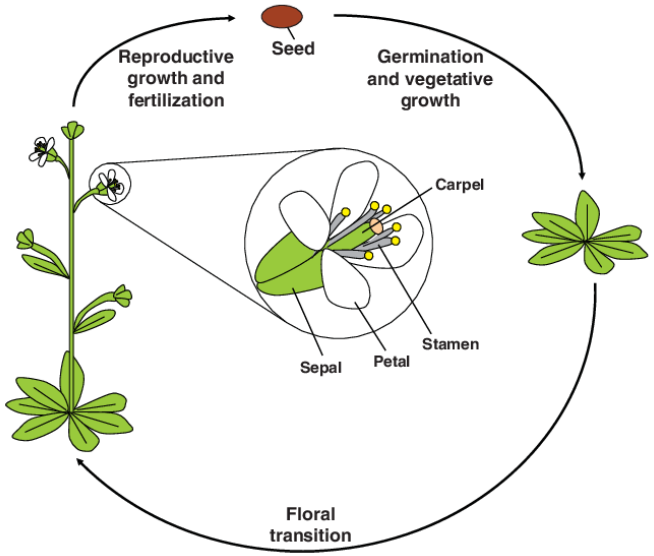
Bharathidasan University

Tiruchirappalli- 620024,
Tamil Nadu, India

Programme: M.Sc., Botany

Course Title: Anatomy, embryology and morphogenesis
Course Code: 22PGBOTCC102



UNIT -V

MORPHOGENESIS

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MORPHOGENESIS

- In term morphogenesis, morphe means shape and genesis means creation. So morphogenesis is defined as the biological process that causes an organism to develop its shape.

- When a cell loss the capacity to divide, it leads to differentiation. Differentiation results in development of structures that is commensurate with the function the cells finally has to perform.

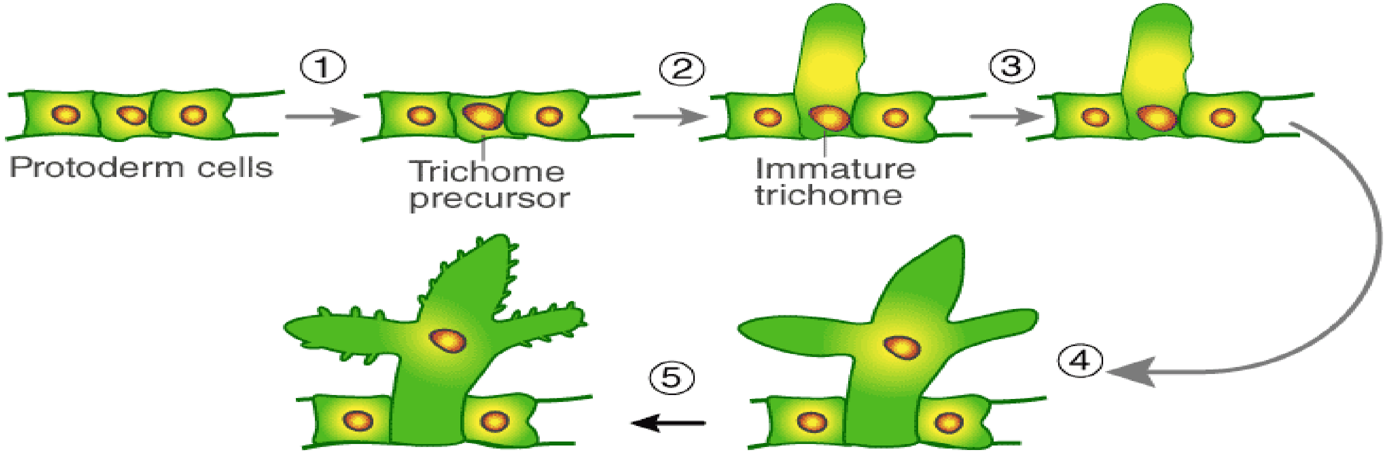
- General principles for differentiation for cell, tissues and organs are similar.

- A differentiated cell may dedifferentiate and then redifferentiate.

DIFFERENTIATION

- Differentiation is a process through which meristematic tissues undergo permanent change to form specialized cells in the plant body.
- Differentiation leads to the formation of permanent tissues which have specialized structures for specific functions.
- For instance, The protoplasm is lost during the formation of tracheary elements.

Example



1. DNA Synthesis
2. Cell Expansion
3. Nuclear Migration
4. Branching
5. Maturation

There are two types of differentiation process:

Dedifferentiation process:

- Through the dedifferentiation process, permanent cells that have lost their ability to divide, regain their ability to divide under certain special conditions.
- For example, under special circumstances, parenchymal cells undergo dedifferentiation to form meristematic cells.

Redifferentiation process:

- Redifferentiation is the process through which cells, which had regained their ability to divide, again lose that ability and mature into permanent tissue to perform their specialized functions.

Transititions to flowering

- Plants undergo several developmental transitions during their life cycle. The first is germination, which is the transition from the embryonic to the postembryonic mode of growth.
- After germination, the seedling passes through a juvenile vegetative phase, where it is not competent to flower.
- This is followed by the transition to the adult vegetative phase, where it can respond to floral inductive signals. With the transition to flowering, the plant enters the reproductive phase.
- The environmental inputs regulating the floral transition overlap considerably with those regulating the juvenile-to-adult vegetative transition.
- Physiological experiments provided the concept of multiple pathways that promote or repress flowering, all of which quantitatively contribute to an activity that switches the shoot apical meristem from producing leaves to forming flowers after reaching a threshold level

Floral meristem

- The meristem can be defined as the tissue or group of plant tissues that contain undifferentiated stem cells, which are capable of producing any type of cell tissue. Their maintenance and development, both in the vegetative meristem or the meristem of the inflorescence is controlled by genetic cell fate determination mechanisms.

