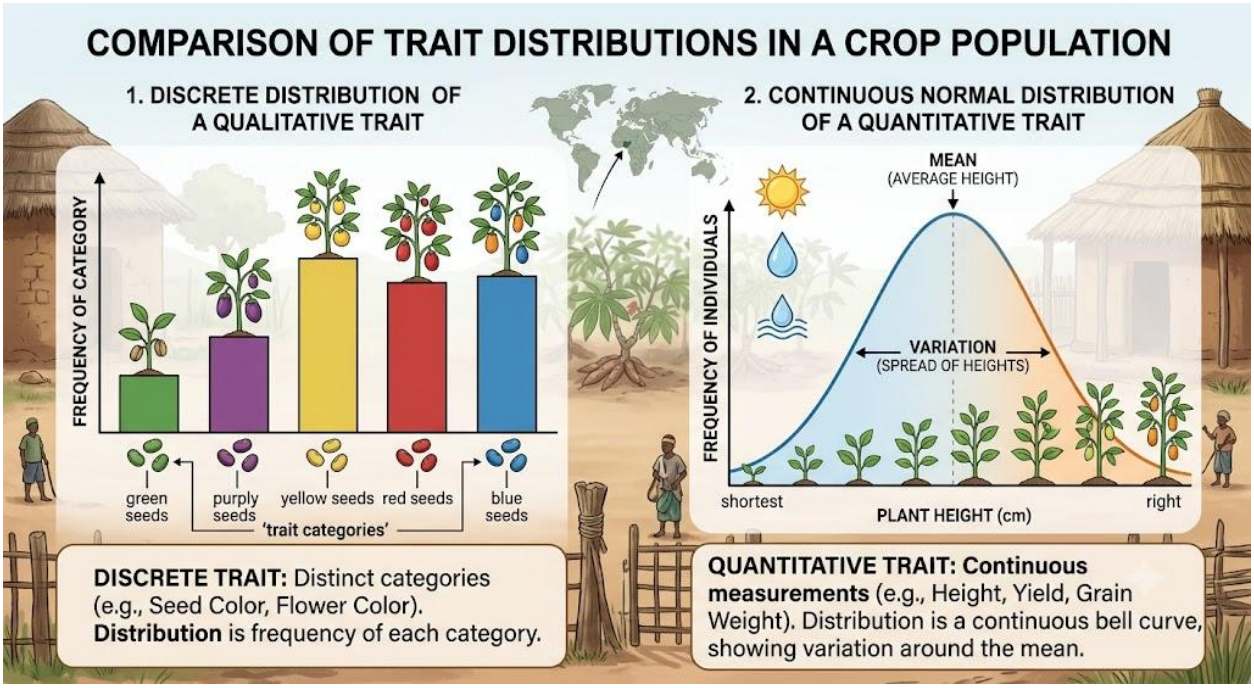

Figure 3.2: Diagram comparing the distribution of a qualitative trait and a quantitative trait in a crop population

3.3.3 Heritability and its estimation

Heritability is the proportion of total phenotypic variance in a population that is attributable to genetic variance. Broad-sense heritability (H2) = VG / VP, where VG is total genetic variance (VA + VD + VI) and VP is total phenotypic variance (VG + VE). It answers the question: "How much of the variation I observe is genetic?" Narrow-sense heritability (h2) = VA / VP, where VA is additive genetic variance only. It answers the question: "How well do offspring resemble their

parents?" and directly predicts the response to selection. Narrow-sense heritability is the more useful measure for the plant breeder.

Heritability is estimated from genetic experiments: parent-offspring regression (the regression coefficient of offspring mean on mid-parent value estimates h2); variance components from replicated trials (VP is estimated from the phenotypic variance of the population, VG from genotypic variance estimated by clonal replication or from line family variances, and VE from the environmental variance estimated from within-genotype variation); and the response to selection method (h2 = R/S, where R is the observed selection response and S is the selection differential, the difference between the mean of the selected parents and the mean of the whole population). Heritability values range from 0 to 1 and are specific to the population and environment in which they are estimated.

Fill in the blank: Narrow-sense heritability (h2) = VA / VP, where VA is _____ genetic variance; it predicts the response to selection and determines how well offspring resemble their parents.

Pilot questions 3.3

1. Distinguish between qualitative and quantitative traits and give two examples of each in Nigerian crops.
2. Explain polygenic inheritance and state what distribution quantitative traits typically show in a population.
3. Write the equation for phenotypic value partitioning (P = G + E) and explain each component.
4. Define broad-sense and narrow-sense heritability and write the formula for each.
5. State three methods of estimating heritability and briefly explain each.

3.4 Chi-Square Analysis and Selection Response

3.4.1 The chi-square test for goodness of fit

The chi-square (x2) test is used in plant breeding to test whether observed offspring frequencies fit the ratios expected from a specific genetic hypothesis (for example, 3:1 or 9:3:3:1 for Mendelian segregation). The null hypothesis states that the observed frequencies do not differ from the expected frequencies in a statistically significant way; deviations are due to chance sampling variation. If the calculated chi-square value exceeds the critical value at the chosen significance level (usually p = 0.05) and the appropriate degrees of freedom, the null hypothesis is rejected, and the data do not fit the expected ratio, indicating that a different genetic model may be operating.

The chi-square test is appropriate when: the data are counts (discrete numbers of individuals in each class, not proportions or continuous measurements); the sample size is adequate (each expected class frequency should be at least 5, ideally at least 10); the observations are independent; and the categories are mutually exclusive and exhaustive. When these conditions are met, the chi-square test provides an objective statistical criterion for accepting or rejecting a specific genetic interpretation of segregation data. Without such a test, breeders cannot distinguish between small deviations due to sampling variation and larger deviations that suggest a different inheritance pattern.

Fill in the blank: The chi-square test requires that each expected class frequency is at least _____, that the data are counts, that observations are independent, and that the categories are mutually exclusive and exhaustive.

3.4.2 Calculating and interpreting chi-square

The chi-square statistic is calculated as: x2 = sum of [(O - E)2 / E] for each class, where O is the observed count and E is the expected count for that class. The degrees of freedom (df) = number of phenotypic classes minus 1 (minus any additional parameters estimated from the data). For a monohybrid 3:1 ratio, df = 2 - 1 = 1. The calculated x2 is compared with the critical value from the chi-square distribution table at the chosen significance level and the appropriate df: for df = 1 and p = 0.05, the critical value is 3.841; for df = 3 (dihybrid) and p = 0.05, the critical value is 7.815.

Worked example: from a monohybrid cross, 150 plants are observed: 120 tall and 30 dwarf. Expected ratio 3:1 gives 112.5 tall and 37.5 dwarf. x2 = (120-112.5)2/112.5 + (30-37.5)2/37.5 = 56.25/112.5 + 56.25/37.5 = 0.500 + 1.500 = 2.000. df = 1; critical value at p = 0.05 is 3.841. Since 2.000 < 3.841, we fail to reject the null hypothesis: the data fit the expected 3:1 ratio. The conclusion is that the observed results are consistent with monohybrid segregation with complete dominance.

Fill in the blank: The chi-square statistic is calculated as the sum of [(O minus E) squared divided by E] for each class; a calculated value less than the critical value means we _____ to reject the null hypothesis and the data fit the expected ratio.

Category	Observed (O)	Expected (E)	O − E	(O − E)²	(O − E)² / E
Tall	120	112.5	7.5	56.25	0.50
Dwarf	30	37.5	-7.5	56.25	1.50
Total	150	150	—	—	**2.00**

Table 3.1: Worked chi-square calculation for a monohybrid 3:1 ratio

Step-by-Step Calculation

1. **Total observed = 120 + 30 = 150**
2. **Expected ratio = 3:1 → Tall = 3/4 × 150 = 112.5; Dwarf = 1/4 × 150 = 37.5**
3. **Chi-square formula:**
   [\chi^2 = \sum \frac{(O - E)^2}{E}]
   - Tall: ((120 - 112.5)^2 / 112.5 = 56.25 / 112.5 = 0.50)
   - Dwarf: ((30 - 37.5)^2 / 37.5 = 56.25 / 37.5 = 1.50)
4. **Chi-square total = 0.50 + 1.50 = 2.00**

Interpretation

- Degrees of freedom (df) = categories − 1 = 2 − 1 = **1**
- At df = 1, critical χ^2 at 0.05 = **3.84**
- Since **2.00 < 3.84**, the difference is **not significant**.

- The observed data **fits the expected 3:1 Mendelian ratio**.

3.4.3 Selection response and the breeder's equation

The breeder's equation predicts the response to selection (R) for a quantitative trait: R = h2 x S, where h2 is the narrow-sense heritability and S is the selection differential (S = mean of selected parents minus mean of the whole population). The selection differential measures how intensively selection has been applied; it depends on the proportion of individuals selected (selection intensity, i) and the phenotypic standard deviation (sigma_P): S = i x sigma_P. Substituting: R = h2 x i x sigma_P. This equation tells the breeder how much improvement to expect per generation of selection and allows planning of the number of generations needed to reach a target performance level.

Worked example: a cowpea breeding programme selects for seed yield. Population mean yield = 800 kg/ha; phenotypic standard deviation = 120 kg/ha; the breeder selects the top 10 per cent of plants (selection intensity i = 1.755 for the top 10%); narrow-sense heritability h2 = 0.35. Selection differential S = 1.755 x 120 = 210.6 kg/ha. Response R = 0.35 x 210.6 = 73.7 kg/ha per generation. The expected mean of the next generation = 800 + 73.7 = 873.7 kg/ha. The breeder can also rearrange the equation to estimate how many generations are needed to achieve a specific breeding target, or to evaluate whether increasing selection intensity or heritability would accelerate progress.

Fill in the blank: The breeder's equation is R = h2 x S, where R is the selection _____, h2 is the narrow-sense heritability, and S is the selection differential (mean of selected parents minus mean of the whole population).

Component	Symbol	Definition	Cowpea Worked Example

Selection Response	R	Expected genetic gain per generation	R=73.7 kg/ha
Heritability	h2	Proportion of phenotypic variance due to genetic variance	h2=0.35
Selection Intensity	i	Standardized selection differential (depends on proportion selected)	i=1.755 (top 10%)
Phenotypic Standard Deviation	σP	Measure of variation in the population	σP=120
Selection Differential	S	Difference between mean of selected parents and population mean	S=i×σP=1.755×120=210.6
Equation	R=h2×i×σP	Predicts genetic gain from selection	R=0.35×1.755×120=73.7 kg/ha
Next Generation Mean	—	Population mean + response	800+73.7=873.7 kg/ha

Box 3.1: Breeder's equation: components and worked cowpea yield example

Pilot questions 3.4

1. Explain what the chi-square test is used for in plant breeding and state the null hypothesis it tests.
2. State four conditions that must be met for the chi-square test to be valid.
3. Write the formula for chi-square and define each symbol.
4. Using the worked example in the text (120 tall, 30 dwarf), verify the chi-square calculation and state your conclusion.
5. Write the breeder's equation and explain each component; use it to calculate the expected selection response for a population with h2 = 0.4, sigma_P = 100, and selection intensity i = 1.40.

Series Summary

This Series covered the Mendelian foundations and statistical tools of plant breeding. We described Mendel's experimental design with garden pea, his Law of Segregation (two alleles separate at meiosis, each gamete carries one), and his Law of Independent Assortment (alleles of different genes on non-homologous chromosomes assort independently at metaphase I). We constructed Punnett squares for monohybrid crosses (3:1 F2 phenotypic ratio) and dihybrid crosses (9:3:3:1), introduced the testcross and backcross, and described modifications of Mendelian ratios including incomplete dominance, codominance, and epistasis.

We distinguished qualitative traits (discrete classes, few genes, little environmental influence, Mendelian inheritance) from quantitative traits (continuous variation, many polygenes, environmental influence, partitioned as P = G + E = A + D + I + E), defined broad-sense and narrow-sense heritability, and described three methods of heritability estimation. Finally, we applied the chi-square test (x2 = sum of (O-E)2/E, compared with critical values at df = classes - 1) for testing goodness of fit to Mendelian ratios, and introduced the breeder's equation (R = h2 x i x sigma_P) for predicting selection response. By completing this Series, you should be able to achieve all eight Series Learning Outcomes (SLO 3.1 to SLO 3.8).

Glossary of Terms

- **Additive genetic variance (VA):** the component of genetic variance due to the average effects of individual alleles; the component that responds to selection and is passed to offspring; used in the denominator of narrow-sense heritability.
- **Backcross:** a cross of an F1 hybrid back to one of the parental genotypes; used in breeding to introgress a specific trait while recovering the recurrent parent genome.

- **Breeder's equation:** R = h2 x S (or R = h2 x i x sigma_P); predicts the response to selection for a quantitative trait per generation.
- **Broad-sense heritability (H2):** VG / VP; the proportion of phenotypic variance attributable to total genetic variance (additive + dominance + epistatic).
- **Chi-square (x2) test:** a statistical test comparing observed and expected frequencies to determine whether deviations from expected Mendelian ratios are due to chance or indicate a different genetic model.
- **Codominance:** the condition in which both alleles at a heterozygous locus are fully expressed, resulting in a phenotype that shows characteristics of both homozygous phenotypes.
- **Degrees of freedom (df):** in chi-square analysis, the number of phenotypic classes minus 1 (minus any additional estimated parameters); determines which row of the chi-square table to use.
- **Dihybrid cross:** a cross between parents that differ at two gene loci; produces a 9:3:3:1 F2 phenotypic ratio when the genes assort independently and show complete dominance.
- **Environmental deviation (E):** the component of an individual's phenotypic value attributable to non-heritable environmental effects; P = G + E.
- **Epistasis:** interaction between alleles at different loci such that alleles at one locus mask or modify the phenotypic expression of alleles at another locus; produces modified dihybrid ratios.
- **Genotypic value (G):** the component of phenotypic value attributable to genotype; G = A + D + I.
- **Heterosis (hybrid vigour):** the superior performance of an F1 hybrid over the mean of its parents; attributable primarily to dominance and epistatic genetic effects.
- **Incomplete dominance:** a situation in which the heterozygote shows a phenotype intermediate between the two homozygotes; produces a 1:2:1 F2 phenotypic ratio.

- **Law of Independent Assortment:** Mendel's second law: alleles of different genes on non-homologous chromosomes assort independently during gamete formation.
- **Law of Segregation:** Mendel's first law: the two alleles of a gene separate (segregate) during gamete formation so that each gamete carries only one allele for each gene.
- **Monohybrid cross:** a cross between parents that differ at a single gene locus; produces a 3:1 F2 phenotypic ratio (with complete dominance) or 1:2:1 (with incomplete dominance or codominance).
- **Narrow-sense heritability (h2):** VA / VP; the proportion of phenotypic variance attributable to additive genetic variance; directly predicts the response to selection and parent-offspring resemblance.
- **Null hypothesis:** in chi-square analysis, the hypothesis that observed frequencies do not differ significantly from expected frequencies and that any deviations are due to chance sampling variation.
- **Polygenic inheritance:** the inheritance of a quantitative trait controlled by many genes (polygenes) each with a small individual effect; produces continuous, approximately normally distributed variation.
- **Punnett square:** a grid method for predicting the genotypic and phenotypic ratios of offspring from a cross by systematically combining gametes of the two parents.
- **Qualitative trait:** a trait controlled by one or a few genes with large effects, showing discrete non-overlapping phenotypic classes with little environmental influence.
- **Quantitative trait:** a trait controlled by many genes (polygenes) each with a small effect, showing continuous variation that approximates a normal distribution and is influenced by the environment.
- **Selection differential (S):** the difference between the mean of selected parents and the mean of the whole population; S = i x sigma_P.
- **Selection intensity (i):** a standardised measure of how stringently selection is applied; the selection differential expressed in units of the phenotypic standard deviation.

- **Selection response (R):** the change in population mean between generations due to selection; R = h2 x S.
- **Testcross:** a cross of a dominant-phenotype individual of unknown genotype with a homozygous recessive to determine whether the individual is homozygous dominant (AA) or heterozygous (Aa).
- **True-breeding line:** a plant line that is homozygous at all relevant loci and therefore produces offspring identical to the parent when self-pollinated; used as parental material in crossing programmes.

Concept Check Questions [Series 3]

Objective Questions

1. Mendel's Law of _____ states that the two alleles of a gene separate during gamete formation so each gamete carries only one allele. (Linked to SLO 3.2)
2. The F2 of a dihybrid cross (AaBb x AaBb) with complete dominance and independent assortment produces the phenotypic ratio 9 A_B_ : 3 A_bb : 3 aaB_ : 1 aabb; this is known as the _____ ratio. (Linked to SLO 3.3)
3. _____ traits are controlled by many genes with small individual effects and show continuous variation approximating a normal distribution. (Linked to SLO 3.5)
4. Narrow-sense heritability h2 = VA / VP, where VA is _____ genetic variance; it directly predicts the response to selection. (Linked to SLO 3.6)
5. The breeder's equation is R = h2 x S; S is the selection _____, the difference between the mean of selected parents and the mean of the whole population. (Linked to SLO 3.8)

Short-Answer Questions

6. State Mendel's two laws of inheritance. (Linked to SLO 3.2)

7. Construct a Punnett square for Aa x Aa and state the genotypic and phenotypic ratios. (Linked to SLO 3.3)
8. Distinguish between qualitative and quantitative traits. (Linked to SLO 3.5)
9. Write the formula for chi-square and state the degrees of freedom for testing a monohybrid 3:1 ratio. (Linked to SLO 3.7)
10. State the breeder's equation and calculate R for a population with h2 = 0.4, sigma_P = 100, and i = 1.40. (Linked to SLO 3.8)

Long-Answer Questions

11. Describe Mendel's experimental design, state and explain his two laws of inheritance with their cellular basis, and demonstrate the use of the Punnett square for monohybrid and dihybrid crosses. (Linked to SLOs 3.1, 3.2, 3.3)
12. Distinguish between qualitative and quantitative traits, explain polygenic inheritance and phenotypic value partitioning (P = G + E = A + D + I + E), and describe broad-sense and narrow-sense heritability and methods of estimation. (Linked to SLOs 3.5, 3.6)
13. Explain the chi-square test for goodness of fit (including conditions, formula, degrees of freedom, and interpretation) and the breeder's equation for selection response, using worked examples. (Linked to SLOs 3.7, 3.8)

Answers to Concept Check Questions [Series 3]

Objective Questions

1. Segregation.
2. 9:3:3:1.
3. Quantitative.
4. Additive.
5. Differential.

Short-Answer Questions

6. Law of Segregation: the two alleles of a gene in an individual separate from each other during gamete formation so that each gamete carries only one allele for each gene. Law of Independent Assortment: alleles of different genes on non-homologous chromosomes assort independently of one another during gamete formation.
7. Punnett square for Aa x Aa: gametes A and a from each parent; four cells: AA, Aa, Aa, aa. Genotypic ratio: 1 AA : 2 Aa : 1 aa. Phenotypic ratio (A dominant over a): 3 A_ (dominant phenotype) : 1 aa (recessive phenotype).
8. Qualitative traits: controlled by one or a few genes with large effects; show discrete non-overlapping phenotypic classes; little influenced by the environment; follow Mendelian inheritance (e.g. seed colour, disease resistance class). Quantitative traits: controlled by many polygenes each with a small effect; show continuous variation approximating a normal distribution; strongly influenced by the environment; measured on a continuous scale (e.g. grain yield, plant height, days to flowering).
9. Chi-square formula: x2 = sum of [(O - E)2 / E] for each class, where O is the observed count and E is the expected count. Degrees of freedom for a monohybrid 3:1 ratio: df = number of classes - 1 = 2 - 1 = 1. Critical value at df=1, p=0.05 is 3.841.
10. Breeder's equation: R = h2 x S = h2 x i x sigma_P. With h2 = 0.4, sigma_P = 100, i = 1.40: S = 1.40 x 100 = 140. R = 0.4 x 140 = 56 units per generation.