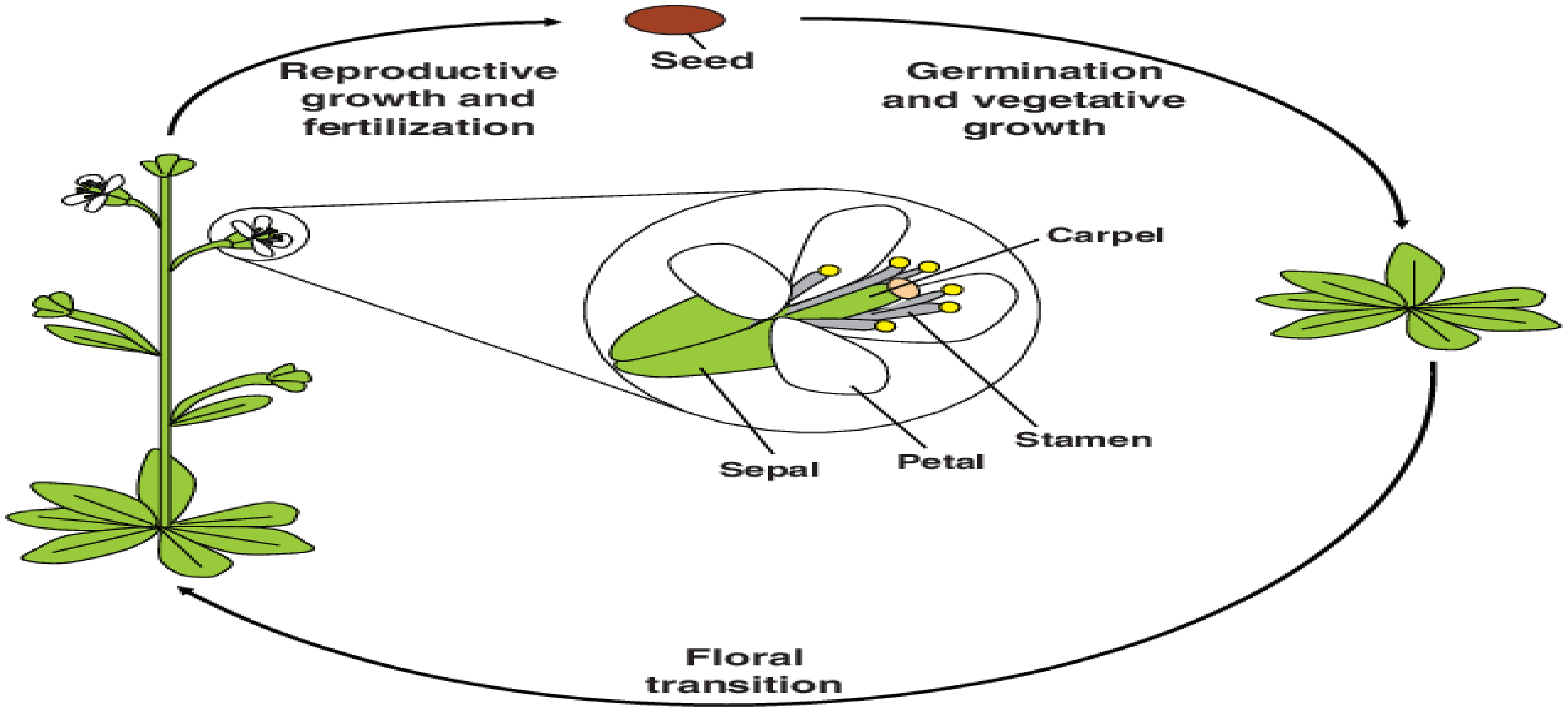
- Along with the WUS gene the SHOOTMERISTEMLESS (STM) gene also represses the differentiation of the meristematic dome. This gene acts by inhibiting the possible differentiation of the stem cells but still allows cell division in the daughter cells, which, had they been allowed to differentiate, would have given rise to distinct organs.

- A flower's anatomy, as defined by the presence of a series of organs (sepals, petals, stamens and carpels) positioned according to a given pattern, facilitate sexual reproduction in flowering plants. The flower arises from the activity of three classes of genes, which regulate floral development:

•**Meristem identity genes**, which code for the transcription factors required to initiate the induction of the identity genes. They are positive regulators of organ identity during floral development.

- **Organ identity genes**, which directly control organ identity and also code for transcription factors that control the expression of other genes, whose products are implicated in the formation or function of the distinct organs of the flower.

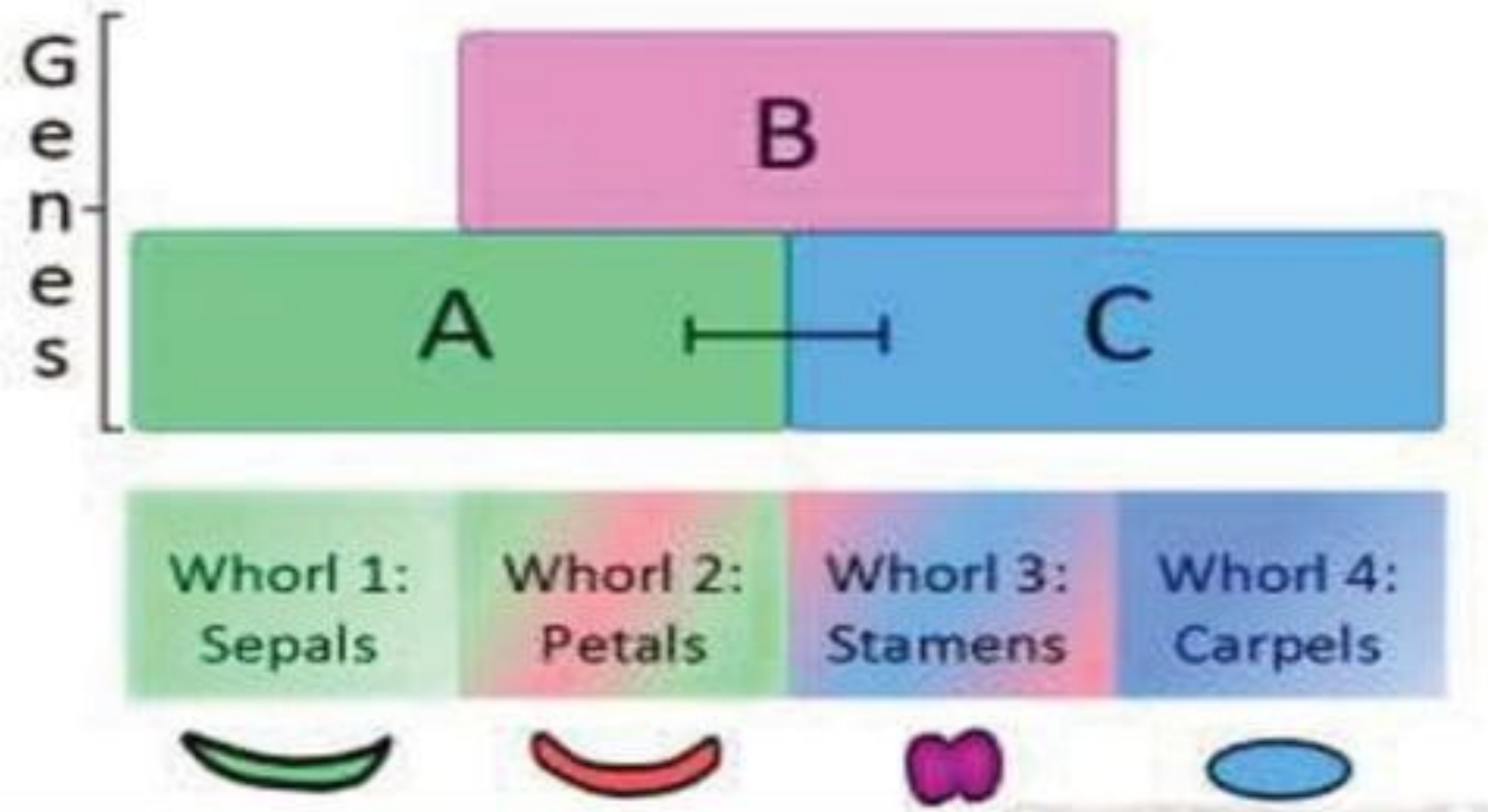
- **Cadastral genes**, which act as spatial regulators for the organ identity genes by defining boundaries for their expression. In this way they control the extent to which genes interact thereby regulating whether they act in the same place at the same time.