Long-Answer Questions

11. Mendel's design: garden pea (self-pollinating, true-breeding lines easily maintained, short generation, large offspring numbers, seven clear-cut alternative trait pairs); methodological innovations (true-breeding parents, reciprocal crosses, large sample sizes, multi-generation tracking). Law of Segregation: two alleles separate at meiosis (cellular basis: homologs separate at anaphase I); each gamete carries one allele; F1 Tt x TT/tt cross all F1 Tt (tall, dominant); F2 selfing gives 3 tall : 1 dwarf (3 T_ : 1 tt). Monohybrid

Punnett (Aa x Aa): gametes A, a x A, a; cells AA, Aa, Aa, aa; genotypic 1:2:1; phenotypic 3:1. Law of Independent Assortment: alleles on non-homologous chromosomes assort independently (cellular basis: random bivalent orientation at metaphase I); dihybrid cross YYRR x yyrr gives all YyRr F1; F2 9 Y_R_ : 3 Y_rr : 3 yyR_ : 1 yyrr; 16 cells in 4x4 Punnett.

12. Qualitative: one or few genes, large effects, discrete classes, little environmental influence, Mendelian ratios; Nigerian examples: Striga resistance in maize (R/r), grain colour in sorghum. Quantitative: many polygenes, each small effect, continuous normal distribution, strong environmental influence, measured on continuous scale; Nigerian examples: grain yield (kg/ha), plant height (cm), days to maturity. Polygenic inheritance: additive effects of many loci produce a distribution that approximates normal; number of genes can be estimated from transgressive segregation in F2. Phenotypic partitioning: P = G + E; G = A + D + I; A = additive (responds to selection, predicts offspring mean); D = dominance deviation (within-locus allele interaction, contributes to heterosis); I = epistatic deviation (between-locus interaction). Broad-sense heritability: H2 = VG / VP = (VA + VD + VI) / VP; proportion of variation that is genetic. Narrow-sense heritability: h2 = VA / VP; predicts selection response and parent-offspring resemblance; more useful for breeder. Estimation methods: parent-offspring regression (b = h2); variance components from replicated trials (VP from phenotypic variance, VE from within-genotype variance, VG = VP - VE, h2 = VA/VP); response method (h2 = R/S after one cycle of selection).
13. Chi-square: used to test whether observed offspring frequencies fit expected Mendelian ratios. Null hypothesis: deviations from expected are due to chance. Conditions: data are counts; each expected class frequency at least 5 (ideally 10); observations independent; categories mutually exclusive and exhaustive. Formula: x2 = sum of [(O-E)2/E]; df = classes - 1. Worked example: 120 tall, 30 dwarf; expected 3:1 from 150 = 112.5 tall, 37.5 dwarf; x2 = (7.5)2/112.5 + (7.5)2/37.5 = 0.5 + 1.5 = 2.0; df=1; critical value 3.841; 2.0 < 3.841; fail to reject null; data consistent with 3:1. Interpretation: if x2 exceeds critical value, reject null; data do not fit expected ratio; investigate alternative model (epistasis, linkage, lethality). Breeder's equation: R = h2 x S = h2 x i x sigma_P. R = selection response (change in population mean per generation); h2 = narrow-sense heritability; S =

selection differential = i x sigma_P; i = selection intensity (standardised, depends on proportion selected; top 10% i=1.755, top 5% i=2.063); sigma_P = phenotypic standard deviation. Cowpea worked example: mean 800, sigma_P=120, i=1.755, h2=0.35; S=210.6; R=73.7 kg/ha; next generation mean=873.7 kg/ha. Uses: predict progress per generation; estimate generations to reach target; optimise selection intensity vs population size trade-off.

Answers to Pilot Questions [Series 3]

Part 3.1: Mendel's Experiments and Laws of Inheritance

1. Any four: the garden pea naturally self-pollinates, making it easy to maintain true-breeding (homozygous) lines for use as parental material; hand-pollination allows controlled crosses; the generation time is short (one growing season), allowing multiple generations to be studied; large numbers of offspring are produced, providing statistical power for counting ratios; and seven pairs of traits show clear-cut, easily distinguishable alternative forms.
2. The Law of Segregation states that the two alleles of a gene in an individual separate (segregate) from each other during gamete formation so that each gamete carries only one allele for each gene. Cellular basis: the two alleles of a gene occupy the same locus on the two homologous chromosomes (one allele per homolog). During meiosis I, homologous chromosomes separate to opposite poles at anaphase I; since the alleles are on homologs, they also separate, so each resulting gamete receives exactly one allele at that locus.
3. In a monohybrid cross between true-breeding tall (TT) and dwarf (tt) plants, Mendel observed that all F1 offspring were tall (Tt), indicating that tallness (T) is dominant over dwarfness (t). When F1 (Tt) plants were selfed, F2 plants appeared in a ratio of approximately 3 tall : 1 dwarf. Mendel interpreted this as evidence that: (1) the F1 heterozygote (Tt) carried both T and t alleles in separate form (they had not blended); (2) the two alleles separated equally during gamete formation, giving 50% T gametes and

50% t gametes; (3) random fusion of gametes at fertilisation gave 1/4 TT (tall) + 2/4 Tt (tall) + 1/4 tt (dwarf) = 3 tall : 1 dwarf.

4. The Law of Independent Assortment states that alleles of different genes assort independently of one another during gamete formation, provided the genes are on different (non-homologous) chromosomes. Cellular basis: during metaphase I of meiosis, each bivalent (pair of homologs) lines up at the cell equator independently of all other bivalents; the orientation of one bivalent (which homolog faces which pole) is completely random and uninfluenced by the orientation of any other bivalent. As a result, the alleles at different loci end up in different gametes in all possible combinations with equal frequency.
5. The Law of Independent Assortment applies only to genes on different (non-homologous) chromosomes. Genes on the same chromosome are physically linked on the same DNA molecule; their alleles therefore tend to be inherited together rather than independently. If two loci are linked, the frequency of recombinant gametes (carrying new allele combinations) is less than 50 per cent and depends on the distance between them on the chromosome: closely linked genes produce very few recombinants; genes far apart on the same chromosome may appear to assort nearly independently (up to 50% recombination) due to multiple crossing over events between them.

Part 3.2: Monohybrid and Dihybrid Crosses

1. Punnett square for Aa x Aa: Gametes from parent 1: A, a (columns). Gametes from parent 2: A, a (rows). Four cells: AA, Aa / Aa, aa. Genotypic ratio: 1 AA : 2 Aa : 1 aa. Phenotypic ratio (A dominant): 3 A_ (dominant phenotype, includes AA and Aa) : 1 aa (recessive phenotype).
2. A testcross involves crossing an individual that shows the dominant phenotype but whose genotype is unknown (either AA or Aa) with a homozygous recessive individual (aa). If the unknown individual is AA: all offspring are Aa (dominant phenotype); ratio 1:0. If the unknown individual is Aa: offspring are 1 Aa (dominant) : 1 aa (recessive); ratio 1:1. The

presence or absence of recessive-phenotype offspring in the testcross progeny reveals the genotype of the unknown parent: no recessives = AA; half recessives = Aa.

3. F2 phenotypic ratio from AaBb x AaBb (complete dominance, independent assortment): 9 A_B_ (dominant for both traits) : 3 A_bb (dominant for first, recessive for second) : 3 aaB_ (recessive for first, dominant for second) : 1 aabb (recessive for both traits). Total: 16 parts. The 9:3:3:1 ratio results from the independent 3:1 segregation of each gene multiplied together: (3:1) x (3:1) = 9:3:3:1.
4. Incomplete dominance occurs when the heterozygote (Aa) shows a phenotype that is intermediate between the two homozygote phenotypes (AA and aa), rather than resembling either parent exactly. Example: in some flowers, red (RR) crossed with white (rr) gives pink F1 (Rr); the pink F1 selfed gives F2 = 1 red (RR) : 2 pink (Rr) : 1 white (rr). The F2 phenotypic ratio is therefore 1:2:1 (same as the genotypic ratio), not 3:1, because the heterozygote is now phenotypically distinguishable from both homozygotes.
5. Epistasis is the interaction between alleles at different loci (gene-by-gene interaction) such that the alleles at one locus mask or modify the phenotypic expression of alleles at a different locus. Its importance for choosing a breeding method: the type of genetic variance present determines the most efficient breeding method. If a trait is primarily controlled by additive variance (VA), mass selection or pure-line selection is effective. If the trait shows strong epistasis (VI is large, as in hybrid vigour), then developing F1 hybrid varieties that exploit the specific allele combinations producing the best phenotype is more effective than recurrent selection for individual loci. A breeder who recognises epistasis will use diallel crossing to identify the best hybrid combinations rather than selecting from segregating populations.

Part 3.3: Qualitative and Quantitative Traits

1. Qualitative traits: controlled by one or a few genes with large individual effects; phenotype appears in discrete, non-overlapping classes that can be identified by visual inspection without measurement; little affected by environmental variation; follow predictable Mendelian ratios. Nigerian crop examples: grain colour in cowpea (black-

eyed vs cream); Striga resistance or susceptibility in sorghum. Quantitative traits: controlled by many genes (polygenes) each with a small additive effect; phenotype shows continuous variation in a population (cannot be divided into discrete classes); strongly influenced by environmental variation; do not follow simple Mendelian ratios. Nigerian crop examples: grain yield (kg/ha) in maize; days to 50% flowering in cowpea.

2. Polygenic inheritance is the control of a trait by many genes (polygenes) each contributing a small, approximately equal, and additive effect to the phenotype. The phenotypic value of any individual is the sum of the small contributions of all polygene loci plus the environmental effect. Because many independent loci each take one of two allele states and their effects add up, the central limit theorem predicts that the sum of many small independent effects will approach a normal (bell-shaped, Gaussian) distribution. In a segregating F2 population derived from a cross between two inbred lines, quantitative traits typically show a normal distribution with the mean approximately equal to the mid-parent value and a variance that reflects both genetic segregation and environmental effects.
3. Phenotypic value partitioning: P = G + E, where P is the phenotypic value of an individual (the observed measurement), G is the genotypic value (the contribution of the individual's genotype to its phenotype, the average phenotypic value of individuals with that genotype across environments), and E is the environmental deviation (the difference between the individual's actual phenotypic value and its genotypic value, caused by non-heritable environmental effects specific to the individual's growing conditions). The genotypic value G is further partitioned as G = A + D + I, where A = additive genetic value (the predictable component transmitted to offspring), D = dominance deviation (non-additive within-locus allele interaction), I = epistatic interaction deviation (non-additive between-locus gene interactions).
4. Broad-sense heritability H2 = VG / VP = (VA + VD + VI) / (VG + VE); the proportion of total phenotypic variance attributable to all genetic variance (additive + dominance + epistatic). Narrow-sense heritability h2 = VA / VP = VA / (VA + VD + VI + VE); the proportion of total phenotypic variance attributable to additive genetic variance only; the more useful measure for the plant breeder because it directly predicts the response to selection.

5. Three methods: (1) Parent-offspring regression: grow parents and measure their phenotypic values; grow their offspring and measure the offspring mean; regress offspring mean on mid-parent value; the regression coefficient b estimates narrow-sense heritability h2 because the resemblance between parents and offspring is due to the additive genetic component. (2) Variance components from replicated trials: grow a set of genotypes in replicated plots; estimate phenotypic variance VP from the among-genotype + within-genotype variation; estimate environmental variance VE from the within-genotype (within-clone or within-pure-line) variation; VG = VP - VE; h2 = VA/VP (VA approximated from family variance components). (3) Realised heritability from selection response: conduct one cycle of selection; measure the selection differential S (mean of selected parents minus population mean) and the selection response R (mean of progeny of selected parents minus original population mean); h2 = R/S.

Part 3.4: Chi-Square Analysis and Selection Response

1. The chi-square test is used in plant breeding to determine whether the observed frequencies of offspring phenotypic classes are consistent with the frequencies expected from a specific genetic hypothesis (such as 3:1 for a monohybrid or 9:3:3:1 for a dihybrid). The null hypothesis tested is: "the observed frequencies do not differ significantly from the expected frequencies, and any deviations are due to random sampling variation." If the null hypothesis is rejected, the data do not fit the hypothesised genetic model and a different model must be considered.
2. Four conditions: (1) the data must be counts (discrete numbers of individuals classified into phenotypic categories), not proportions or continuous measurements; (2) each expected class frequency must be at least 5 (ideally at least 10) to ensure that the chi-square approximation is valid; (3) observations must be independent of each other (the classification of one plant must not influence the classification of another); (4) the phenotypic categories must be mutually exclusive (each individual fits in exactly one class) and exhaustive (all individuals are classified, none excluded).

3. Formula: x2 = sum of [(O - E)2 / E] summed over all phenotypic classes. O = observed count (number of individuals actually counted in that class from the experiment); E = expected count (number predicted from the genetic hypothesis, calculated as total offspring x expected proportion for that class); (O - E) = the deviation of the observed from the expected count; (O - E)2 = the squared deviation (to remove negative signs); (O - E)2 / E = the deviation standardised for the magnitude of the expected count; the sum over all classes = x2, a single test statistic that is then compared with the critical value from the chi-square distribution table at df = number of classes - 1.
4. Verification: total offspring = 120 + 30 = 150. Expected for 3:1: tall = 3/4 x 150 = 112.5; dwarf = 1/4 x 150 = 37.5. x2 = (120-112.5)2/112.5 + (30-37.5)2/37.5 = (7.5)2/112.5 + (-7.5)2/37.5 = 56.25/112.5 + 56.25/37.5 = 0.500 + 1.500 = 2.000. df = 2 - 1 = 1; critical value at df=1, p=0.05 is 3.841. Since 2.000 < 3.841, we fail to reject the null hypothesis. Conclusion: the observed data (120 tall : 30 dwarf) are consistent with the expected 3:1 Mendelian ratio; there is no statistically significant evidence against the monohybrid segregation hypothesis with complete dominance.
5. Breeder's equation: R = h2 x S = h2 x i x sigma_P, where R = selection response (expected change in population mean per generation); h2 = narrow-sense heritability; S = selection differential (mean of selected parents minus mean of whole population); i = selection intensity (standardised); sigma_P = phenotypic standard deviation. Calculation: h2 = 0.4, sigma_P = 100, i = 1.40. S = i x sigma_P = 1.40 x 100 = 140 units. R = h2 x S = 0.4 x 140 = 56 units per generation. The expected mean of the next generation = original mean + R = original mean + 56 units. This tells the breeder that at h2 = 0.4 and selecting the proportion corresponding to i = 1.40, approximately 56 units of improvement per generation is expected, regardless of the original population mean.

References and Attributions [Series 3]

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Figure 3.1: Dihybrid cross and 9:3:3:1 ratio Attribution: AI generated. Suggested OER search string: "dihybrid cross Punnett square F2 ratio 9:3:3:1 Mendel independent assortment OER".
- Figure 3.2: Qualitative vs quantitative trait distributions Attribution: AI generated. Suggested OER search string: "qualitative vs quantitative trait distribution discrete continuous crop breeding OER".
- Table 3.1: Chi-square worked example for 3:1 ratio Attribution: AI generated. Suggested OER search string: "chi-square calculation monohybrid 3:1 ratio worked example table plant breeding OER".
- Box 3.1: Breeder's equation worked cowpea example Attribution: AI generated. Suggested OER search string: "breeder equation selection response heritability differential worked example cowpea OER box".

Course code: AGE 304

Course title: Technology of Breeding Crop

Course credit load: 2 Units

Series 4: Sexual Reproduction, Controlled Crosses, and Breeding Materials

- **Part 4.1: Methods of Sexual Reproduction in Crop Plants**
    - Sub Part 4.1.1: Self-pollination and its genetic consequences
    - Sub Part 4.1.2: Cross-pollination and its genetic consequences
    - Sub Part 4.1.3: Identifying the mating system of a crop
- **Part 4.2: Self-Incompatibility and Male Sterility**
    - Sub Part 4.2.1: Self-incompatibility: types and mechanisms
    - Sub Part 4.2.2: Male sterility: cytoplasmic and genetic
    - Sub Part 4.2.3: Use of self-incompatibility and male sterility in hybrid seed production
- **Part 4.3: Steps for Controlled Crosses**
    - Sub Part 4.3.1: Tools and preparation for crossing
    - Sub Part 4.3.2: Emasculation techniques
    - Sub Part 4.3.3: Pollination, bagging, and labelling
- **Part 4.4: Sourcing for Breeding Materials**
    - Sub Part 4.4.1: Sources of breeding materials

- Sub Part 4.4.2: Evaluating and selecting parental lines
- Sub Part 4.4.3: Managing a crossing nursery

Introduction

The practical starting point of every breeding programme is understanding how a crop reproduces sexually and then manipulating that reproduction to make the crosses required by the breeding plan. Whether a crop self-pollinates or cross-pollinates determines which breeding methods are applicable and what precautions must be taken to control pollination. Some crops have evolved mechanisms (self-incompatibility and male sterility) that prevent selfing and enforce cross-pollination; these same mechanisms can be exploited by the breeder to produce hybrid seed efficiently.