- The **ABC model of flower development** is a scientific model of the process by which flowering plants produce a pattern of gene expression in meristems that leads to the appearance of an organ oriented towards sexual reproduction, **(a flower).**

- In the early 1990's, genetic studies on **Arabidopsis thaliana** and **Antirrhinum majus** led to the isolation and characterization of floral-organ identity genes **(Floral homeotic genes)** and the establishment of the seminal ABC model for flower development.
- This model proposed that different organ- identity genes act alone and in various combinations to specify each of the four types of floral organs.

ABC model

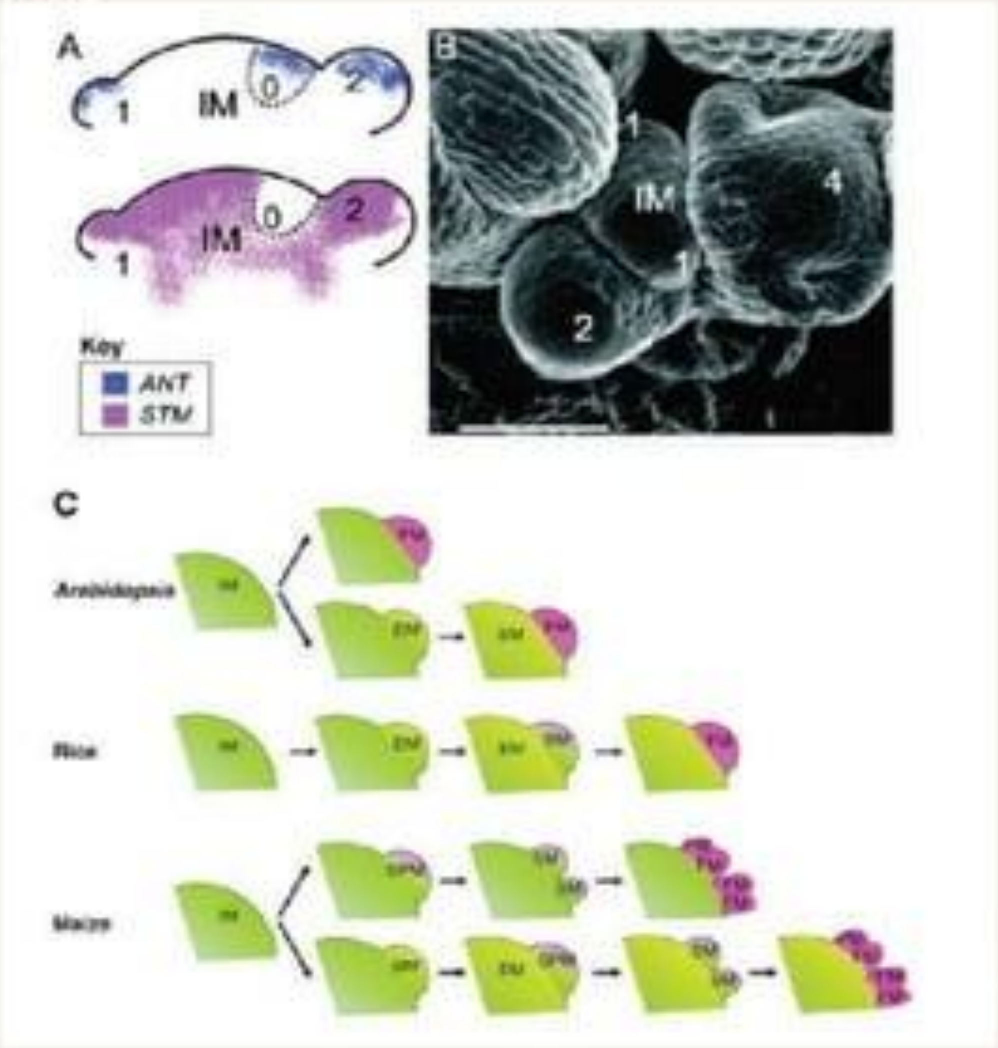

Genes
B
A
C
Whorl 1: Sepals
Whorl 2: Petals
Whorl 3: Stamens
Whorl 4: Carpels

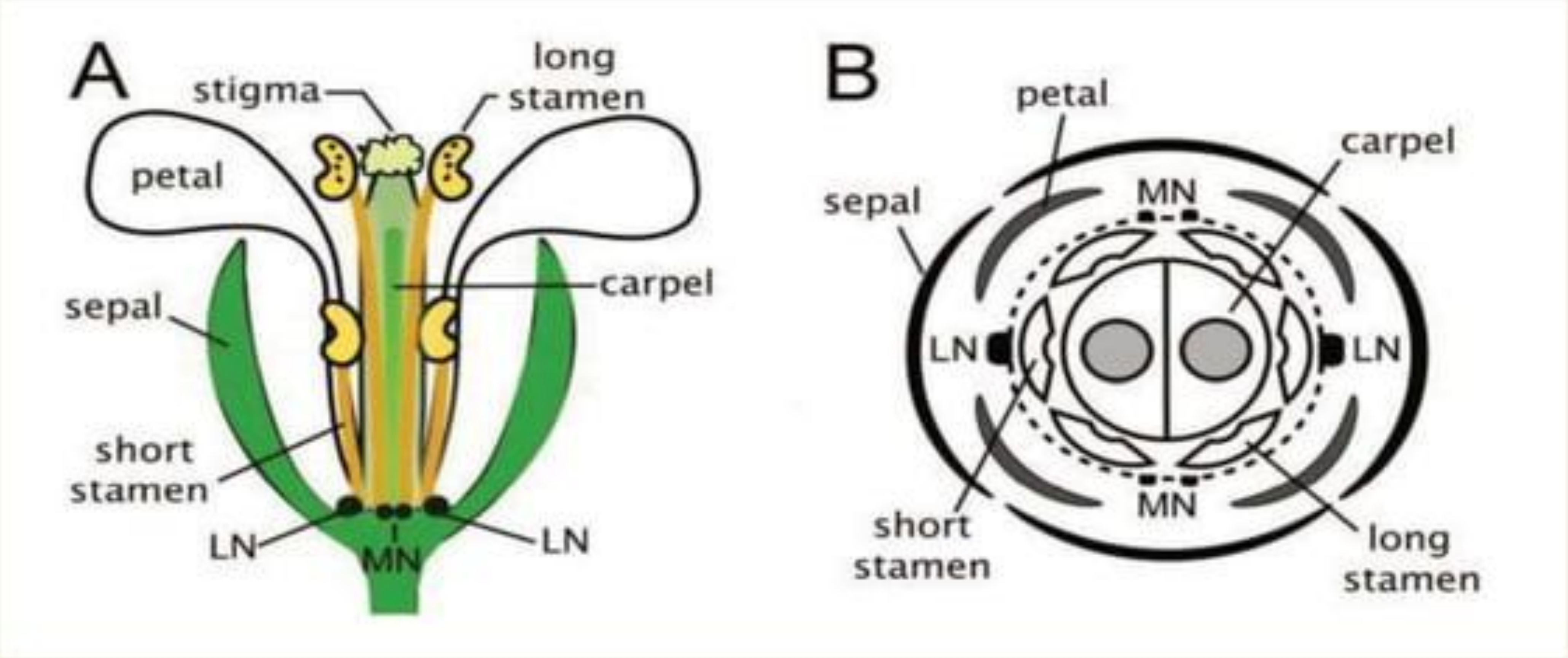