This Series covers the methods of sexual reproduction in crop plants and their genetic consequences, the mechanisms of self-incompatibility and male sterility and their use in hybrid seed production, the practical steps for making controlled crosses (emasculation, pollination, bagging, and labelling), and the sourcing and evaluation of parental breeding materials. Together these topics provide the practical foundation for the breeding methods described in Series 5.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 4.1** describe self-pollination and cross-pollination and explain their genetic consequences for crop improvement (Linked to Part 4.1),
- **SLO 4.2** identify the mating system of a given crop and explain its implications for breeding method selection (Linked to Part 4.1),
- **SLO 4.3** explain the mechanisms of self-incompatibility and cytoplasmic and genetic male sterility (Linked to Part 4.2),

- **SLO 4.4** describe how self-incompatibility and male sterility are used in hybrid seed production (Linked to Part 4.2),
- **SLO 4.5** describe the tools and preparation required for making a controlled cross (Linked to Part 4.3),
- **SLO 4.6** describe the emasculation techniques appropriate for different crop flowers (Linked to Part 4.3),
- **SLO 4.7** describe the correct procedures for pollination, bagging, and labelling in a crossing programme (Linked to Part 4.3), and
- **SLO 4.8** identify the sources of breeding materials, explain how parental lines are evaluated and selected, and describe the management of a crossing nursery (Linked to Part 4.4).

4.1 Methods of Sexual Reproduction in Crop Plants

4.1.1 Self-pollination and its genetic consequences

Self-pollination occurs when pollen from a flower fertilises the egg cell of the same flower or another flower on the same plant. Crops that normally self-pollinate include rice, wheat, barley, sorghum, cowpea, groundnut, soybean, and tomato. Self-pollination leads to increased homozygosity with each generation: in a heterozygous plant (Aa), each round of selfing halves the frequency of heterozygotes and doubles the frequency of homozygotes; after six to seven generations of selfing, approximately 99 per cent of loci are homozygous. This natural tendency toward homozygosity is the basis of pure-line selection in self-pollinated crops.

The genetic consequences of self-pollination for breeding are: (1) Increased homozygosity makes it easier to fix desirable genotypes and maintain true-breeding lines. (2) Inbreeding depression is generally mild in naturally self-pollinated crops because deleterious recessive alleles have been purged over evolutionary time by exposure to selection in the homozygous state. (3) Varieties of self-pollinated crops are typically pure lines (homozygous) and do not require isolation in seed production because selfing maintains variety identity. (4) Controlled

crosses (hybridisation) between pure lines must be made deliberately because self-pollination is the default; emasculation is required to prevent selfing of the female parent.

Fill in the blank: Self-pollination leads to increased _____ with each generation; after six to seven generations of selfing, approximately 99 per cent of loci in the population are homozygous.

4.1.2 Cross-pollination and its genetic consequences

Cross-pollination occurs when pollen from one plant fertilises the egg cells of a different plant. Crops that naturally cross-pollinate include maize, sorghum (partially), pearl millet, cassava, oil palm, cocoa, and most forages. Cross-pollination is enforced by structural or physiological mechanisms that prevent or reduce selfing (protandry, protogyny, dioecy, self-incompatibility, male sterility). Cross-pollinated crops are typically genetically heterogeneous: each plant in a population differs from its neighbours, and the population as a whole maintains a wide range of genotypes.

The genetic consequences of cross-pollination for breeding are: (1) High heterozygosity is maintained, which supports heterosis (hybrid vigour) in F1 combinations. (2) Inbreeding depression is severe in naturally cross-pollinated crops because selfing exposes previously hidden deleterious recessives; this makes it difficult to develop pure inbred lines for hybrid seed production (large population sizes and many cycles of selection are needed). (3) Open-pollinated variety seed production requires isolation from other varieties to prevent pollen contamination. (4) Hybridisation is the natural state; the breeder must control crosses carefully to ensure the desired pollen parent is used.

Fill in the blank: Cross-pollinated crops maintain high _____ because pollen from different plants combines at each generation; inbreeding depression is severe when these crops are selfed.

Crop	Mating System	Mechanism	Breeding Implications
Maize (Zea mays)	Cross-pollinated	Monoecious plant with separate male (tassel) and	Requires controlled pollination for hybrid

		female (ear) flowers; wind pollination	seed; heterosis exploited in breeding
Rice (Oryza sativa)	Self-pollinated	Bisexual flowers with closed florets; natural selfing predominates	Pure-line selection effective; hybrids possible but require controlled crossing
Cowpea (Vigna unguiculata)	Self-pollinated	Cleistogamous flowers (self-fertilization before opening)	Breeding relies on pedigree selection; hybrids are rare and labor-intensive
Cassava (Manihot esculenta)	Cross-pollinated (vegetatively propagated)	Separate male and female flowers on same plant; natural outcrossing	Genetic improvement via clonal selection; heterozygosity maintained
Groundnut (Arachis hypogaea)	Self-pollinated	Flowers self-fertilize before geocarpy (peg penetrates soil)	Pure-line breeding effective; limited hybridization
Sorghum (Sorghum bicolor)	Mostly self-pollinated (some cross-pollination)	Bisexual florets; occasional outcrossing via wind	Line breeding common; hybrids used for yield improvement
Wheat (Triticum aestivum)	Self-pollinated	Bisexual florets; selfing occurs before anthesis	Pure-line selection effective; hybrid wheat requires special techniques

Table 4.1: Classification of major Nigerian food crops by mating system

4.1.3 Identifying the mating system of a crop

The mating system of a crop is identified from: (1) Floral biology: flowers with long styles and short stamens (or vice versa) favour cross-pollination; flowers with stamens surrounding the stigma and opening before the flower opens (cleistogamy) favour selfing. (2) Protandry and

protogyny: if anthers shed pollen before the stigma is receptive in the same flower (protandry, as in maize), cross-pollination is favoured; if the stigma is receptive before pollen is shed (protogyny, as in some grasses), cross-pollination is also promoted. (3) Genetic markers: crossing two phenotypically different pure lines and examining the offspring for segregation tests whether cross-pollination has occurred.

Practical observation methods include: bagging individual flowers before anthesis (pollen release) and observing whether seed set occurs (if seed sets under a bag without pollinator access, the crop is self-pollinated; if no seed set occurs, the crop requires cross-pollination); and applying a pollen trap (such as petroleum jelly on a microscope slide) near the crop to detect airborne pollen (wind-pollinated crops) versus observing pollinator visits (insect-pollinated crops). Understanding the mating system is not merely academic: it directly determines which breeding methods, which crossing procedures, and which seed production systems are appropriate for the crop.

Fill in the blank: The mating system of a crop is identified from floral biology, _____ (pollen released before stigma is receptive) or protogyny, and by bagging flowers to observe whether seed set occurs without pollinator access.

Pilot questions 4.1

1. Define self-pollination and state four Nigerian crops that normally self-pollinate.
2. State three genetic consequences of self-pollination for plant breeding.
3. Define cross-pollination and explain why inbreeding depression is more severe in cross-pollinated than in self-pollinated crops.
4. Name three mechanisms that enforce cross-pollination in crop plants.
5. Describe two practical methods for identifying the mating system of an unknown crop.

4.2 Self-Incompatibility and Male Sterility

4.2.1 Self-incompatibility: types and mechanisms

Self-incompatibility (SI) is a genetically controlled mechanism that prevents fertilisation when pollen and stigma carry the same alleles at the S (self-incompatibility) locus, thus enforcing cross-pollination. The most common type is sporophytic self-incompatibility (SSI), in which the SI phenotype of the pollen is determined by the genotype of the pollen-producing plant (the sporophyte) rather than the pollen grain itself. SSI is controlled by the S locus with many alleles; if the pollen donor and pollen recipient share any S allele, the pollen tube is arrested on the stigma surface. SSI is found in Brassica (cabbage, kale), sunflower, and sweet potato.

Gametophytic self-incompatibility (GSI) is the type in which the SI phenotype is determined by the haploid genotype of the pollen grain itself. If the S allele in the pollen matches either S allele in the pistil, the pollen tube is arrested in the style (not on the stigma surface as in SSI). GSI is found in tobacco, potato, clover, rye, and many fruit crops. In both types, SI is the natural mechanism maintaining cross-pollination and genetic diversity in the species. The breeder exploits SI by selecting parents with different S alleles as crossing partners to ensure high seed set in controlled crosses.

Fill in the blank: In _____ self-incompatibility, pollen tube growth is arrested in the style when the pollen S allele matches either S allele in the pistil; this type is found in tobacco, potato, clover, and rye.

4.2.2 Male sterility: cytoplasmic and genetic

Male sterility (MS) is the inability of a plant to produce functional pollen; plants with male sterility can be fertilised only by pollen from other plants, making them ideal female parents in hybrid seed production. Cytoplasmic male sterility (CMS) is caused by mutations in the mitochondrial genome that produce non-functional or absent pollen; it is maternally inherited (like all cytoplasmic traits) and does not follow Mendelian ratios. CMS is maintained by crossing the CMS line (A line) with a maintainer line (B line) that has the same nuclear genotype but

normal cytoplasm (N cytoplasm); all offspring of A x B are CMS because the CMS cytoplasm is contributed by the A-line mother.

Genetic male sterility (GMS) is caused by nuclear gene mutations (typically a recessive gene ms/ms) that disrupt pollen formation; it follows Mendelian inheritance. GMS is less useful than CMS for commercial hybrid seed production because it cannot be maintained as a stable male-sterile line (ms/ms plants cannot be pollinated by ms/ms pollen). Fertility restoration in CMS is achieved by crossing the CMS female (A line) with a restorer line (R line) that carries nuclear restorer genes (Rf) which suppress the CMS mitochondrial effect; the F1 hybrid produced is male fertile (CMS cytoplasm + Rf nuclear genes) and can produce its own seed.

Fill in the blank: Cytoplasmic male sterility (CMS) is maintained by crossing the A line (CMS cytoplasm) with the B line (_____ cytoplasm, same nuclear genotype) to produce all CMS offspring.

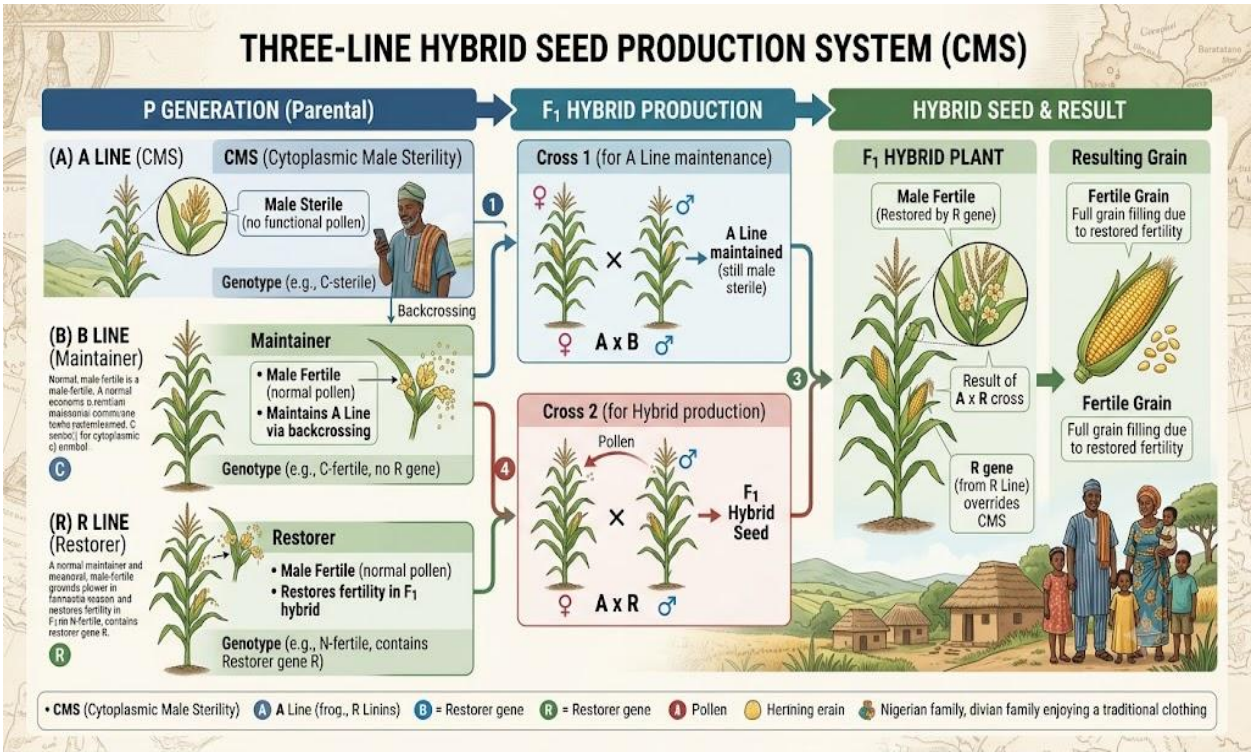

Figure 4.1: Diagram of the three-line hybrid seed production system using CMS

4.2.3 Use of self-incompatibility and male sterility in hybrid seed production

Self-incompatibility is used for hybrid seed production in crops where SI is natural and manageable. In Brassica vegetables (cabbage, broccoli, cauliflower), two SI inbred lines with different S alleles are planted alternately in rows; bees or other pollinators transfer pollen between the two rows, and all seeds on the SI plants are cross-pollinated (hybrid) seed. The cost of SI-based hybrid seed production is that the SI parent lines must be maintained by bud pollination (pollinating buds before the SI system is fully active) or by temporarily suppressing SI with CO2 treatment or high temperature.

CMS-based hybrid seed production uses the three-line system (A line x R line, maintained using B line) and is commercially used for maize, sorghum, pearl millet, sunflower, and rice. In Nigeria, the IITA and the National Centre for Genetic Resources and Biotechnology use CMS-based systems for the production of hybrid maize seed. The advantage of CMS over SI for hybrid seed production is that CMS is complete and stable (no pollen is produced by the A line), the hybrids are male fertile (can produce grain), and the system can be applied in any crop where a CMS source is available. CMS has transformed the commercial hybrid seed industry worldwide.

Fill in the blank: In the three-line CMS hybrid system, the commercial F1 hybrid is produced by crossing the _____ line (CMS female) with the R line (restorer male); the F1 is male fertile because the R line restorer genes suppress the CMS effect.

Pilot questions 4.2

1. Explain the difference between sporophytic and gametophytic self-incompatibility.
2. Define cytoplasmic male sterility and explain how it is maintained using the A and B line system.
3. Explain the role of the restorer (R) line in the three-line CMS hybrid system.
4. Distinguish between cytoplasmic male sterility and genetic male sterility.
5. Explain how self-incompatibility is used in the production of hybrid Brassica seed.

4.3 Steps for Controlled Crosses

4.3.1 Tools and preparation for crossing

Making a controlled cross requires careful preparation of tools, materials, and the crossing nursery. Essential tools and materials include: forceps (for removing anthers during emasculation), scissors or fine-pointed scissors (for opening flower buds), glassine or paper bags (for bagging emasculated flowers to exclude unwanted pollen and for bagging pollinated flowers to prevent contamination), adhesive labels or waterproof tags (for recording cross information on each bagged flower), a dissecting needle or camel-hair brush (for transferring pollen), a notebook for recording all cross combinations and dates, and vials or petri dishes for collecting and storing pollen.

Preparation of the crossing nursery involves: synchronising the flowering of the intended parents by staggered planting (the male parent is usually planted 1 to 2 weeks before or after the female to ensure their flowering periods overlap); growing sufficient plants to make the required number of cross combinations (typically 5 to 20 crosses per combination for security); and confirming the identity of each parent line before crossing begins by checking morphological characteristics against the variety description. Crossing should be done in the early morning when temperatures are cool and flowers are fresh; pollen viability decreases rapidly in high temperatures and humidity.

Fill in the blank: The flowering of intended cross parents is synchronised by _____ planting, typically planting the male parent 1 to 2 weeks before or after the female to ensure their flowering periods overlap.

4.3.2 Emasculation techniques

Emasculation is the removal or inactivation of the anthers from the female parent flower before they shed pollen, to prevent self-pollination of the female parent. The technique varies by crop. In cowpea and soybean (small self-pollinating flowers): the flower bud is opened 1 to 2 days before anthesis using forceps; the anthers are removed one by one with fine forceps; the emasculated bud is bagged immediately. In sorghum and pearl millet (large panicles): the

immature panicle is enclosed in a bag before anthesis; hot water (43 to 45 degrees Celsius for 10 minutes) is poured through the bag to kill pollen on the panicle; the treated panicle is rebagged as the female parent.

In maize, emasculation is achieved by detasseling: the tassel (which bears the male flowers) is physically removed from the female parent plants before anthesis (before pollen is shed). This is practical because maize has separate male (tassel) and female (silk) flowers on the same plant. In rice, emasculation uses the hot-water method (43 degrees Celsius for 7 to 10 minutes to kill pollen in the enclosed panicle) or vacuum emasculation with a special device that sucks pollen out of the flowers. In cross-pollinated crops where male sterility is used, no emasculation is needed because the female parent plants already produce no pollen.

Fill in the blank: In maize, emasculation is achieved by _____, the physical removal of the tassel from female parent plants before anthesis, because maize has separate male and female flowers on the same plant.