- The ABC model of flower development was first formulated by **George Haughn** and **Chris Somerville** in 1988.
- It was first used as a model to describe the collection of genetic mechanisms that establish floral organ identity in the **Rosids**, as exemplified by ***Arabidopsis thaliana,*** and the **Asterids,** as demonstrated by ***Antirrhinum majus***.

- The ABC model of flower development in angiosperm demonstrates the presence of three classes of genes that regulate the development of floral organs.
- The genes are referred to as **Class A genes**, **Class B genes**, and **Class C genes**.

  These genes and the interaction between them induce the development of floral organs.
- During reproductive development.

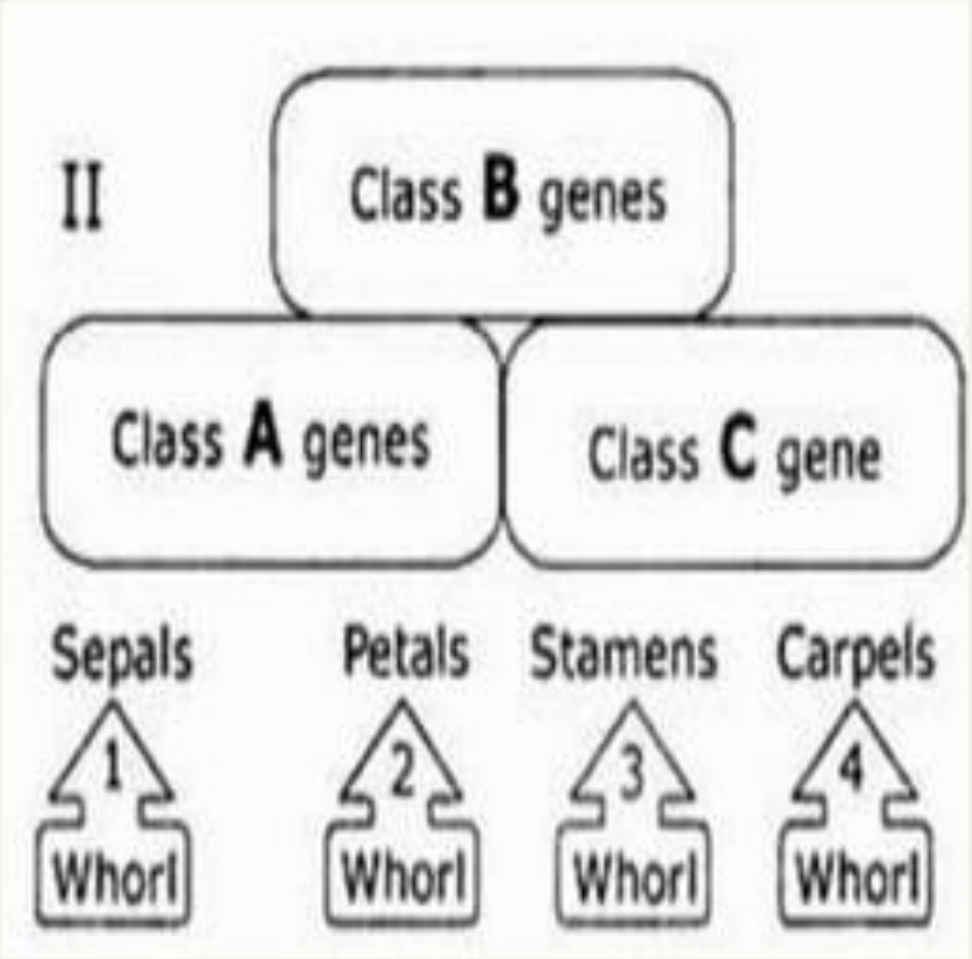
  The **shoot apical meristems (SAM)** initiates **floral meristems (FMs)** along its flanks.