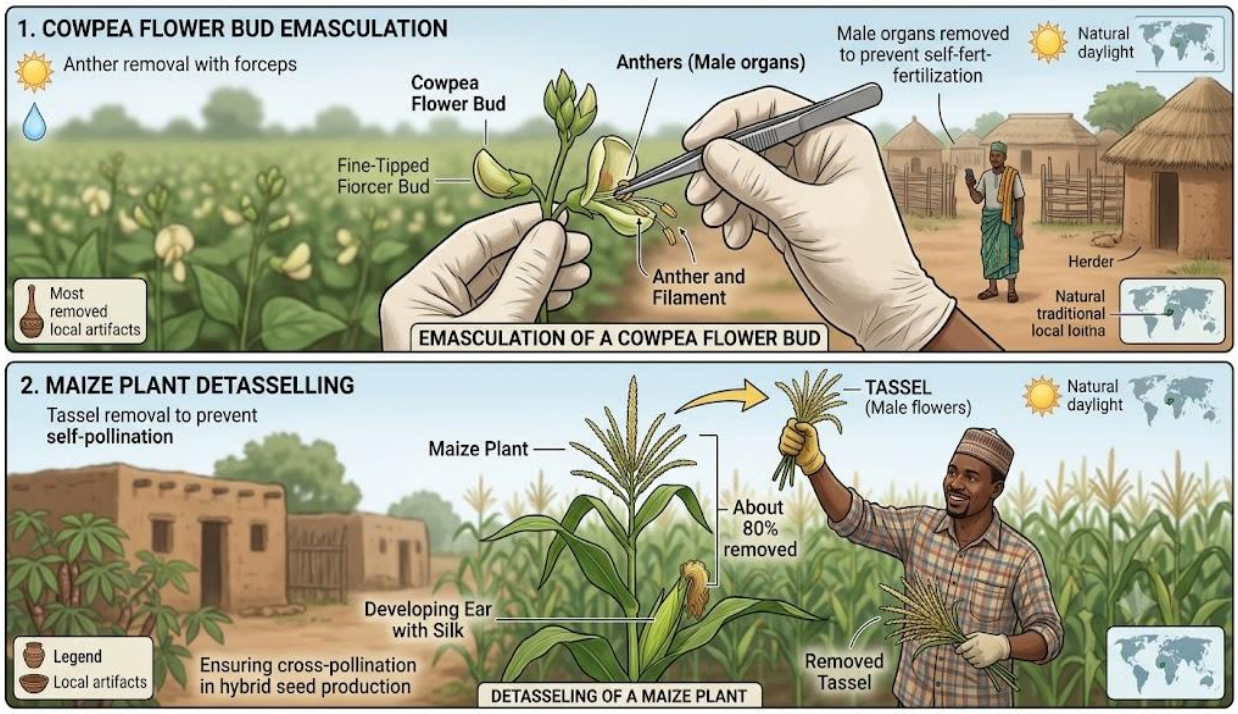

Figure 4.2: Diagram showing emasculation steps for cowpea and detasseling in maize

4.3.3 Pollination, bagging, and labelling

Pollination of the emasculated female parent is done at the time the stigma is receptive (usually 1 to 3 days after emasculation, when the stigma becomes sticky and shiny). Pollen is collected from the male parent by: enclosing the male parent's flower or panicle in a paper bag before anthesis, shaking the bag to collect pollen after anthesis, and transferring the pollen to the female parent's stigma using the bag (by inverting it over the stigma), a brush, or a pollen applicator. In maize, the pollen-filled bag from the detasseled male row is shaken over the exposed silks of the emasculated female row.

Immediately after pollination, the flower or ear is rebagged to exclude unwanted pollen and left in place until the cross is confirmed by seed set (typically 1 to 2 weeks). Labelling is critical: each bagged cross must be labelled with a waterproof tag showing the cross notation (female parent name x male parent name), the date of pollination, and the plot or row number. The standard notation is: female parent listed first (to the left of the multiplication sign), male parent second: "TGx 536-02D x IT93K-277-2" means TGx 536-02D is the female (pod-bearing) parent and IT93K-277-2 is the male (pollen-donating) parent. All cross records must be entered in the crossing notebook on the day they are made.

Fill in the blank: In cross notation, the _____ parent is written first (to the left of the multiplication sign) and the male (pollen donor) parent is written second, as in "Female x Male".

Pilot questions 4.3

1. List five tools or materials required for making a controlled cross.
2. Explain why parents are planted at staggered dates in a crossing nursery.
3. Describe the emasculation procedure for cowpea.
4. Explain how the hot-water method is used for emasculation in sorghum.
5. Describe the correct pollination, bagging, and labelling procedure after emasculation.

4.4 Sourcing for Breeding Materials

4.4.1 Sources of breeding materials

Breeding materials are the parental lines, populations, and genetic stocks used as the starting point or as parents in a breeding programme. The main sources are: (1) National and international gene banks (NACGRAB in Nigeria; IITA gene bank in Ibadan; CGIAR centre collections such as CIMMYT for maize and wheat, IRRI for rice, ICRISAT for sorghum and pearl millet, and IITA for cowpea, cassava, and yam); accessions from these collections provide the widest range of genetic diversity. (2) Existing improved varieties and elite lines from national programmes or private companies; these are genetically narrow but agronomically adapted and serve as recurrent parents in backcross programmes.

(3) Farmer landraces and traditional varieties collected from farming communities; these provide locally adapted genotypes that may carry valuable alleles not present in modern varieties. (4) Wild relatives of the cultivated crop; these are used as donors of disease resistance and stress tolerance genes but require extensive backcrossing to eliminate wild-type phenotypic defects (undesirable traits linked to the donor genome). (5) Mutant and transgenic lines; these provide specific novel alleles not available in natural populations. In Nigeria, international exchange of germplasm is governed by the ITPGRFA (2004) and bilateral material transfer agreements with the relevant CGIAR centres.

Fill in the blank: The main institutional source of genetic diversity for Nigerian breeders working on cowpea, cassava, and yam is the gene bank of the _____ (International Institute of Tropical Agriculture) in Ibadan.

4.4.2 Evaluating and selecting parental lines

Before committing to a crossing programme, the breeder must evaluate potential parents to confirm they have the complementary traits needed for the cross to produce the desired outcome. Evaluation involves: agronomic characterisation (growing potential parents in the target environment and measuring yield, maturity, plant height, disease scores, and other relevant traits); quality assessment (nutritional composition, cooking quality, market acceptability); and molecular characterisation (genotyping potential parents with DNA markers to assess genetic distance, heterotic group membership, and the presence of specific alleles for target traits).

The criteria for selecting parents for a cross are: (1) complementarity (each parent should contribute traits that the other lacks: parent A is high-yielding but susceptible; parent B is low-yielding but resistant); (2) genetic distance (parents that are genetically diverse produce greater heterosis in F1 and more transgressive segregation in F2 populations); (3) adaptation to the target environment (at least one parent should be well-adapted to the target environment to ensure the offspring are not maladapted); and (4) commercial acceptability (the parents and their offspring must meet market quality requirements for grain size, colour, and taste). General combining ability (GCA) tests can be used to identify parental lines that consistently produce good progenies.

Fill in the blank: The four criteria for selecting parents for a cross are complementarity, genetic _____, adaptation to the target environment, and commercial acceptability of the product.

4.4.3 Managing a crossing nursery

A crossing nursery is a planting of parent lines specifically designed to support a crossing programme. Key management considerations are: spatial arrangement (plant female and male parents in adjacent rows or plots so that the breeder can move easily between them during crossing; for cross-pollinated crops, consider wind direction when placing male rows); plant density (grow enough plants per parent line to make all required crosses plus a surplus in case some crosses fail or are lost to disease or weather); and isolation (isolate the crossing nursery from other plantings of the same or related crops to prevent contamination of female parents with unwanted pollen).

Detailed record keeping is essential in the crossing nursery. The crossing book records: each cross combination (female x male), the date of emasculation, the date of pollination, the number of flowers pollinated, and the number of seeds harvested from each cross. Seeds from each successful cross are labelled with the cross code, the cross notation, and the harvest date, and stored separately. After the crossing season, the breeder evaluates the success rate of each cross combination (number of seeds obtained / number of flowers pollinated) and uses this information to plan the next crossing season with more flowers pollinated for low-success crosses.

Fill in the blank: The crossing book records each cross combination, the date of emasculation and pollination, the number of flowers pollinated, and the number of _____ harvested from each cross.

Management Action	Purpose
Parent selection	Choose diverse, superior parents with desired traits for crossing
Nursery layout	Organize plots to facilitate controlled pollination and record keeping
Pollination control	Use hand emasculation, bagging, or controlled pollination to ensure desired crosses
Accurate labeling	Tag each cross with parent IDs, date, and method to avoid mix-ups
Record keeping	Maintain detailed logs of crosses, success rates, and seed collection
Seed harvesting	Collect mature seeds from successful crosses carefully to avoid contamination
Post-harvest handling	Dry, clean, and store seeds under proper conditions for future evaluation

Box 4.1: Crossing nursery management checklist

Pilot questions 4.4

1. Name four sources of breeding materials available to Nigerian plant breeders.
2. Explain the role of IITA's gene bank in Nigerian plant breeding.
3. State the four criteria for selecting parents for a cross.
4. Explain what general combining ability (GCA) is and how it helps in parent selection.
5. Describe three key management considerations for a crossing nursery.

Series Summary

This Series covered sexual reproduction in crop plants, controlled crossing procedures, and the sourcing of breeding materials. We distinguished self-pollinated crops (rice, wheat, cowpea, groundnut; increased homozygosity, mild inbreeding depression, pure-line varieties) from cross-

pollinated crops (maize, pearl millet, cassava, oil palm; maintained heterozygosity, severe inbreeding depression, open-pollinated or hybrid varieties) and described methods for identifying the mating system. We explained self-incompatibility (sporophytic in Brassica; gametophytic in tobacco, potato, rye) and male sterility (CMS maintained by A and B lines; fertility restored by R line in the three-line system) and their use in hybrid seed production.

We covered the practical steps for controlled crosses: tools and nursery preparation (staggered planting for flowering synchrony), emasculation techniques by crop (forceps removal in cowpea, detasseling in maize, hot-water treatment in sorghum and rice), and pollination, bagging, and labelling (female x male notation, waterproof tags, crossing book records). Finally, we described sources of breeding materials (gene banks, improved varieties, landraces, wild relatives, mutant lines), criteria for parent selection (complementarity, genetic distance, adaptation, market acceptability), and crossing nursery management (spatial arrangement, isolation, record keeping). By completing this Series, you should be able to achieve all eight Series Learning Outcomes (SLO 4.1 to SLO 4.8).

Glossary of Terms

- **A line (CMS line):** the cytoplasmic male sterile female parent line in the three-line hybrid system; it produces no functional pollen and must be maintained by crossing with the B line.
- **B line (maintainer line):** the male-fertile line with normal (N) cytoplasm and the same nuclear genotype as the A line; crossing A x B produces all CMS (A-line type) offspring.
- **Bagging:** enclosing an emasculated or pollinated flower in a paper or glassine bag to exclude unwanted pollen until cross-pollination is complete and confirmed by seed set.
- **Cleistogamy:** the condition in which flowers pollinate themselves before opening, a mechanism that enforces self-pollination; found in some cowpea and groundnut varieties.
- **Cross-pollination:** the transfer of pollen from the anthers of one plant to the stigma of a genetically different plant.

- **Crossing book:** the breeder's detailed record of all crosses made in a crossing nursery, including cross notation, dates of emasculation and pollination, flowers pollinated, and seeds harvested.
- **Crossing nursery:** a planting of parent lines specifically managed to support a crossing programme, with controlled spatial arrangement, plant density, and isolation from unwanted pollen sources.
- **Cytoplasmic male sterility (CMS):** male sterility caused by mutations in the mitochondrial genome; maternally inherited; exploited in three-line hybrid seed production systems.
- **Detasseling:** the physical removal of the tassel (male inflorescence) from maize plants to achieve emasculation; used in maize hybrid seed production.
- **Emasculation:** the removal or inactivation of anthers from the female parent flower before pollen shed to prevent self-pollination and permit controlled cross-pollination.
- **Gametophytic self-incompatibility (GSI):** SI in which the pollen phenotype is determined by the haploid genotype of the pollen grain itself; pollen is rejected if its S allele matches either S allele of the pistil.
- **General combining ability (GCA):** the average performance of a line in all hybrid combinations relative to the population mean; a measure of the line's additive genetic value as a parent.
- **Hot-water emasculation:** the use of hot water (43 to 45 degrees Celsius for 7 to 10 minutes) applied to a bagged panicle of sorghum or rice to kill pollen and achieve emasculation without manual anther removal.
- **Inbreeding depression:** the reduction in vigour, fertility, and productivity observed when a naturally cross-pollinated crop is selfed, caused by the expression of previously hidden deleterious recessive alleles.
- **Male sterility (MS):** the inability of a plant to produce or shed functional pollen; used as a practical tool for producing hybrid seed without manual emasculation.

- **Protandry:** the condition in which anthers shed pollen before the stigma of the same flower is receptive, promoting cross-pollination; found in maize.
- **Protogyny:** the condition in which the stigma is receptive before pollen is shed in the same flower, promoting cross-pollination; found in some grasses.
- **R line (restorer line):** the male-fertile pollen parent in the three-line hybrid system; carries nuclear restorer genes (Rf) that suppress the CMS effect, producing male-fertile F1 hybrids.
- **Self-incompatibility (SI):** a genetically controlled mechanism that prevents fertilisation when pollen and stigma share the same alleles at the S locus, enforcing cross-pollination.
- **Self-pollination:** the transfer of pollen from the anthers of a flower to the stigma of the same flower or another flower on the same plant.
- **Sporophytic self-incompatibility (SSI):** SI in which the pollen phenotype is determined by the diploid genotype of the pollen-producing plant (sporophyte); pollen is rejected on the stigma surface if it shares an S allele with the pistil.
- **Staggered planting:** planting different parent lines at different dates to synchronise their flowering periods so that pollen availability and stigma receptivity coincide.
- **Three-line hybrid system:** a commercial hybrid seed production system using A line (CMS female), B line (maintainer), and R line (restorer) to produce hybrid seed without manual emasculation.
- **Wild relative:** a wild species related to a cultivated crop used as a donor of disease resistance or stress tolerance genes in wide hybridisation programmes.

Concept Check Questions [Series 4]

Objective Questions

1. Self-pollination leads to increased _____ with each generation; after 6 to 7 generations of selfing, approximately 99 per cent of loci are homozygous. (Linked to SLO 4.1)
2. Cytoplasmic male sterility is maintained by crossing the A line with the _____ line, which has normal cytoplasm and the same nuclear genotype. (Linked to SLO 4.3)
3. In maize, emasculation is achieved by _____, the physical removal of the tassel from female parent plants before anthesis. (Linked to SLO 4.6)
4. In cross notation, the _____ parent is written first (left of the multiplication sign) and the male (pollen donor) second. (Linked to SLO 4.7)
5. The four criteria for selecting parents for a cross are complementarity, genetic _____, adaptation to target environment, and commercial acceptability. (Linked to SLO 4.8)

Short-Answer Questions

6. State three genetic consequences of self-pollination for plant breeding. (Linked to SLO 4.1)
7. Distinguish between sporophytic and gametophytic self-incompatibility. (Linked to SLO 4.3)
8. Describe the three-line CMS hybrid seed production system. (Linked to SLO 4.4)
9. Describe the emasculation procedures for cowpea and sorghum. (Linked to SLO 4.6)
10. State four sources of breeding materials available to Nigerian plant breeders. (Linked to SLO 4.8)

Long-Answer Questions

11. Describe self-pollination and cross-pollination in crop plants, explain their genetic consequences for breeding, and describe the mechanisms of self-incompatibility and male sterility and their use in hybrid seed production. (Linked to SLOs 4.1, 4.2, 4.3, 4.4)

12. Describe the complete procedure for making a controlled cross in a self-pollinated crop, covering tools and preparation, emasculation, pollination, bagging, and labelling, with reference to specific crops practised in Nigeria. (Linked to SLOs 4.5, 4.6, 4.7)
13. Describe the sources of breeding materials available to Nigerian plant breeders, the criteria for selecting parental lines, and the management of a crossing nursery. (Linked to SLO 4.8)

Answers to Concept Check Questions [Series 4]

Objective Questions

1. Homozygosity.
2. B.
3. Detasseling.
4. Female.
5. Distance.

Short-Answer Questions

6. Any three: increased homozygosity with each generation of selfing, making it easier to fix desirable genotypes and maintain true-breeding lines; mild inbreeding depression in naturally self-pollinated crops because deleterious recessives have been purged over evolutionary time; varieties are typically pure lines requiring no isolation in seed production; controlled crosses must be made deliberately by emasculation because selfing is the default.
7. Sporophytic SI (SSI): the SI phenotype of the pollen is determined by the diploid genotype of the pollen-producing plant (sporophyte); pollen is rejected on the stigma surface if it shares an S allele with the pistil; found in Brassica, sunflower, and sweet potato. Gametophytic SI (GSI): the SI phenotype is determined by the haploid genotype

of the pollen grain itself; pollen tube is arrested in the style if the pollen S allele matches either S allele in the pistil; found in tobacco, potato, clover, and rye.

8. Three-line CMS system: A line (CMS, male sterile, female parent, cannot self) x B line (maintainer, normal cytoplasm, same nuclear genotype as A) produces A-line seed (all CMS, maintained for the next season). A line x R line (restorer, carries nuclear Rf genes that suppress CMS) produces commercial F1 hybrid seed that is male fertile. The F1 hybrid carries CMS cytoplasm but the Rf restorer genes make it male fertile so it can produce grain. Three lines serve different roles: B maintains A, R produces the commercial hybrid.
9. Cowpea emasculation: select flower bud 1 to 2 days before anthesis; open the bud carefully with fine forceps; remove all anthers one by one without damaging the stigma; bag the emasculated bud immediately with a glassine bag. Sorghum emasculation (hot-water method): enclose an immature sorghum panicle in a paper bag before anthesis; pour hot water (43 to 45 degrees Celsius) through the bag for approximately 10 minutes to kill pollen in the spikelets; remove the bag and rebag the treated panicle as the female for pollination.
10. National and international gene banks (NACGRAB Nigeria; IITA Ibadan; CIMMYT, IRRI, ICRISAT, IITA CGIAR collections); existing improved varieties and elite lines from national programmes; farmer landraces collected from farming communities; wild relatives of the cultivated crop.

Long-Answer Questions

11. Self-pollination: pollen fertilises egg of same plant; self-pollinated crops: rice, wheat, cowpea, groundnut, soybean; genetic consequences: increased homozygosity (99% after 6-7 generations selfing), mild inbreeding depression (deleterious recessives purged), pure-line varieties, deliberate emasculation needed for crossing. Cross-pollination: pollen from different plant; cross-pollinated crops: maize, pearl millet, cassava, oil palm; mechanisms: protandry, protogyny, dioecy, SI, MS; genetic consequences: maintained heterozygosity, severe inbreeding depression on selfing, open-pollinated or hybrid

varieties, isolation needed in seed production. Self-incompatibility: prevents fertilisation when pollen and stigma share S alleles; SSI (Brassica, pollen rejected on stigma surface, sporophyte genotype determines pollen SI); GSI (tobacco, potato, rye, pollen tube arrested in style, pollen grain genotype determines SI). CMS: mitochondrial mutation, maternally inherited, no pollen produced; maintained by A(CMS) x B(N cytoplasm, same nuclear) = all CMS offspring; fertility restored by R line (Rf nuclear genes suppress CMS); three-line system produces male-fertile F1 hybrid; used for maize, sorghum, pearl millet, sunflower, rice; IITA uses CMS for Nigerian hybrid maize seed.

12. Preparation: tools (forceps, fine scissors, glassine bags, adhesive labels, camel-hair brush or pollen applicator, crossing notebook, pollen vials); crossing nursery (staggered planting to synchronise flowering, male parent 1-2 weeks before or after female; adequate plant numbers for all required crosses plus surplus; isolation from other plantings; confirm parent identity). Emasculation by crop: cowpea (select bud 1-2 days before anthesis, open with forceps, remove anthers, bag immediately); sorghum (bag immature panicle, hot water 43-45 degrees Celsius 10 minutes, rebag as female); maize (detasseling before anthesis, remove tassel from female parent rows); rice (hot water 43 degrees Celsius 7-10 minutes or vacuum emasculation). Pollination: wait 1-3 days for stigma to become sticky and receptive; collect pollen from male parent in bag by shaking at anthesis; transfer pollen to receptive stigma by inverting bag over stigma, using brush, or shaking pollen-bag over silks (maize). Bagging and labelling: immediately rebag pollinated flower; label with waterproof tag showing Female x Male notation, date, plot number; enter all crosses in crossing book on the day; check for seed set after 1-2 weeks.
13. Sources: gene banks (NACGRAB Nigeria, IITA Ibadan, CIMMYT for maize/wheat, IRRI for rice, ICRISAT for sorghum/millet, IITA for cowpea/cassava/yam; widest genetic diversity); improved varieties and elite lines from national programmes (agronomically adapted, genetically narrow, used as recurrent parents); farmer landraces from communities (locally adapted, carry unique stress tolerance and quality alleles); wild relatives (disease resistance, stress tolerance genes, require extensive backcrossing); mutant and transgenic lines (specific novel alleles). Parent selection criteria: complementarity (parent A high-yield but susceptible; parent B resistant but low-yield; cross combines both); genetic distance (diverse parents produce greater heterosis and

transgressive segregation); adaptation (at least one parent adapted to target environment); commercial acceptability (grain size, colour, taste meet market requirements). GCA test: cross each candidate line with a common tester; average performance across all hybrid combinations = GCA; lines with high GCA consistently produce good progenies regardless of the cross partner. Crossing nursery management: spatial arrangement (female and male rows adjacent, consider wind direction for cross-pollinated crops); isolation from other plantings; adequate plant numbers per parent; synchronise flowering; detailed crossing book records (cross notation, emasculation date, pollination date, flowers pollinated, seeds harvested); label and store seeds by cross; evaluate success rate after season to plan improvements.

Answers to Pilot Questions [Series 4]

Part 4.1: Methods of Sexual Reproduction in Crop Plants

1. Self-pollination is the transfer of pollen from the anthers of a flower to the stigma of the same flower or another flower on the same plant. Four Nigerian crops that normally self-pollinate: rice (Oryza sativa), cowpea (Vigna unguiculata), groundnut (Arachis hypogaea), sorghum (Sorghum bicolor; predominantly self-pollinating with some natural outcrossing).
2. Any three: increased homozygosity with each generation of selfing (the frequency of heterozygotes is halved with each selfing cycle; after 6 to 7 generations approximately 99 per cent of loci are homozygous); mild inbreeding depression in naturally self-pollinated crops because deleterious recessive alleles have been progressively purged from the population over evolutionary time by being exposed to selection in the homozygous state; varieties of self-pollinated crops are typically pure lines (nearly completely homozygous) that maintain their genetic identity through selfing, requiring no isolation plots in seed production.
3. Cross-pollination is the transfer of pollen from the anthers of one plant to the stigma of a genetically different plant. Inbreeding depression is more severe in naturally cross-

pollinated crops because these species have evolved under conditions of continuous outcrossing and have accumulated many deleterious recessive alleles in the heterozygous state in their populations; when a cross-pollinated crop is selfed, homozygosity increases rapidly and the previously hidden recessive alleles are exposed in the homozygous state, where they reduce vigour, fertility, and productivity. In contrast, self-pollinated crops have been regularly selfing throughout their evolution, exposing and eliminating deleterious recessives generation after generation, so very few remain in the population to cause inbreeding depression.

4. Any three: protandry (anthers shed pollen before stigma of same flower is receptive, as in maize; promotes cross-pollination); protogyny (stigma is receptive before pollen is shed from same flower; also promotes cross-pollination); dioecy (male and female flowers on different plants, as in oil palm; makes selfing impossible); self-incompatibility (genetic mechanism at the S locus that prevents pollen from fertilising the stigma if they share S alleles); male sterility (plants that produce no functional pollen and can only be fertilised by pollen from other plants).
5. Any two: bagging method (enclose individual flowers in paper or glassine bags before anthesis to exclude pollinators and pollen; after a set period, observe whether seed set has occurred; if seeds set under the bag without pollinator access, the crop can self-pollinate; if no seed sets, the crop requires cross-pollination or has some SI mechanism); flowering observation (observe whether the stigma and anthers of the same flower are both functional at the same time; protandry or protogyny indicates cross-pollination is favoured; cleistogamy indicates selfing).

Part 4.2: Self-Incompatibility and Male Sterility

1. Sporophytic self-incompatibility (SSI): the self-incompatibility phenotype of the pollen is determined by the diploid genotype of the pollen-producing plant (the sporophyte); even if the pollen grain itself carries only one S allele, it is rejected on the stigma surface if either of the S alleles of the sporophyte matches either of the stigma's S alleles; found in Brassica (cabbage, cauliflower, broccoli), sunflower, and sweet potato. Gametophytic

self-incompatibility (GSI): the SI phenotype is determined by the haploid genotype of the pollen grain itself; pollen is rejected in the style (after germination) if its single S allele matches either S allele of the pistil; found in tobacco, potato, clover, and rye.

2. Cytoplasmic male sterility (CMS) is caused by a mutation in the mitochondrial genome that disrupts normal pollen development, resulting in plants that produce no functional pollen; it is maternally inherited because mitochondria are contributed almost entirely by the egg cell. CMS is maintained as a stable male-sterile line by crossing the CMS line (A line, with CMS mitochondria and nuclear genotype N) with the maintainer line (B line, with normal mitochondria and the same nuclear genotype N); because the CMS cytoplasm is contributed by the A line mother, all offspring (A x B) have CMS cytoplasm and are male sterile (A-line type). The B line is kept as a separate male-fertile line and used every season to regenerate the A line.
3. The restorer line (R line) is a male-fertile line that carries nuclear restorer genes (Rf alleles) in its genome. When the A line (CMS cytoplasm) is crossed with the R line (normal cytoplasm, Rf nuclear genes), the F1 hybrid offspring inherit the CMS cytoplasm from the A-line mother but also inherit the Rf restorer genes from the R-line father; the Rf genes suppress the effect of the CMS mitochondrial mutation, allowing normal pollen development. The commercial F1 hybrid is therefore male fertile and can produce its own seed (grain), which is the commercial product sold to farmers. Without the R line, the F1 hybrid would be male sterile and could not produce grain.
4. CMS: caused by a mitochondrial genome mutation; maternally inherited; does not follow Mendelian ratios; completely stable (no pollen produced); maintained by A line x B line system; fertility restored by R line; commercially applicable for large-scale hybrid seed production. GMS (Genetic male sterility): caused by a nuclear gene mutation (typically recessive ms/ms); follows Mendelian inheritance; male-sterile plants (ms/ms) cannot be maintained as a pure male-sterile line because ms/ms plants cannot donate ms/ms pollen to maintain themselves; a ms/ms plant can only be pollinated by a male-fertile plant, producing 50% ms/ms (sterile) and 50% Msms (fertile) offspring; less useful than CMS for commercial hybrid seed production because male-sterile plants cannot be distinguished from heterozygous male-fertile plants at the seedling stage.

5. In Brassica hybrid seed production using SI: two inbred lines with different S alleles are selected as parents (for example, S1S2 x S3S4, where neither pair of S alleles is shared). The two parent lines are planted in alternating rows in a seed production field. Bees or other insect pollinators move freely between the rows, transferring pollen from line 1 to line 2 and vice versa. Because the two lines have different S alleles, cross-pollination is compatible and seed sets normally on both parent lines; self-pollination is blocked by SI so no selfed seed is produced. The seed harvested from one of the parent lines (designated the female parent) is the F1 hybrid commercial product. SI parent lines are maintained by bud pollination (pollinating very young buds before the SI system is fully active) or by temporary CO2 or heat treatment to suppress SI.

Part 4.3: Steps for Controlled Crosses

1. Any five: forceps (for removing anthers during emasculation); fine-pointed scissors (for opening flower buds); glassine or paper bags (for bagging emasculated and pollinated flowers); adhesive waterproof labels or tags (for labelling each cross with cross notation, date, and plot number); camel-hair brush or pollen applicator (for transferring pollen to stigma); crossing notebook (for recording all cross combinations and dates on the day); pollen collection vials or petri dishes (for storing pollen from the male parent).
2. Parents are planted at staggered dates to synchronise their flowering periods so that the male parent is shedding pollen at the same time as the female parent's stigmas are receptive. Different parental lines often have different days-to-flowering; if both are planted on the same day, one may flower and finish before the other begins, making crossing impossible. By planting the earlier-flowering parent later (or the later-flowering parent earlier), both are brought into flowering simultaneously, ensuring that both pollen availability and stigma receptivity coincide for the crossing window.
3. Cowpea emasculation procedure: (1) Select a flower bud that is 1 to 2 days before anthesis (the bud should be fully expanded but not yet open and the petals should be coloured but tightly closed). (2) Gently open the bud using fine-pointed forceps by carefully separating the petals. (3) Locate the anthers (the small yellow pollen-producing

structures surrounding the style) and remove each one carefully with the forceps tips, taking care not to damage the stigma or style. (4) Inspect the emasculated flower to confirm all anthers have been removed and the stigma is intact. (5) Bag the emasculated bud immediately with a glassine bag and fasten securely to exclude any airborne or insect-carried pollen until pollination is performed.

4. Hot-water emasculation in sorghum: (1) Identify a sorghum panicle that is at the boot stage (enclosed within the flag leaf sheath, about 2 to 3 days before the panicle emerges). (2) Enclose the entire panicle within the flag leaf sheath in a paper bag, sealing the bag around the peduncle to create a closed chamber. (3) Pour hot water at 43 to 45 degrees Celsius into the bag through the top, ensuring the panicle is fully immersed in the hot water for approximately 10 minutes; the hot water kills the pollen inside the developing spikelets while the stigmas remain viable because they are more heat-tolerant than pollen. (4) Remove the bag, allow excess water to drain, and rebag the treated panicle with a fresh dry paper bag. (5) The treated panicle is now the emasculated female parent ready for pollination when the stigmas emerge.
5. After emasculation: wait 1 to 3 days for the stigma to become fully receptive (glossy and sticky in cowpea; feathery and exerted in sorghum; silky and elongated in maize). To collect pollen: enclose a mature male-parent panicle or flower in a paper bag before anthesis; shake the bag gently after anthesis to collect shed pollen in the bag. To pollinate: invert the pollen-filled bag over the receptive stigma (cowpea, sorghum) or shake the pollen-filled bag over the exposed silks (maize) to deposit pollen on the stigma. Rebagging: immediately after pollination, rebag the pollinated flower with a fresh bag and fasten securely. Labelling: attach a waterproof label to the bagged cross showing the cross notation in the format "Female parent x Male parent", the date of pollination, and the plot or row number. Recording: enter all cross details in the crossing notebook on the same day the cross is made.

Part 4.4: Sourcing for Breeding Materials

1. Any four: national and international gene banks (NACGRAB in Nigeria; IITA gene bank in Ibadan; CGIAR centre collections including CIMMYT for maize and wheat, IRRI for rice, ICRISAT for sorghum and pearl millet); existing improved varieties and elite lines from national breeding programmes or private companies; farmer landraces and traditional varieties collected from farming communities; wild relatives of the cultivated crop used as donors of disease resistance and stress tolerance genes.
2. IITA (International Institute of Tropical Agriculture), headquartered in Ibadan, Nigeria, maintains one of the most important gene bank collections for tropical food crops in the world. It holds large collections of cowpea accessions (the world's largest cowpea collection), cassava, yam, maize, soybean, and other crops important to Nigerian agriculture. Nigerian plant breeders can access this germplasm for use in breeding programmes through material transfer agreements governed by the ITPGRFA (2004). The IITA gene bank also characterises accessions for agronomic, quality, and disease resistance traits, providing passport data that helps breeders select accessions most likely to contain the traits they need.
3. Complementarity (each parent should contribute traits the other lacks: if the programme aims to combine high yield with disease resistance, parent A should be high-yielding but susceptible and parent B low-yielding but resistant); genetic distance (parents that are genetically diverse produce greater heterosis in F1 and more transgressive segregation in F2 populations, giving the breeder more opportunity to select superior recombinants); adaptation to the target environment (at least one parent should be well-adapted to the target environment to ensure that offspring are not maladapted to local soil, climate, and pest conditions); commercial acceptability (the parents and their offspring must meet the market quality requirements for grain size, colour, cooking quality, and taste that determine whether farmers can sell their harvest).
4. General combining ability (GCA) is a measure of the average performance of a parental line across all hybrid combinations in which it is tested, expressed relative to the mean of all crosses. It is estimated by crossing each candidate parental line with a common tester (a line of known performance) or with all other candidate lines in a diallel cross and measuring the performance of all hybrids produced. Lines with high GCA consistently produce above-average hybrids regardless of the cross partner and are therefore valuable

as parents; their superiority is attributable to the additive genetic effects of their alleles, which are passed reliably to offspring. In hybrid breeding programmes, GCA is used to identify lines that will generate consistently high-performing F1 hybrids for commercial release.

5. Any three: spatial arrangement (plant female and male parent rows adjacently and close enough for efficient movement between them during crossing; in cross-pollinated crops, consider the prevailing wind direction when positioning male rows relative to female rows so pollen drift does not contaminate the female rows with the wrong pollen); isolation of the crossing nursery from other plantings of the same or related crop species to prevent unwanted pollen from contaminating the emasculated female parents and producing non-hybrid seed; adequate plant density per parent (grow enough plants to make all required cross combinations with a surplus of 50 to 100 per cent above the target, because some flowers may fail to set seed due to weather, pest damage, or handling errors, and some crosses may need to be repeated).

References and Attributions [Series 4]

Textual References (Books and External Sources)

- Acquaah, G. (2012). Principles of plant genetics and breeding (2nd ed.). Wiley-Blackwell.
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Figures, Plates, Tables, and Boxes

- Table 4.1: Nigerian food crops classified by mating system Attribution: AI generated. Suggested OER search string: "Nigerian food crops mating system self cross pollinated breeding implications OER table".
- Figure 4.1: Three-line CMS hybrid seed production system Attribution: AI generated. Suggested OER search string: "CMS three line hybrid seed production system A B R line diagram OER".
- Figure 4.2: Emasculation in cowpea and maize detasseling Attribution: AI generated. Suggested OER search string: "emasculation cowpea forceps anther removal maize detasseling diagram OER".
- Box 4.1: Crossing nursery management checklist Attribution: AI generated. Suggested OER search string: "crossing nursery management checklist plant breeding emasculation pollination OER box".

Course code: AGE 304

Course title: Technology of Breeding Crop

Course credit load: 2 Units

Series 5: Breeding Methodologies for Self- and Cross-Pollinated Crops

- **Part 5.1: Breeding Methods for Self-Pollinated Crops**
  - Sub Part 5.1.1: Pure-line selection
  - Sub Part 5.1.2: Mass selection in self-pollinated crops
  - Sub Part 5.1.3: Hybridisation and pedigree selection
- **Part 5.2: Additional Methods for Self-Pollinated Crops**
  - Sub Part 5.2.1: Bulk population method
  - Sub Part 5.2.2: Backcross breeding
  - Sub Part 5.2.3: Single seed descent
- **Part 5.3: Breeding Methods for Cross-Pollinated Crops**
  - Sub Part 5.3.1: Mass selection in cross-pollinated crops
  - Sub Part 5.3.2: Recurrent selection
  - Sub Part 5.3.3: Hybrid variety development in maize
- **Part 5.4: Synthetic Varieties, Seed Production, and Distribution**
  - Sub Part 5.4.1: Synthetic varieties in maize
  - Sub Part 5.4.2: Seed production and quality control

- Sub Part 5.4.3: Seed distribution systems in Nigeria

Introduction

The mating system of a crop plant determines which breeding methods are applicable and efficient. Self-pollinated crops, which naturally achieve high homozygosity, are amenable to selection within genetically uniform lines; the breeder's task is to identify the best line, fix its genotype, and multiply it for distribution. Cross-pollinated crops, which maintain heterozygosity and suffer from inbreeding depression, require population improvement methods or the exploitation of heterosis through hybrid variety development. Understanding both groups of methods is essential for any crop improvement scientist working in Nigerian agriculture.

This final Series covers the major breeding methodologies for self-pollinated crops (pure-line selection, mass selection, hybridisation with pedigree selection, bulk method, backcross breeding, and single seed descent) and for cross-pollinated crops (mass selection, recurrent selection, hybrid variety development in maize, and synthetic varieties). We conclude with seed production, quality control, and the seed distribution systems that determine whether improved varieties reach farmers. This Series completes the practical methodology component of the course.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 5.1** describe pure-line selection and mass selection as breeding methods for self-pollinated crops (Linked to Part 5.1),
- **SLO 5.2** describe hybridisation and pedigree selection as breeding methods for self-pollinated crops (Linked to Part 5.1),

- **SLO 5.3** describe the bulk population method, backcross breeding, and single seed descent (Linked to Part 5.2),
- **SLO 5.4** describe mass selection and recurrent selection as breeding methods for cross-pollinated crops (Linked to Part 5.3),
- **SLO 5.5** describe hybrid variety development in maize including the development of inbred lines and the three-line CMS system (Linked to Part 5.3),
- **SLO 5.6** explain synthetic variety development and state its advantages over hybrid varieties for resource-poor farmers (Linked to Part 5.4),
- **SLO 5.7** describe seed production systems and quality control requirements for improved crop varieties (Linked to Part 5.4), and
- **SLO 5.8** describe the formal and informal seed distribution systems in Nigeria and explain how improved varieties reach farmers (Linked to Part 5.4).