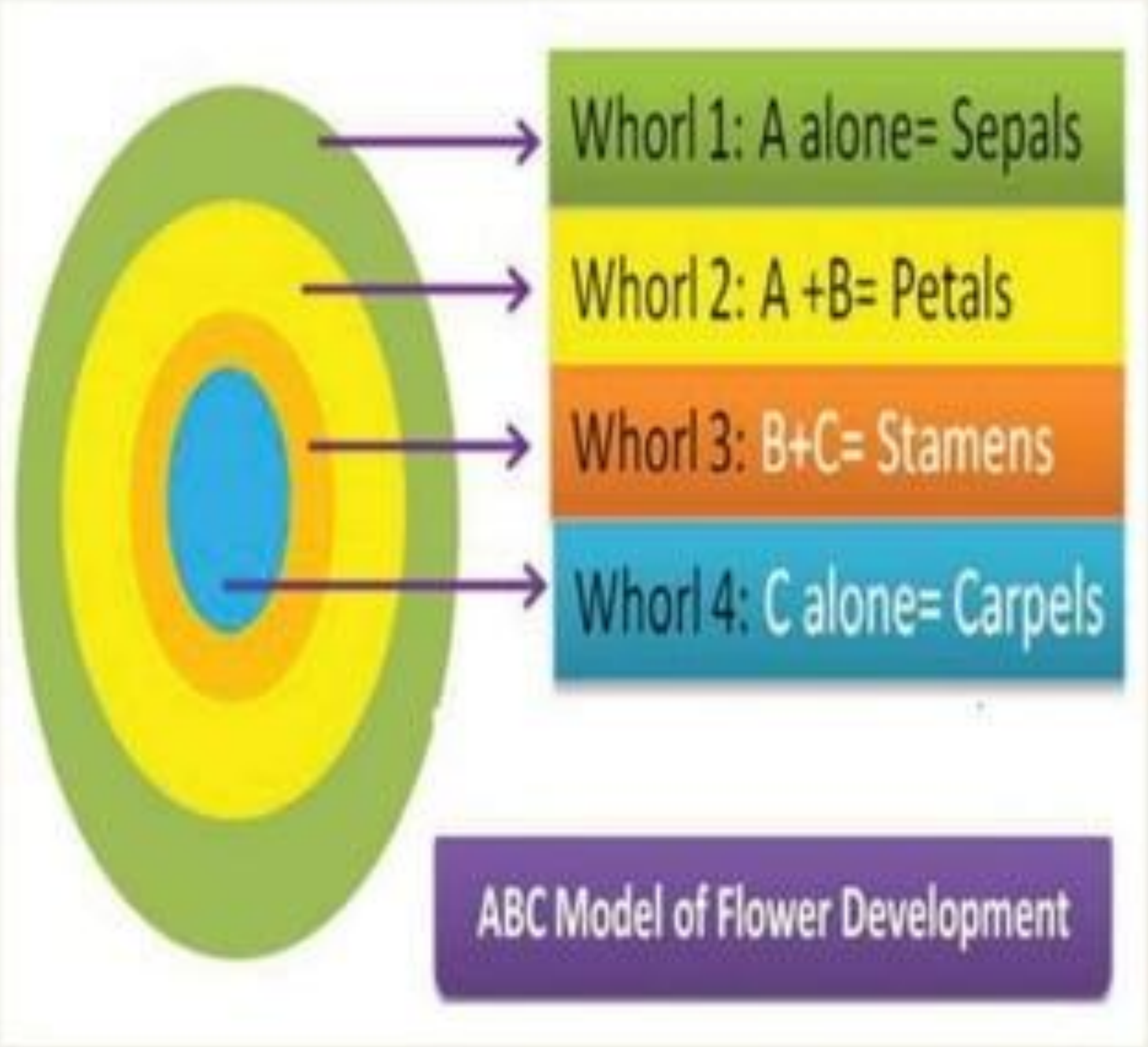
- The identities of these different organs are specified by the actions of floral organ- identity genes in different regions of a developing flower.

- The ABC model for flower development proposed that three classes of these organ identity genes functions in overlapping domains to specify:



- In the flower of angiosperms there are usually four concentric whorls of organs, **(i.e. sepal, petal, stamen, and carpel)** that are form in whorl 1, whorl 2, whorl 3, and whorl 4 respectively, the whorl 1 being on the peripheral side.

- The identities of different organs are specified by the actions of floral organ-identity genes in different regions of developing a flower.



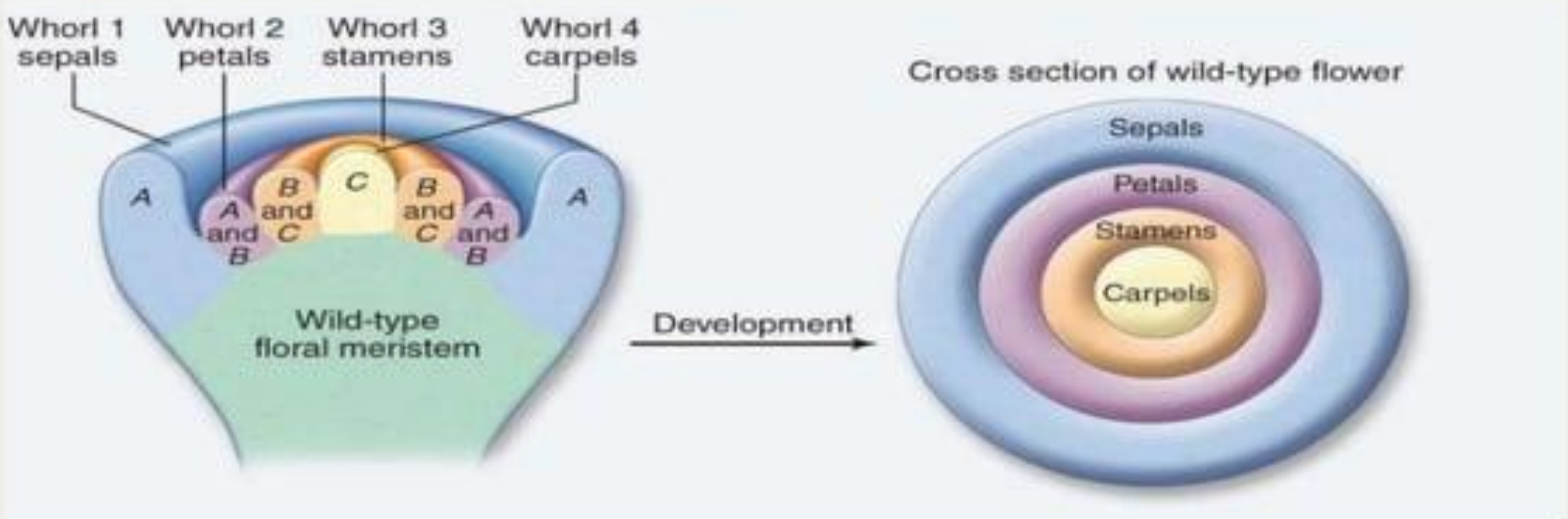
Whorl 1: A alone= Sepals

Whorl 2: A +B= Petals

Whorl 3: B+C= Stamens

Whorl 4: C alone= Carpels

ABC Model of Flower Development

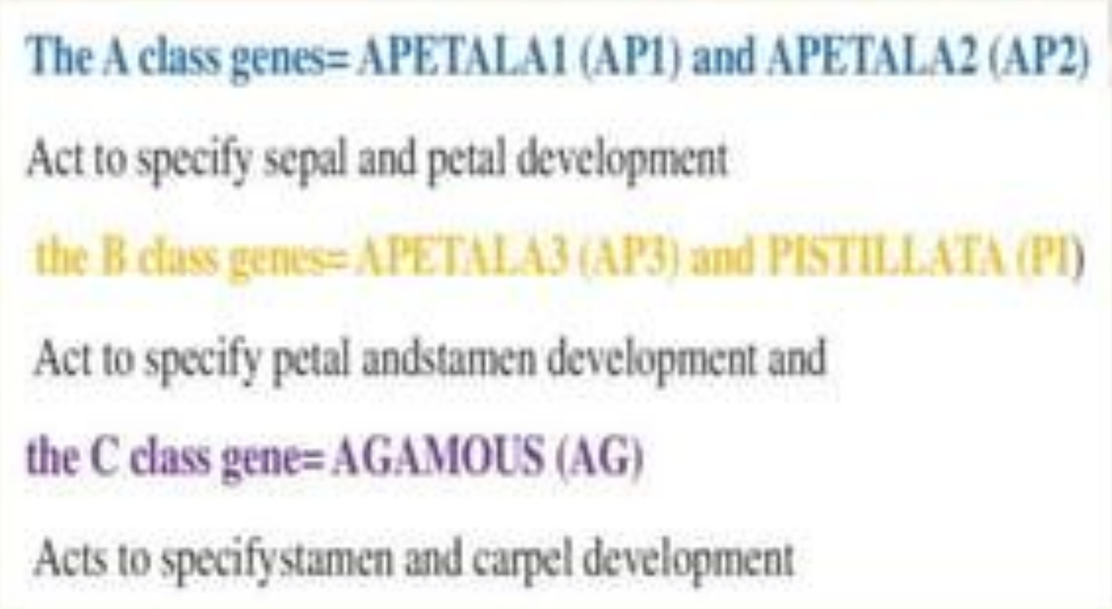


Where, in the **whorl 1 (Class A genes)** when it is expressed it induce the development of sepals.

Where, the interaction of **Class A** & **Class B genes** induce the development of petals in the whorl 2. **Stamens** are formed in the whorl 3 as a result of interaction between **Class B** & **Class C genes.**

Where, in the **whorl 4 (Class C genes),** it induces the formation of carpel.

- So therefore, the **ABC model** is that:
- **Class A genes** together with **Class C genes** alone are responsible for the development of sepals and carpel respectively.
- The **Class B genes** and **Class A genes** function cooperatively to determine the development of petals.
- The **Class B genes** and **Class C genes** acts together to induce the development of stamens. ***(or it goes this way)***



The A class genes= APETALA1 (AP1) and APETALA2 (AP2)

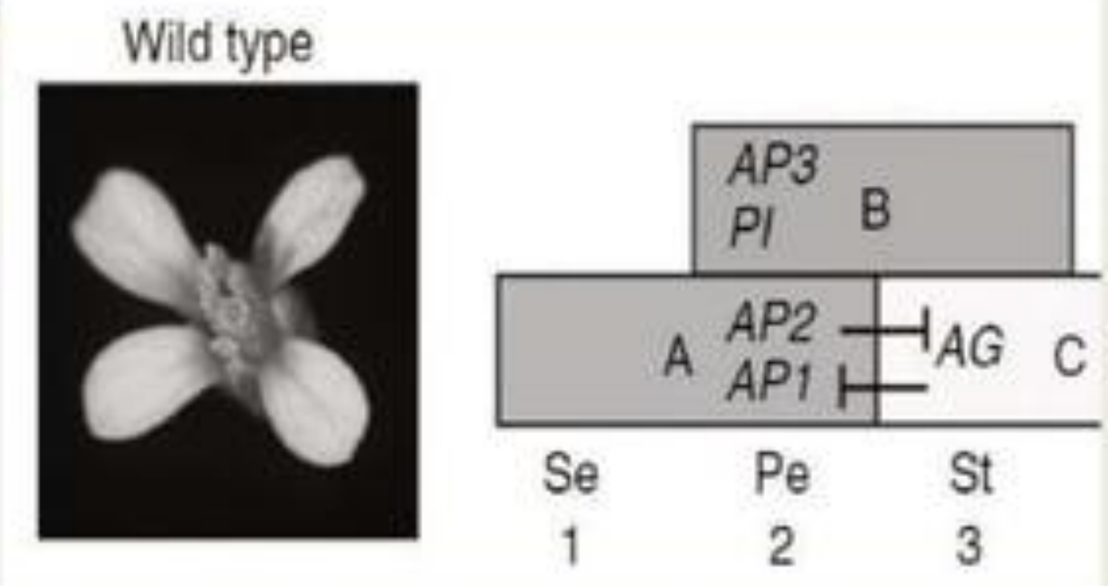
Act to specify sepal and petal development

the B class genes= APETALA3 (AP3) and PISTILLATA (PI)

Act to specify petal andstamen development and

the C class gene= AGAMOUS (AG)

Acts to specifystamen and carpel development



- It was **Coen et al., (1991)** formulated the ABC model while analyzing the mutations affecting flower structure they identified the class ABC genes that direct flower development.
- They also formulated the molecular models of how floral meristem and organ identity may be specified.
- They have shown that the distantly related angiosperm plants use homologous mechanism in pattern formation of floral organs.
- **i.e. *Arabidopsis thaliana*** and ***Antirrhinum majus***
- The following two have led to formulate the ABC model:

1. The discovery of homeotic mutants **(homeotic genes identify specific floral organs and help the organ to develop in respective whorl)**. The homeotic mutants has inappropriate expression – that it, it induces right organ to develop in wrong whorl. **(i.e. petals emerge in the whorl where normally stamens develop).**

2. The observation that each of the genes tat induce the formation of an organ in a flower has an effect on two groups of floral organs, **(i.e. sepal** and **petals or petals and stamens)**

- **Class A** and **Class B genes** are homeotic genes. They determine the identity of different floral organs and induce the organs to develop in their respective whorls.
- The **homeotic mutants** have defects in floral organ development and induce the right organs to develop in wrong whorls/place.