5.1 Breeding Methods for Self-Pollinated Crops

5.1.1 Pure-line selection

Pure-line selection is the simplest breeding method for self-pollinated crops. It involves: (1) collecting seeds from a large number of individual plants in an existing landrace or old variety population; (2) growing each plant's progeny as a separate line (a pure line) and evaluating the lines for yield, quality, and disease resistance over one or more seasons; (3) selecting the best pure lines based on their performance; and (4) multiplying and releasing the best line as a new cultivar. The method works because a landrace or old variety population contains many different pure lines (each internally homozygous but genetically different from other lines), among which variation exists for the breeder to select.

Pure-line selection does not create new genetic variation; it merely identifies and separates the best genotypes already present in the starting population. Once the best line is identified, no further genetic improvement is possible by this method in that population. The method is therefore most appropriate as a first step in improving a neglected crop or variety, or in exploiting existing diversity in landraces. In Nigeria, several improved cowpea, groundnut, and

sorghum varieties were developed by pure-line selection from farmer landraces in the early decades of the national breeding programme. The main advantage is its simplicity and low cost.

Fill in the blank: Pure-line selection identifies the best genotypes _____ present in a landrace population; it does not create new genetic variation and is most appropriate as a first improvement step.

5.1.2 Mass selection in self-pollinated crops

Mass selection involves selecting a large number of plants (50 to several hundred) based on their phenotype (visual appearance and measurable traits), bulking their seeds together, and growing the bulk seed as the next generation. It differs from pure-line selection in that individual plant progenies are not grown separately; the selected plants are bulked and their combined seed is used without individual line evaluation. Mass selection is faster and cheaper than pure-line selection but less precise, because it does not distinguish between genetic and environmental causes of the phenotypic differences among selected plants.

In self-pollinated crops, mass selection is most effective for highly heritable traits (those where phenotypic differences among plants are mostly genetic rather than environmental), such as seed size, seed colour, plant height, and maturity. It is less effective for yield and other traits with low heritability because the phenotypic value of an individual plant is a poor predictor of its genetic worth. Mass selection has been used in Nigeria to select for seed size and colour in cowpea and for grain type in sorghum, and it is commonly practised by progressive farmers who save seed from their best-looking plants each season.

Fill in the blank: Mass selection involves selecting plants based on _____ and bulking their seeds without individual line evaluation; it is most effective for highly heritable traits such as seed size and colour.

5.1.3 Hybridisation and pedigree selection

Hybridisation (crossing) creates new genetic combinations that do not exist in either parent. The standard procedure for self-pollinated crops is: (1) Cross two parents with complementary traits

to produce F1 hybrids; (2) Self F1 plants to produce F2, which segregates for all the traits where parents differed; (3) Select individual plants from the F2 population for all desired traits; (4) Grow selected F2 plants as F3 families, and select within and among families; (5) Continue selection and selfing through F4, F5, F6, and F7 until lines are sufficiently homozygous (approximately 99 per cent); (6) Evaluate promising lines in replicated yield trials; (7) Release the best line as a new cultivar.

In pedigree selection, a detailed pedigree record is kept for each selected individual showing its lineage back to the original parents, allowing the breeder to trace the history of any line at any point. Selection is applied in every generation (F2 to F7) for qualitative traits visible on individual plants (disease resistance, plant type, maturity) and for quantitative traits at the family level. Pedigree selection is the most widely used method for self-pollinated crops and has been used by IITA and national programmes in Nigeria to develop most improved cowpea, rice, and groundnut varieties.

Fill in the blank: In pedigree selection, a detailed _____ record is kept for each selected individual tracing its lineage back to the original parents through all generations of selection.

Figure 5.1: DIAGRAM SHOWING THE PEDIGREE SELECTION METHOD FOR A SELF-POLLINATED CROP FROM F1 TO VARIETY RELEASE

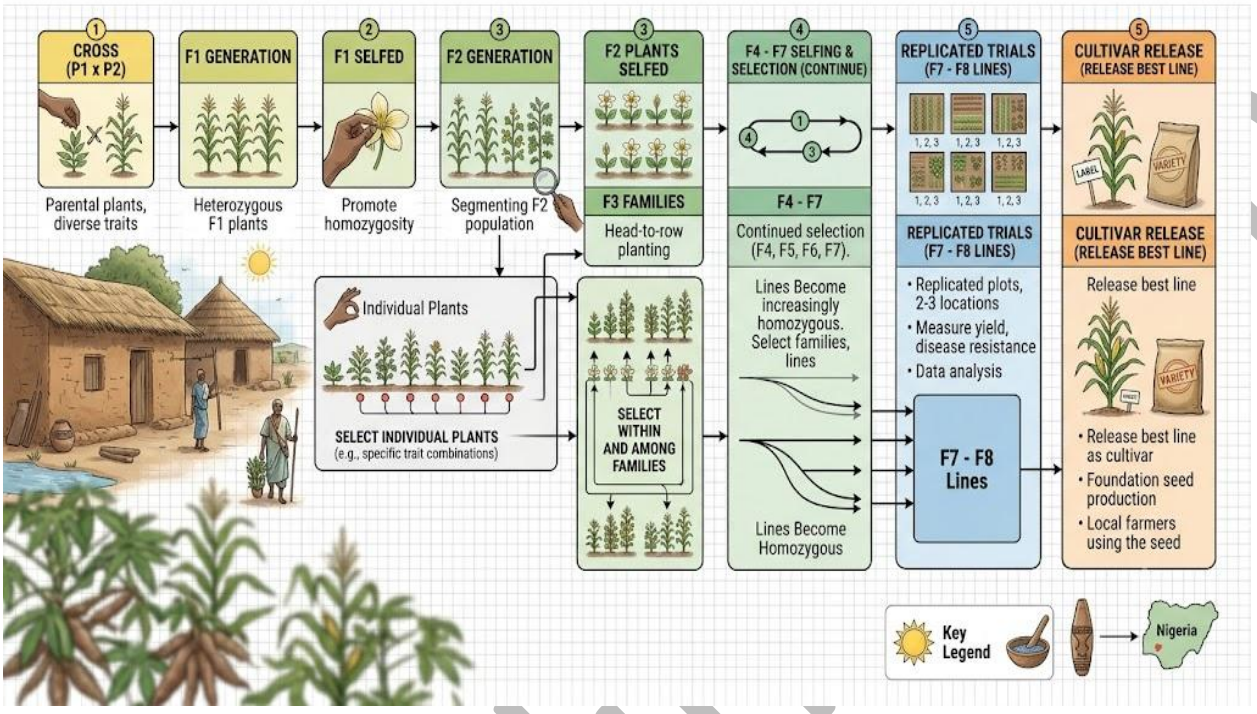

Figure 5.1: Diagram showing the pedigree selection method for a self-pollinated crop from F1 to variety release

Pilot questions 5.1

1. Describe the steps of pure-line selection and state its main limitation.
2. Explain how mass selection differs from pure-line selection in self-pollinated crops.
3. Describe the pedigree selection method from the initial cross through to variety release.
4. Explain why pedigree selection is suitable for self-pollinated crops.
5. State two Nigerian crops for which pedigree selection has been used and name the institutional breeders.

5.2 Additional Methods for Self-Pollinated Crops

5.2.1 Bulk population method

The bulk population (bulk) method involves crossing two parents, then growing the F2 and subsequent generations as a bulk population (all plants together in one plot) without individual selection, for several generations (F2 to F5 or F6). During this period natural selection acts on the bulk, eliminating poorly adapted genotypes; the proportion of superior genotypes in the bulk increases progressively as inferior genotypes fail to reproduce or die. After several bulk generations, individual plants are selected from the bulk, selfed to produce F7 or F8 lines, and evaluated in replicated trials.

The advantage of the bulk method is its low cost: no individual pedigree records are maintained, the population is managed as a single bulk rather than many individual rows, and the breeder can delay intensive selection until lines are nearly homozygous, making selection for complex traits more reliable. The disadvantage is that natural selection in the bulk may favour genotypes that are adapted to the nursery environment but not to the target farmer environment; and the breeder has less control over which allele combinations survive in the population compared with pedigree selection. The bulk method is used at IITA and national programmes for cowpea and soybean.

Fill in the blank: In the bulk population method, the F2 and subsequent generations are grown as a _____ without individual selection; natural selection eliminates poorly adapted genotypes before individual plant selection is begun.

5.2.2 Backcross breeding

Backcross breeding is used to transfer a specific trait (usually a single dominant or simply-inherited gene for disease resistance) from a donor parent into an otherwise agronomically superior elite variety (the recurrent parent), while recovering the genotype of the elite variety. Procedure: (1) Cross the elite variety (recurrent parent, RP) with the donor parent (DP) to produce F1; (2) Backcross F1 to RP to produce BC1F1; (3) Select BC1F1 plants carrying the desired donor trait and backcross to RP again to produce BC2F1; (4) Repeat for 5 to 6 backcross generations; (5) Self the final backcross generation to fix the desired trait in homozygous form.

After each backcross cycle, the proportion of the recurrent parent genome in the selected plants increases: BC1F1 = 75% RP; BC2F1 = 87.5% RP; BC3F1 = 93.75% RP; BC5F1 = 98.44% RP.

After 5 to 6 backcross generations, the backcross-derived line is nearly identical to the elite recurrent parent in all traits except the introgressed resistance gene. Molecular marker-assisted backcrossing (MABC) uses DNA markers to accelerate background recovery, reducing the number of backcross cycles required. Backcross breeding has been widely used in Nigeria to introduce Striga resistance, drought tolerance, and virus resistance into elite cowpea, maize, and cassava varieties.

Fill in the blank: After five backcross generations (BC5F1), the proportion of the recurrent parent genome in the selected backcross lines is approximately _____ per cent, making them nearly identical to the elite variety except for the introgressed trait.

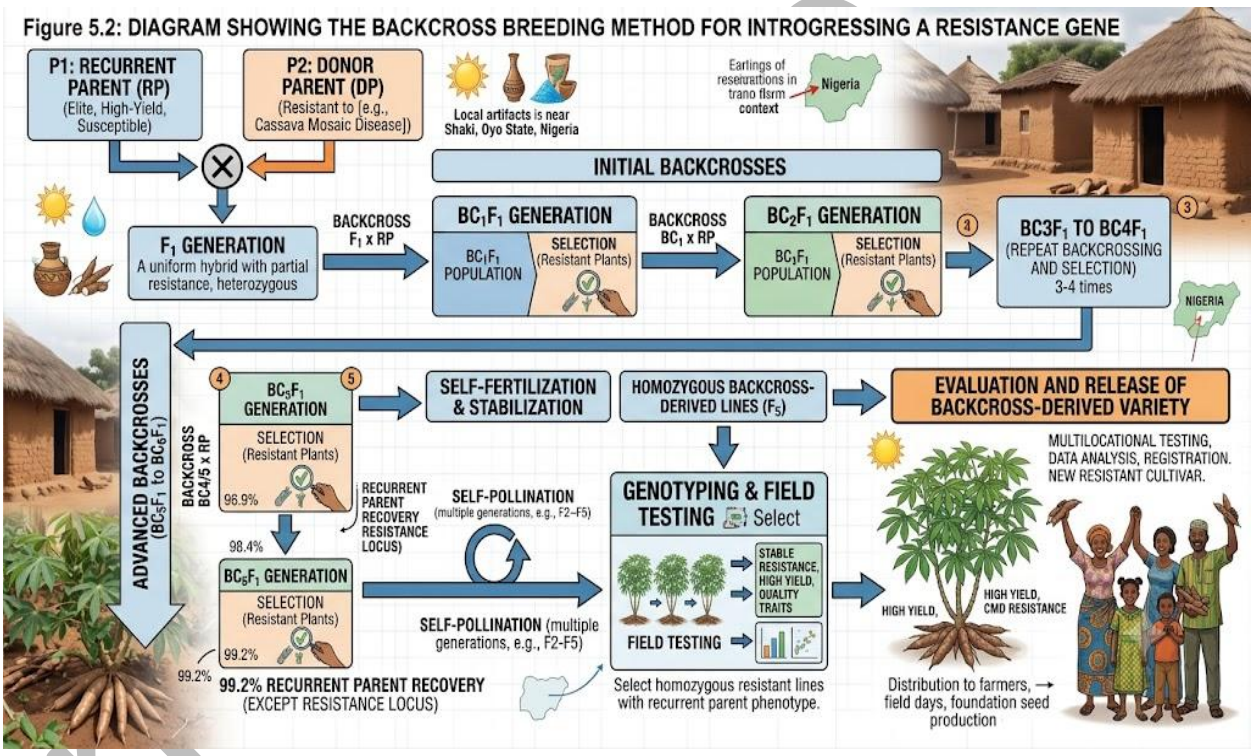

Figure 5.2: Diagram showing the backcross breeding method for introgressing a resistance gene

5.2.3 Single seed descent

Single seed descent (SSD) is a rapid method for advancing segregating populations to homozygosity in self-pollinated crops by taking one seed from each plant in each generation and growing the next generation from this set of single seeds. No selection is applied during the advance from F2 to F6 or F7; all plants are advanced regardless of their phenotype. This allows

the breeder to maintain the genetic diversity of the original F2 population without the sampling loss that occurs in pedigree or bulk selection, and to reach near-homozygosity (F6 or F7) rapidly by growing multiple generations per year in a controlled environment (greenhouse or off-season nursery).

Once the F6 or F7 generation is reached, the breeder evaluates the individual SSD lines in replicated trials and selects the best for variety release. SSD can be combined with doubled haploid (DH) technology: haploid plants are produced from F1 anther culture or in vivo haploid induction, and their chromosomes are doubled with colchicine to produce completely homozygous lines in a single generation rather than the six to seven required by SSD or pedigree selection. DH technology is increasingly used in maize and barley breeding to accelerate programme cycles. At IITA, SSD has been used for cowpea improvement programmes.

Fill in the blank: Single seed descent advances populations to homozygosity by taking _____ seed from each plant per generation without selection; it preserves the genetic diversity of the original F2 population.

Pilot questions 5.2

1. Describe the bulk population method and state one advantage and one disadvantage.
2. State the objective of backcross breeding and describe its procedure.
3. Calculate the percentage of the recurrent parent genome in BC3F1 plants.
4. Explain what single seed descent is and state its main advantage over pedigree selection.
5. Explain how doubled haploid technology relates to single seed descent.

5.3 Breeding Methods for Cross-Pollinated Crops

5.3.1 Mass selection in cross-pollinated crops

Mass selection in cross-pollinated crops involves selecting a proportion of the best-looking individual plants from an open-pollinated population based on their phenotype, bulking their seed together, and using this bulk seed as the next generation. Because the crop is cross-

pollinated, both the selected female parents (seed-bearing plants) and the unselected male parents (which provide pollen) contribute to the next generation; improvement is made only through the female gametes. This means mass selection in cross-pollinated crops is half as effective per generation as selection in self-pollinated crops where both gamete types are controlled.

Modified mass selection improves effectiveness by also controlling the pollen source: only selected plants are allowed to contribute pollen (by detasseling non-selected plants in maize, or isolating selected plants). This is called half-sib mass selection (when the selected plants are pollinated by each other) or full-sib selection (when specific controlled crosses are made). Mass selection is most effective for highly heritable traits (ear length, grain colour, plant height in maize); it is less effective for yield. Traditional Nigerian farmers practice mass selection when they save seed from their best-looking plants at harvest each season.

Fill in the blank: In mass selection for cross-pollinated crops, improvement is made only through the female gametes because the pollen parents are _____ and contribute to the next generation without being selected.

5.3.2 Recurrent selection

Recurrent selection is a cyclic population improvement method for cross-pollinated crops designed to increase the frequency of favourable alleles in the population over successive cycles while maintaining genetic diversity. The basic cycle consists of: (1) evaluation of a large number of individuals or families from the base population; (2) selection of the best individuals or families; (3) recombination of the selected individuals by intercrossing to form the next cycle's population. Each cycle takes one or more seasons; after 5 to 10 cycles, the population mean for the target trait improves substantially, though the population remains heterogeneous.

Types of recurrent selection vary by the unit of selection: simple recurrent selection (individuals selected on own performance), half-sib recurrent selection (individuals selected based on the performance of half-sib family progeny), full-sib recurrent selection (based on full-sib family performance), and reciprocal recurrent selection (RRS, simultaneous improvement of two populations for combining ability, used to develop superior hybrid parents). Recurrent selection has been used at IITA to improve cowpea and maize populations for yield, protein content, and

disease resistance. The IITA maize open-pollinated variety TZPB was developed through recurrent selection.

Fill in the blank: The basic recurrent selection cycle consists of _____ of individuals or families, selection of the best, and recombination of selected individuals to form the next population.

5.3.3 Hybrid variety development in maize

Hybrid variety development in maize exploits heterosis (hybrid vigour): the superior performance of F1 hybrids over the mean of their parents. The process involves: (1) Development of inbred lines by repeated selfing of open-pollinated varieties or population selections for 6 to 8 generations until lines are essentially homozygous; (2) Evaluation of inbred lines per se (their own performance) and in testcrosses (crossed with a standard tester line) to identify lines with high general combining ability (GCA); (3) Diallel crossing among the best inbred lines to identify the best specific combinations (specific combining ability, SCA); (4) Identifying the best single-cross (two inbred lines), three-way cross (single cross x inbred), or double cross (single cross x single cross) hybrid combination.

Commercial hybrid maize production in Nigeria uses the three-line CMS system (described in Series 4): the A line (CMS, female parent), the B line (maintainer), and the R line (restorer, male parent). The commercial hybrid seed is the F1 of A x R. IITA has developed numerous hybrid maize varieties for Nigerian conditions, including early-maturing varieties for the Sudan and Sahel zones. The advantage of hybrid maize over open-pollinated varieties is typically 20 to 30 per cent higher yield; the disadvantage is that farmers must purchase fresh hybrid seed each season because the F2 of a hybrid segregates and yields much less than the F1.