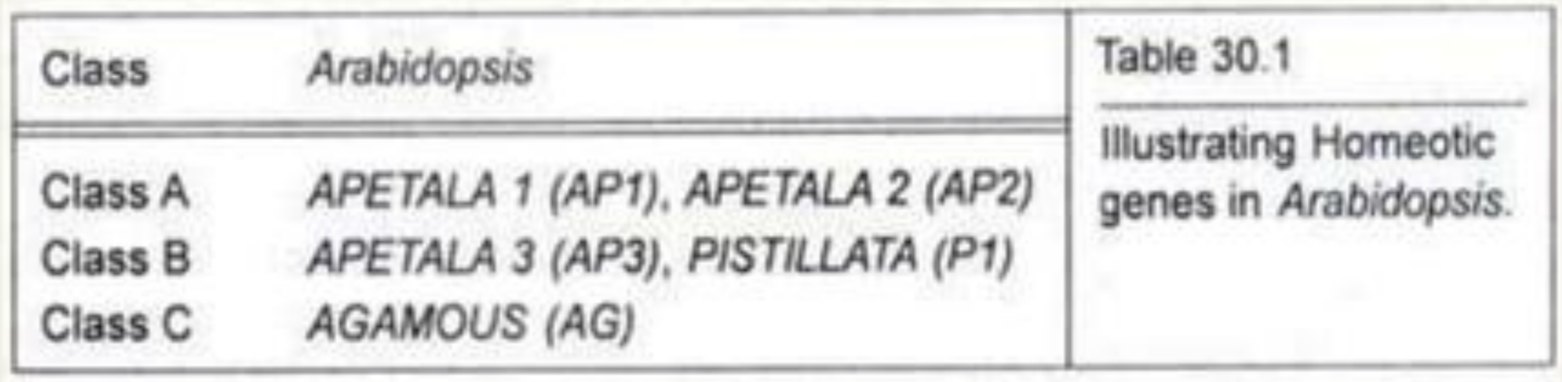
i.e. one floral organ develops in the whorl, which is the normal position of another floral organs.
Petals for example develop in the whorl where stamens are normally to be formed.

- In each whorl of a flower there is one or more homeotic genes and their cooperative functions determine the organ to be formed in that whorl.

i.e. the activity of Class A gene is restricted to whorls 1 & 2. The Class B gene have function in whorls 2 & 3. The

- Another was of describing the function of **Class A**, **B**, and **C genes** is that – in **whorl 1**, the Class A gene function alone determines the formation of sepals. In **whorl 2**, Class A & B gene functions both determine the formation of petals. In **whorl 3**, Class B & C gene functions both determine the emergence of stamens and in **whorl 4**, Class C gene function alone determines the carpel formation.

- In ***Arabidopsis thaliana*** there are two genes in class A, two genes in class B, and one gene in class C.
- The most characteristic feature of these homeotic genes is in the identification of floral organs and in the determinacy of position or in the whorl of their emergence in a floral meristem.
- The two genes of class A and the two genes of class B act cooperatively.

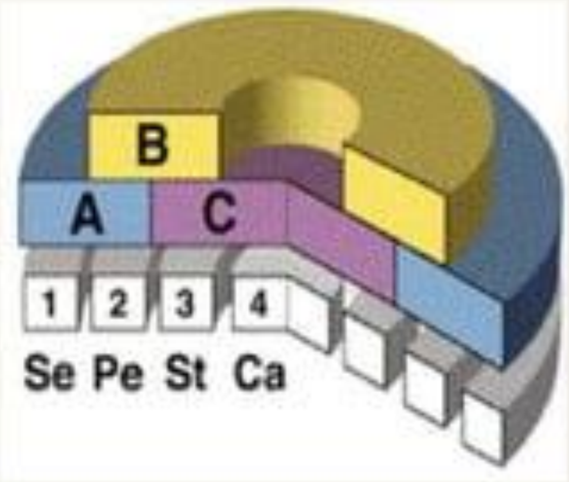


Class	*Arabidopsis*
Class A	*APETALA 1 (AP1), APETALA 2 (AP2)*
Class B	*APETALA 3 (AP3), PISTILLATA (P1)*
Class C	*AGAMOUS (AG)*