Fill in the blank: Hybrid variety development in maize exploits _____ (the superior performance of F1 hybrids over their parents); commercial hybrids typically yield 20 to 30 per cent more than open-pollinated varieties but require fresh seed each season.

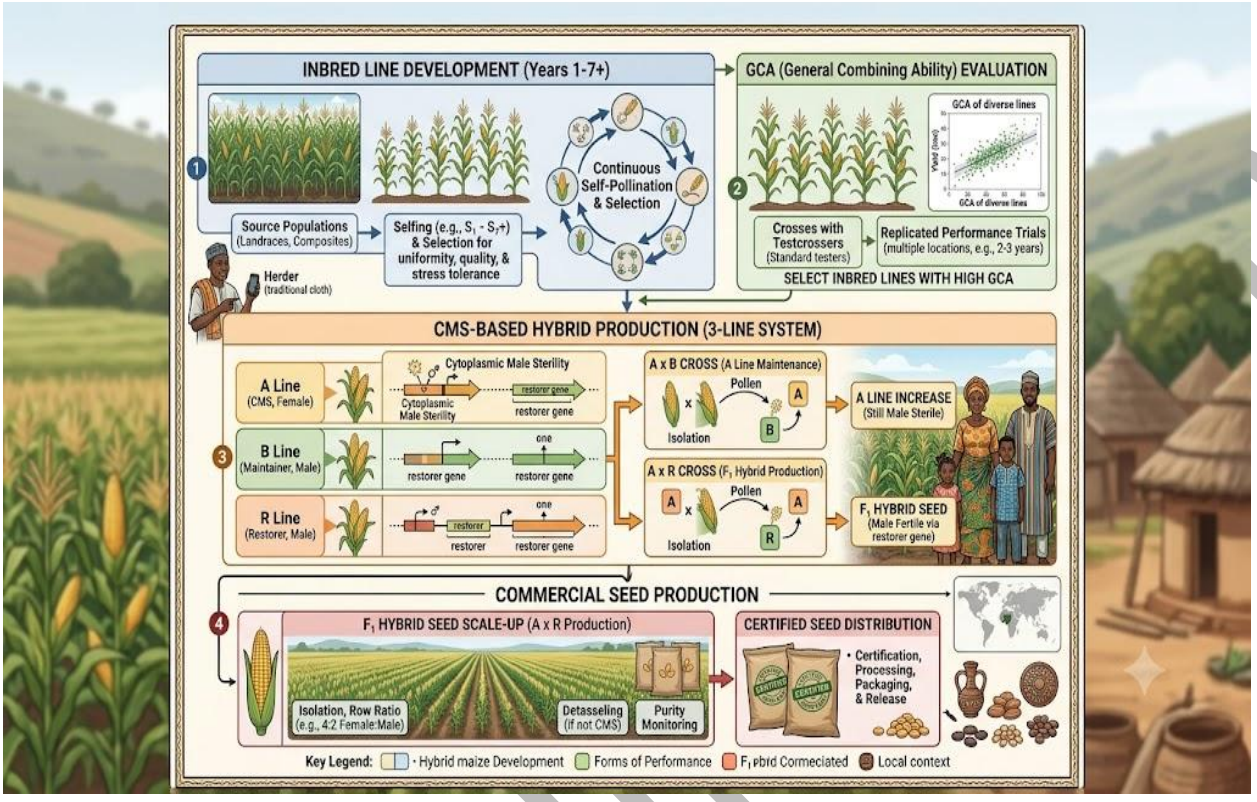

Figure 5.3: Diagram summarising hybrid maize development from inbred line development to commercial seed production

Pilot questions 5.3

1. Explain why mass selection is only half as effective in cross-pollinated crops as in self-pollinated crops.
2. Describe the basic cycle of recurrent selection.
3. Explain what heterosis is and why it is exploited in hybrid maize breeding.
4. Describe the steps in developing inbred lines for hybrid maize production.
5. Explain the difference between general combining ability (GCA) and specific combining ability (SCA).

5.4 Synthetic Varieties, Seed Production, and Distribution

5.4.1 Synthetic varieties in maize

A synthetic variety is developed by intercrossing a number of selected inbred lines or open-pollinated varieties with high GCA among themselves (in all pairwise combinations, a diallel cross) and then allowing the resulting population to open-pollinate for several generations to reach a new Hardy-Weinberg equilibrium. The seed of this equilibrium population is the synthetic variety. Synthetic varieties typically yield slightly less than single-cross hybrids (because they are heterozygous rather than uniformly F1) but significantly more than old open-pollinated varieties, because the contributing parents were selected for high GCA and the population maintains considerable heterosis.

The key advantage of a synthetic variety over a hybrid for resource-poor Nigerian farmers is that farmers can save and replant seed from the synthetic variety for several generations without the severe yield loss that occurs when hybrid seed is saved. Because the synthetic is an open-pollinated variety, it maintains adequate yield for 3 to 5 generations before significant inbreeding reduces performance. Synthetic varieties in maize are also more genetically diverse than hybrids, making them more resilient to pest, disease, and climate variability. IITA and the national programme have developed synthetic maize varieties such as TZPB for smallholder use in Nigeria.

Fill in the blank: A synthetic variety can be saved and replanted by farmers for _____ to 5 generations without severe yield loss, unlike hybrid varieties where F2 seed yields much less than the F1.

Variety Type	Genetic Structure	Yield Potential	Saved Seed Yield	Cost	Smallholder Suitability
Open-pollinated (OPV)	Heterogeneous, maintains variability	Moderate (lower than hybrids)	Stable across generations	Low seed cost	Highly suitable (seed can be recycled)
Synthetic	Developed from selected OPVs, intermated	Intermediate between OPVs and hybrids	Moderate, some decline if recycled	Moderate seed cost	Suitable, but less stable than OPVs

Hybrid	Cross of inbred lines, highly uniform	High yield potential (heterosis)	Sharp yield decline if seed is recycled	High seed cost	Less suitable (requires new seed purchase each season)

Table 5.1: Comparison of open-pollinated varieties, synthetic varieties, and hybrid varieties in maize

5.4.2 Seed production and quality control

Seed production is the multiplication of an improved variety under controlled conditions to maintain genetic purity, physical quality, and vigour. The seed certification system in Nigeria operates through three classes: breeder seed (produced by the original breeder at the research station under the most stringent conditions, in small quantities sufficient only for the next multiplication stage); foundation seed (multiplied from breeder seed under supervision; the seed from which certified seed is produced); and certified seed (the commercial seed distributed to farmers, multiplied from foundation seed with statutory isolation distances from other varieties).

Quality control in seed production involves: varietal purity (roguing: removing off-type plants during the growing season; maintaining statutory isolation distances from other plantings of the same crop; labelling each seed lot with variety name, seed class, lot number, germination percentage, moisture content, and purity); physical purity (cleaning seed to remove inert matter, other crop seeds, and weed seeds); seed health (testing for seed-borne pathogens and treating with fungicide or insecticide dressings where necessary); and germination testing (minimum acceptable germination for certified seed in Nigeria is 80 per cent for most cereals and legumes). The National Agricultural Seeds Council (NASC) oversees seed certification in Nigeria.

Fill in the blank: The three classes of seed in Nigeria's certification system are breeder seed, _____ seed, and certified seed, with each class multiplied from the previous one under progressively less stringent conditions.

5.4.3 Seed distribution systems in Nigeria

Two parallel systems distribute improved seed to farmers in Nigeria. The formal seed system involves public sector research institutions (IITA, national programmes) developing varieties, releasing breeder seed to the National Agricultural Seeds Council (NASC) and to private agro-dealers, seed companies multiplying foundation and certified seed, and government or private distribution networks selling packaged certified seed to farmers through agro-input dealers, cooperative societies, extension agents, and government subsidy programmes. The formal system produces high-quality certified seed but is often unable to reach remote rural farmers due to high cost, poor road infrastructure, and inadequate distribution networks.

The informal seed system is how most Nigerian farmers obtain their planting material: seed saved from their own harvest, seed exchanged with neighbours and community members, seed purchased from local markets in bulk without certification or labelling, and seed supplied by community seed banks and farmer seed networks. The informal system is highly accessible, locally trusted, and culturally appropriate, but the seed it distributes is often the product of several years of farmer saving, resulting in genetic drift, admixture, and loss of the performance characteristics of the original improved variety. Bridging the formal and informal systems through community-based seed production schemes is a priority for improving seed access in Nigerian agriculture.

Fill in the blank: The _____ seed system distributes improved seed through research institutions, seed companies, and agro-dealers but often fails to reach remote rural farmers due to high cost and poor distribution infrastructure.

Certification Class	Production Conditions	Quality Requirements
Breeder Seed	Produced under direct supervision of the crop breeder or research institute	Genetic purity must be 100%; foundation for all other seed classes
Foundation Seed	Grown from breeder seed under strict isolation and field standards	High genetic purity, free from admixtures, meets strict field inspection standards

Certified Seed	Produced from foundation seed by registered seed growers under official certification	Maintains varietal identity, acceptable germination rate, free from weeds and diseases, meets national seed certification standards

Box 5.1: Seed certification classes and quality control requirements in Nigeria

Pilot questions 5.4

1. Explain what a synthetic variety is and how it is developed.
2. State two advantages of synthetic varieties over hybrids for resource-poor Nigerian smallholders.
3. Describe the three seed certification classes in Nigeria and state the role of each.
4. State four quality control requirements for certified seed in Nigeria.
5. Distinguish between the formal and informal seed distribution systems in Nigeria.

Series Summary

This final Series covered the breeding methodologies for self-pollinated and cross-pollinated crops. For self-pollinated crops: pure-line selection (identifies best existing genotypes from landraces, no new variation created), mass selection (phenotypic selection bulked without individual line evaluation, suitable for high-heritability traits), pedigree selection following hybridisation (F1 to F7, individual and family selection with pedigree records, most widely used method for cowpea, rice, and groundnut in Nigeria), bulk population method (natural selection in bulk without individual records until near-homozygosity), backcross breeding (introgressing a specific trait into an elite variety over 5 to 6 backcross cycles recovering 98% of the recurrent parent genome), and single seed descent (rapid advance to homozygosity with one seed per plant, no selection, optionally combined with doubled haploidy).

For cross-pollinated crops: mass selection (phenotypic, only female gametes controlled; modified by detasseling to also control pollen), recurrent selection (cyclic evaluation-selection-recombination over multiple generations, improving population mean while maintaining diversity), and hybrid variety development in maize (inbred line development by 6 to 8 generations of selfing; GCA and SCA testing; single-cross hybrid production using CMS three-line system; 20 to 30 per cent yield advantage over OPVs). We described synthetic varieties (intercrossed inbred lines or high-GCA OPVs, open-pollinated at equilibrium, saveable for 3 to 5 seasons, more resilient than hybrids), seed certification (breeder, foundation, certified seed classes; NASC oversight; 80 per cent minimum germination), and formal vs informal seed distribution in Nigeria. By completing this Series and the course as a whole, you should be able to achieve all eight Series Learning Outcomes (SLO 5.1 to SLO 5.8) and all seven course learning outcomes.

Glossary of Terms

- **Backcross breeding:** a method for introgressing a specific trait from a donor parent into an elite recurrent parent by repeated crossing back to the recurrent parent, recovering its genome progressively over 5 to 6 backcross cycles.
- **Breeder seed:** the first class of seed in the certification system, produced by the original plant breeder under the most stringent conditions to maintain genetic purity; used to produce foundation seed.
- **Bulk population method:** a breeding method for self-pollinated crops in which the F2 and subsequent generations are grown as a bulk without individual selection; natural selection eliminates poorly adapted genotypes before individual plant selection.
- **Certified seed:** the commercial seed class distributed to farmers, multiplied from foundation seed with statutory isolation distances, roguing, germination testing, and labelling.

- **Diallel cross:** a set of crosses in which all possible pairs from a group of parental lines are crossed; used to estimate GCA and SCA of each line and to identify the best hybrid combinations.
- **Doubled haploid (DH):** a completely homozygous line produced from a haploid plant (derived from anther culture or in vivo haploid induction) by chromosome doubling with colchicine; achieves in one generation what takes six to seven generations by selfing.
- **Foundation seed:** the second seed class, multiplied from breeder seed under supervision; used to produce certified seed.
- **General combining ability (GCA):** the average performance of a line across all hybrid combinations in which it is tested; reflects the additive genetic effects of the line's alleles.
- **Half-sib selection:** a form of recurrent selection in which individuals are selected based on the performance of their half-sib families (sharing one common parent).
- **Heterosis (hybrid vigour):** the superior performance of an F1 hybrid over the mean or better parent of the cross; exploited in hybrid variety development in maize, sorghum, and other cross-pollinated crops.
- **Inbred line:** a line of a cross-pollinated crop produced by 6 to 8 generations of selfing; nearly completely homozygous; used as a parent in hybrid variety development.
- **Mass selection:** a breeding method in which individual plants are selected based on phenotype, their seeds are bulked, and the bulk is grown as the next generation; applicable to both self- and cross-pollinated crops.
- **NASC (National Agricultural Seeds Council):** the Nigerian government body responsible for seed certification, quality control, and regulation of the commercial seed industry.
- **Pedigree selection:** a breeding method for self-pollinated crops following hybridisation, in which individual plants are selected in each generation from F2 to F7 and detailed pedigree records are maintained for each selected line.

- **Pure-line selection:** a breeding method for self-pollinated crops in which individual plants are selected from a landrace or old variety, their progenies are grown as pure lines, and the best line is selected as a new cultivar.
- **Reciprocal recurrent selection (RRS):** a form of recurrent selection that simultaneously improves two populations (or heterotic groups) for their combining ability with each other; used to develop superior hybrid parents in maize.
- **Recurrent selection:** a cyclic population improvement method for cross-pollinated crops consisting of evaluation, selection, and recombination of selected individuals or families; progressively increases the frequency of favourable alleles.
- **Roguing:** the physical removal of off-type or diseased plants from a seed production field to maintain genetic purity of the seed lot.
- **Single cross hybrid:** an F1 hybrid produced by crossing two inbred lines; the most common type of commercial maize hybrid; typically the highest-yielding hybrid type.
- **Single seed descent (SSD):** a breeding method for advancing segregating populations to homozygosity by taking one seed per plant per generation without selection; preserves original F2 genetic diversity.
- **Specific combining ability (SCA):** the deviation of a specific hybrid's performance from what would be expected based on the GCA of its two parents; reflects non-additive (dominance and epistatic) genetic effects.
- **Synthetic variety:** an open-pollinated variety developed by intercrossing selected inbred lines or high-GCA OPVs and allowing the population to reach Hardy-Weinberg equilibrium; maintains heterosis, saveable for 3 to 5 seasons.
- **Testcross:** a cross of a candidate inbred line with a standard tester line to evaluate its GCA; commonly used in inbred line evaluation for hybrid breeding programmes.

Concept Check Questions [Series 5]

Objective Questions

1. Pure-line selection identifies the best genotypes _____ present in a landrace population; it does not create new variation. (Linked to SLO 5.1)
2. After five backcross generations (BC5F1), the proportion of the recurrent parent genome is approximately _____ per cent. (Linked to SLO 5.3)
3. In mass selection for cross-pollinated crops, improvement occurs only through the _____ gametes because pollen parents are unselected. (Linked to SLO 5.4)
4. Hybrid varieties in maize typically yield _____ to 30 per cent more than open-pollinated varieties but farmers must buy fresh seed each season. (Linked to SLO 5.5)
5. A synthetic variety can be saved and replanted by farmers for 3 to _____ generations without severe yield loss. (Linked to SLO 5.6)

Short-Answer Questions

6. Describe the steps of pedigree selection from the initial cross to variety release. (Linked to SLO 5.2)
7. Describe the bulk population method and state one advantage over pedigree selection. (Linked to SLO 5.3)
8. Explain what recurrent selection is and describe its basic cycle. (Linked to SLO 5.4)
9. Describe the steps in developing inbred lines for hybrid maize production. (Linked to SLO 5.5)
10. Distinguish between the formal and informal seed distribution systems in Nigeria. (Linked to SLO 5.8)

Long-Answer Questions

11. Describe the breeding methods applicable to self-pollinated crops, covering pure-line selection, mass selection, pedigree selection following hybridisation, bulk population

method, backcross breeding, and single seed descent, explaining the purpose, procedure, and appropriate use of each. (Linked to SLOs 5.1, 5.2, 5.3)

12. Describe the breeding methods applicable to cross-pollinated crops, covering mass selection, recurrent selection, and hybrid variety development in maize, including the role of inbred lines, GCA, SCA, and the CMS three-line system. (Linked to SLOs 5.4, 5.5)
13. Describe synthetic variety development in maize, explain the seed certification system and quality control requirements, and compare the formal and informal seed distribution systems in Nigeria. (Linked to SLOs 5.6, 5.7, 5.8)

Answers to Concept Check Questions [Series 5]

Objective Questions

1. Already.
2. 98.44.
3. Female.
4. 20.
5. 5.

Short-Answer Questions

6. (1) Cross two parents with complementary traits to produce F1; (2) Self F1 to produce F2 which segregates; (3) Select individual F2 plants for desired traits; (4) Grow selected F2 plants as F3 families, select within and among families; (5) Continue selection and selfing through F4, F5, F6, F7 with pedigree records maintained; (6) Evaluate promising F7-F8 lines in replicated yield trials; (7) Release the best line as a new cultivar.
7. In the bulk method, F2 and subsequent generations (to F5 or F6) are grown as a bulk population without individual selection or pedigree records; natural selection progressively eliminates poorly adapted genotypes; after the bulk phase, individual plants

are selected and selfed to produce nearly homozygous lines for evaluation. Advantage over pedigree selection: much lower cost because no individual plant records are maintained and the population is managed as one bulk rather than hundreds of individual rows.

8. Recurrent selection is a cyclic population improvement method for cross-pollinated crops that increases the frequency of favourable alleles over successive cycles while maintaining genetic diversity. Basic cycle: (1) evaluate a large number of individuals or families from the base population; (2) select the best individuals or families; (3) intercross selected individuals to recombine selected alleles and form the next cycle's base population. The cycle is repeated for 5 to 10 or more cycles to progressively improve the population mean.
9. Self the base open-pollinated variety or selected plants; grow F1 selfed plants as S1 families and self again; continue selfing through S2, S3, S4, S5, S6 (6 to 8 generations total) until lines are essentially homozygous (99%); evaluate lines per se and in testcrosses for yield and adaptation; select the best lines for further evaluation; make diallel crosses among the best inbred lines to estimate GCA and SCA and identify the best single-cross or other hybrid combinations.
10. Formal seed system: research institutions develop varieties; NASC certifies seed; seed companies multiply foundation and certified seed; agro-dealers, cooperatives, extension agents, and government subsidy programmes distribute packaged certified seed to farmers; high quality but limited reach to remote rural areas. Informal seed system: seed saved from own harvest; seed exchanged with neighbours; seed bought in local markets without certification; accessible and trusted but often genetically drifted and of unknown quality.

Long-Answer Questions

11. Pure-line selection: collect individual plants from landrace; grow progenies as separate pure lines; select best line; release as cultivar; limitation: no new variation created, only identifies existing genotypes. Mass selection: select large number of plants by phenotype;

bulk seeds; grow bulk as next generation; cheaper but less precise than pure-line; effective for high-heritability traits (seed size, colour). Pedigree selection: cross two complementary parents (F1); self F1 to F2 (select individual plants); F2 to F3 families (select within and among); continue to F7 with pedigree records; replicated trials; release best line; widely used for cowpea, rice, groundnut in Nigeria. Bulk method: F2 to F5-F6 grown as bulk without records; natural selection acts; then individual plant selection to homozygous F7-F8 lines; advantage: lower cost. Backcross breeding: transfer specific gene from donor to elite recurrent parent; 5-6 backcross cycles (BC1F1 to BC6F1); each cycle recovers 50% more RP genome; BC5F1 = 98.44% RP; self final BC to fix trait; MABC accelerates background recovery; used for Striga resistance, drought tolerance, virus resistance in Nigeria. SSD: one seed per plant per generation, no selection, F2 to F6-F7; preserves F2 diversity; rapid advance; combined with DH (anther culture + colchicine doubling) to achieve complete homozygosity in one generation.

12. Mass selection: select plants on phenotype, bulk seeds, grow next generation; only female gametes controlled unless pollen also controlled by detasseling (modified mass selection); half as effective per generation as in self-pollinated crops; effective for high-heritability traits; practised by Nigerian farmers. Recurrent selection: cyclic evaluation-selection-recombination; types: simple (own performance), half-sib (half-sib family performance), full-sib, reciprocal recurrent selection (RRS, two heterotic populations improved simultaneously for combining ability); IITA TZPB open-pollinated maize variety developed by recurrent selection. Hybrid maize: heterosis exploited (F1 superior by 20-30% over OPV); inbred line development (6-8 selfing generations to homozygosity); testcross evaluation for GCA (crosses with standard tester); diallel crosses for SCA; best single-cross hybrid identified; CMS three-line production system (A line x R line, maintained by B line); IITA developed early-maturing hybrid maize varieties for Sudan/Sahel zones of Nigeria; disadvantage: farmers must buy fresh seed each season because F2 of hybrid segregates and yields much less.
13. Synthetic variety: developed by intercrossing selected inbred lines or high-GCA OPVs in all pairwise combinations (diallel cross); resulting population open-pollinates to Hardy-Weinberg equilibrium; maintains heterosis (less than single cross but more than old OPV); saveable for 3-5 seasons without severe yield loss; more genetically diverse =

more resilient to pests, diseases, climate variability; IITA TZPB example; advantage for resource-poor farmers: no annual seed purchase required. Seed certification: three classes: breeder seed (produced by breeder, highest purity, small quantity, produces foundation seed); foundation seed (multiplied from breeder seed under strict supervision, produces certified seed); certified seed (commercial distribution, statutory isolation distances, roguing of off-types, minimum 80% germination, labelled with variety name, seed class, lot number, germination %, moisture %, purity); NASC oversees certification. Formal system: research institutions develop varieties; NASC certifies; seed companies multiply; agro-dealers/cooperatives/extension agents/government distribute; high quality but high cost, poor rural reach. Informal system: farmer-saved seed, community exchange, local market purchase; accessible, low cost, culturally trusted; but genetically drifted, no quality assurance; community-based seed production schemes bridge the two systems.

Answers to Pilot Questions [Series 5]

Part 5.1: Breeding Methods for Self-Pollinated Crops

1. Steps of pure-line selection: (1) collect seeds from a large number of individual plants in an existing landrace or old variety population; (2) grow each plant's progeny as a separate line (a pure line) in a separate plot; (3) evaluate all lines for yield, quality, disease resistance, and other target traits over one or more seasons; (4) identify the best pure line based on its performance; (5) multiply and release the best line as a new cultivar. Main limitation: pure-line selection does not create new genetic variation; it can only identify and separate the best genotypes already present in the starting population. Once the best line is identified and released, no further genetic improvement is possible using this method in that same population; a new cross or new population must be made to create new variation for further selection.
2. Mass selection and pure-line selection both involve selecting superior plants from an existing population, but differ in the unit of evaluation and the fate of selected seed. In

pure-line selection, seed from each selected plant is grown as a separate progeny row (pure line) and each line is evaluated individually, allowing the breeder to identify which specific genotype is best based on family performance over one or more seasons. In mass selection, seed from all selected plants is bulked together and grown as a single mixed population in the next season; no individual line evaluation is done, and the breeder cannot distinguish which selected plant contributed the best genotype. Mass selection is faster and cheaper but less precise.

3. Pedigree selection procedure: (1) Make a cross between two parents with complementary traits to produce the F1 hybrid; (2) Self F1 plants to produce the F2 generation, which segregates for all traits where parents differed; (3) Select individual plants from the F2 population for all visually distinguishable desired traits (disease resistance, plant type, maturity) and record the pedigree of each selected plant; (4) Grow each selected F2 plant as a separate F3 family and select within and among families; (5) Continue selection and selfing, maintaining pedigree records, through F4, F5, F6, and F7 until lines are approximately 99 per cent homozygous; (6) Evaluate the most promising lines from F7 or F8 in replicated multi-location yield trials for 2 to 3 seasons; (7) Submit the best line to national performance trials and, if superior, release it as a new cultivar.
4. Pedigree selection is well-suited to self-pollinated crops for several reasons: the natural tendency of self-pollinated crops toward homozygosity means that each generation of selfing increases homozygosity predictably, allowing the breeder to know when lines are sufficiently fixed for evaluation; individual plant selection in F2 and subsequent generations is meaningful because self-pollination produces distinct progeny lines that remain true to the selected plant's genotype; maintaining pedigree records is straightforward because each selected plant produces its own distinct selfed progeny line; and the method allows selection for both qualitative traits (using individual plant phenotypes in early generations) and quantitative traits (using family means in later generations when lines are more homozygous and environmental effects are averaged out).
5. Any two crops with appropriate breeders: cowpea (Vigna unguiculata): pedigree selection following hybridisation has been used at IITA (International Institute of Tropical Agriculture) in Ibadan and at the University of Agriculture Makurdi and other national

centres to develop improved cowpea varieties such as IT90K-284-2 and IT93K-277-2. Rice (Oryza sativa): pedigree selection has been used at the National Cereals Research Institute (NCRI) Badeggi and through collaboration with IRRI to develop improved rice varieties suited to Nigerian upland and irrigated conditions.

Part 5.2: Additional Methods for Self-Pollinated Crops

1. In the bulk population method, the F2 and subsequent generations (typically F2 to F5 or F6) derived from an initial cross are grown together as a single bulk population without any deliberate individual plant selection and without maintaining pedigree records; all plants are harvested and their seeds are mixed and replanted as the next bulk generation. During the bulk phase, natural selection acts on the population, progressively eliminating genotypes that are poorly adapted to the growing environment and increasing the frequency of adapted genotypes. After 4 to 5 bulk generations, individual plants are selected from the bulk, selfed to produce nearly homozygous lines (F7 or F8), and the lines are evaluated in replicated trials. Advantage: much lower management cost because no individual progeny rows, no pedigree records, and no selection labour are required during the bulk phase. Disadvantage: the breeder has less control over which allele combinations survive; natural selection may favour genotypes adapted to the nursery environment rather than the target farmer environment.
2. Objective of backcross breeding: to transfer a specific trait (usually a single dominant or simply inherited gene for disease resistance, pest resistance, or quality) from a donor parent into an agronomically superior elite variety (the recurrent parent) while recovering the genetic background of the elite variety. Procedure: (1) Cross the elite recurrent parent (RP) with the donor parent (DP) to produce F1; (2) Backcross F1 to RP, selecting for the desired donor trait, to produce BC1F1; (3) Select BC1F1 plants carrying the desired trait and backcross again to RP to produce BC2F1; (4) Repeat for a total of 5 to 6 backcross cycles, selecting for the desired trait at each cycle; (5) Self the final backcross generation plants carrying the desired trait to produce BC5F2 or BC6F2 lines; (6) Select

homozygous lines for the desired trait and evaluate in replicated trials; (7) Release the best line as a backcross-derived improved variety.

3. After each backcross cycle, the proportion of the recurrent parent genome in selected plants = 1 - (1/2)^n where n is the number of backcross generations. For BC3F1: proportion of RP = 1 - (1/2)^3 = 1 - 1/8 = 7/8 = 87.5 per cent. The proportion of donor genome is 12.5 per cent (1/2^3 = 1/8). This means that after three backcross cycles, 87.5 per cent of the backcross line's genome comes from the elite recurrent parent and only 12.5 per cent from the donor, though the donor trait of interest is retained because it was selected at each cycle.
4. Single seed descent (SSD) is a method for rapidly advancing a segregating population from F2 to near-homozygosity (F6 or F7) by taking exactly one seed from each plant in every generation, without applying any deliberate selection during the advance. All plants, regardless of their phenotype, contribute one seed to the next generation. The resulting F6 or F7 lines are then evaluated in replicated trials and the best are selected for variety release. Main advantage over pedigree selection: SSD preserves the genetic diversity of the original F2 population because all F2 genotypes are equally represented in the advance (no genotypes are preferentially eliminated by selection during the advance phase); this is particularly important when the target traits have low heritability and are difficult to select in early segregating generations.
5. Single seed descent advances populations to near-homozygosity by selfing, taking one seed per plant per generation, without selection. Doubled haploid (DH) technology achieves the same endpoint (completely homozygous lines) in a single generation rather than six to seven, by producing haploid plants from F1 pollen (via anther culture in a tissue culture laboratory, or via in vivo haploid induction using a haploid inducer line in maize) and then doubling the chromosomes of the resulting haploid plants with colchicine treatment to produce completely homozygous (DH) lines. DH is essentially an instantaneous replacement for SSD: instead of waiting 6 to 7 seasons to reach F6-F7, the breeder can produce completely homozygous DH lines in one generation and immediately begin replicated evaluation. The disadvantage of DH is its high cost and the need for specialised tissue culture or haploid induction facilities.

Part 5.3: Breeding Methods for Cross-Pollinated Crops

1. In self-pollinated crops, selection controls both the female gametes (the seeds on the selected plant) and the male gametes (the pollen, which comes from the same selected plant through selfing), so genetic improvement occurs through both gametic types simultaneously. In cross-pollinated crops, mass selection controls only the female gametes (the selected plants produce the seed); the male gametes (pollen) come from unselected plants in the surrounding population that pollinate the selected females. Because only half the gametes in the next generation (the female half) are from selected superior parents, the gain from mass selection is effectively halved compared with selection in self-pollinated crops where both gamete types are from selected parents.
2. The basic cycle of recurrent selection consists of three steps: (1) Evaluation: grow a large number of individuals or families from the current cycle's base population and measure their performance for the target trait or traits; (2) Selection: identify and retain the best individuals or families based on their evaluated performance, typically the top 10 to 20 per cent; (3) Recombination: intercross all selected individuals among themselves (by open pollination, hand pollination, or detasseling in maize) to combine their alleles in a new base population for the next cycle. This cycle (evaluation, selection, recombination) is repeated for many cycles; over time the frequency of favourable alleles in the population increases progressively toward fixation.
3. Heterosis (hybrid vigour) is the phenomenon in which the F1 hybrid offspring of two genetically different parents outperforms the average (or in some definitions the better) of its parents for a given trait, particularly yield. It is exploited in hybrid maize breeding because: (1) the yield advantage is large (F1 hybrids typically yield 20 to 30 per cent more than the best open-pollinated varieties from the same genetic background); (2) the F1 is uniform (all plants from the same cross are genetically identical, giving a consistent, predictable product); and (3) maize's cross-pollination biology (separate male and female flowers, wind pollination) makes it practical to control crosses for large-scale hybrid seed production. The exploitation of heterosis through hybrid breeding transformed maize productivity in the 20th century.

4. Steps in developing inbred lines for hybrid maize: (1) Select individuals with desirable agronomic traits from an open-pollinated variety, landrace, or improved population as starting material. (2) Self-pollinate selected plants to produce S1 families (first selfing generation); self-pollination of maize requires hand-pollination by collecting pollen from the tassel and applying it to the silks of the same plant while the plant is enclosed in bags on both. (3) Evaluate S1 families, select the best, and self again to produce S2 families; continue selection and selfing through S3, S4, S5, S6, S7, and S8 (6 to 8 generations total); with each selfing, heterozygosity is halved and by S7-S8 lines are approximately 99 per cent homozygous. (4) Evaluate lines per se (own performance) and in testcrosses with a standard tester to estimate GCA. (5) Select the best inbred lines based on combining ability for use in hybrid crosses.
5. General combining ability (GCA) is the average performance of a line across all hybrid combinations in which it is tested, relative to the overall population mean; it reflects the additive genetic effects of the line's alleles that are consistently transmitted to all its hybrid offspring. A line with high GCA produces above-average hybrids regardless of the cross partner. GCA is estimated by crossing each candidate line with a common tester and averaging performance across all hybrid combinations. Specific combining ability (SCA) is the deviation of a specific hybrid's performance from what would be predicted on the basis of the GCA values of its two parents alone; a positive SCA means the specific combination performs better than expected from GCA alone. SCA reflects non-additive genetic effects (dominance and epistasis). In practice, breeders first screen lines for high GCA to identify broadly useful parents, then conduct diallel or factorial crosses among the best GCA lines to identify high-SCA combinations for commercial hybrid release.

Part 5.4: Synthetic Varieties, Seed Production, and Distribution

1. A synthetic variety is developed as follows: (1) Select a group of inbred lines or open-pollinated varieties with high GCA (demonstrating they produce good hybrid combinations); (2) Intercross all selected parents in all possible pairwise combinations (a diallel cross) to produce a set of F1 hybrids; (3) Bulk the seeds of all F1 hybrid

combinations and grow the bulk together in an isolated open-pollination nursery; (4) Allow the population to open-pollinate for 2 to 3 generations to reach a new Hardy-Weinberg allele frequency equilibrium; (5) The seed of this equilibrium population is the synthetic variety (Syn-1 or Syn-2). The synthetic variety maintains considerable heterosis because the population contains many heterozygous loci (from the high-GCA parents), though less than a single-cross F1 hybrid.

2. Any two: Farmers can save and replant seed from a synthetic variety for 3 to 5 generations without the severe yield penalty that occurs with hybrid varieties (where the F2 of a hybrid segregates and yields much less than the F1), reducing the recurring cost of seed purchase for resource-poor smallholders. The synthetic variety is more genetically diverse than a single-cross hybrid (it is an open-pollinated population rather than a fixed F1 genotype), making it more resilient to variable pest, disease, and climate conditions that are common in smallholder farming environments in Nigeria.
3. Breeder seed: the original seed class produced by the plant breeder at the research station under the most stringent conditions (maximum isolation, intensive roguing, small quantities); it is the genetic standard for the variety and is used to produce foundation seed. Foundation seed: the second class, produced by multiplying breeder seed under supervision and with statutory isolation distances; it is used to produce certified seed; quantities are larger than breeder seed but still limited. Certified seed: the commercial class distributed directly to farmers; produced by multiplying foundation seed with statutory isolation distances from other plantings of the same crop, roguing of off-types, germination testing (minimum 80 per cent), labelling with variety name, seed class, lot number, germination and purity percentages; NASC (National Agricultural Seeds Council) oversees certification of all three classes in Nigeria.
4. Any four: varietal purity (roguing: physically removing all off-type plants from the seed production field before they shed pollen; maintaining statutory isolation distances from other plantings of the same crop to prevent pollen contamination); physical purity (cleaning and processing seed to remove inert material, other crop seeds, and weed seeds to meet minimum purity standards); seed health (testing for seed-borne pathogens and treating with approved fungicide or insecticide dressings where required); germination rate (testing each seed lot in the laboratory to confirm that a minimum of 80 per cent of

seeds germinate within the specified period; seed lots that fail the germination test cannot be certified).

5. Formal seed system: improved varieties are developed by research institutions (IITA, national programmes, universities); breeder seed is certified by NASC; seed companies and NGO partners multiply foundation and certified seed under NASC supervision; packaged certified seed is distributed through agro-input dealers, cooperative societies, extension agents, and government subsidy or distribution programmes; strengths: high quality, genetically pure, labelled seed; weaknesses: high cost to farmers, limited distribution reach to remote rural areas, dependence on government subsidy for affordability. Informal seed system: farmers save seed from their own harvest for the next season; seed is exchanged with neighbours and community members; seed is purchased in local markets in bulk without certification or labelling; strengths: locally accessible, affordable or free, culturally trusted, suited to local conditions; weaknesses: seed quality declines through genetic drift, admixture, and loss of original improved variety characteristics after multiple seasons of farmer saving.

References and Attributions [Series 5]

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Figure 5.1: Pedigree selection method flowchart Attribution: AI generated. Suggested OER search string: "pedigree selection method self-pollinated crop F1 F2 F7 cultivar release flowchart OER".
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- Table 5.1: OPV vs synthetic vs hybrid maize comparison Attribution: AI generated. Suggested OER search string: "maize variety types open-pollinated synthetic hybrid comparison table OER".
- Box 5.1: Seed certification classes and quality requirements Attribution: AI generated. Suggested OER search string: "seed certification Nigeria breeder foundation certified quality control NASC OER box".