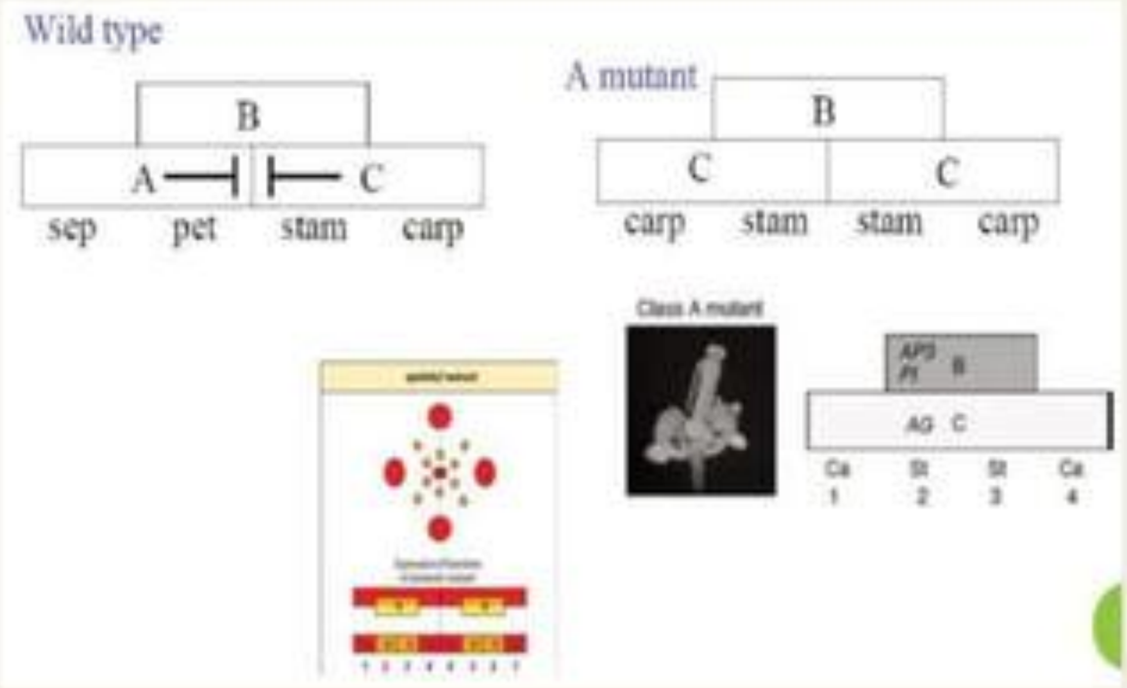
Table 30.1

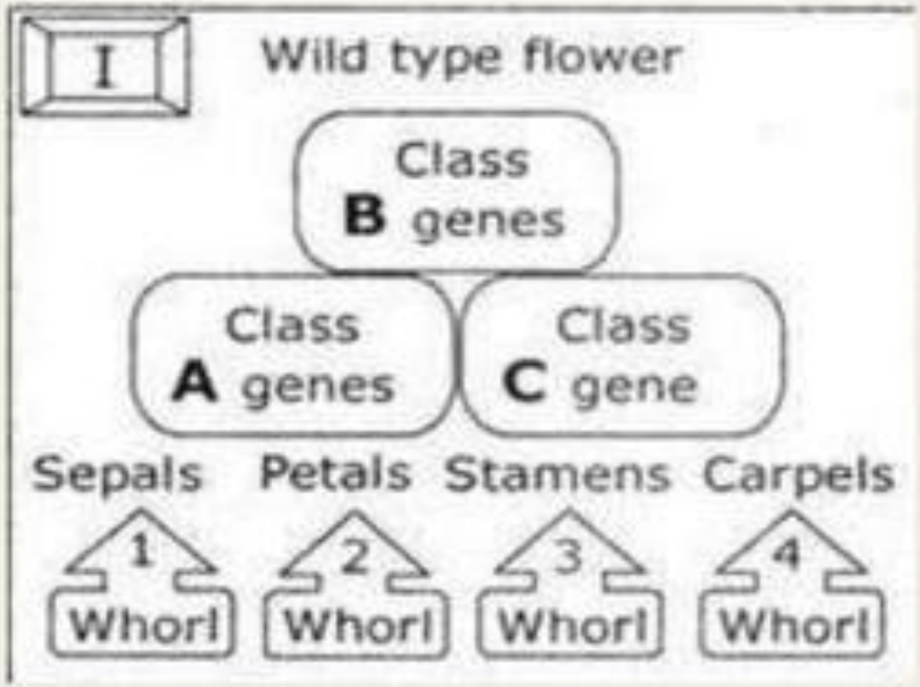
Illustrating Homeotic genes in *Arabidopsis*.

- The function of class A genes is confined to whorls 1 & 2. Similarly the functions of class C gene is restricted in whorl 3 & 4.
- This can be interpreted in another way. In the whorls 1 & 2 the function of class A genes prevents class C gene from functioning in the same whorls.
- Similarly, the function of class C gene prevents class A genes from functioning in whorl 3 & 4.



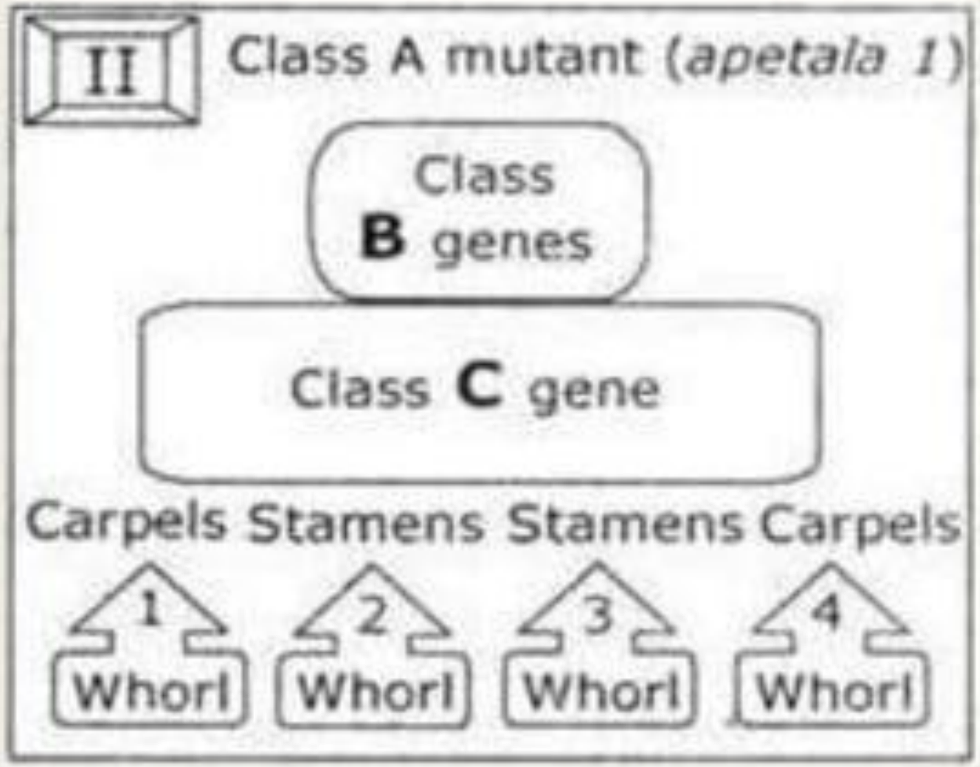
- Any mutation in class A with defects in floral organ development will invite class C gene to express whorl 1 & 2. the class C gene, in class A mutants, will express in whorl 1 & 2 in addition to the normal whorls 3 & 4.
- Similarly, any mutations in class C gene with defects in floral organ development will lead to the encroachment of the function of class A genes.
- The class A genes will express in the whorls 3 & 4 in addition to the normal whorls 1 & 2.
- **Mutations** in the class **A gene AP2** result in **C activity** spreading into whorls 1 and 2, and consequently homeotic transformations in organ identity with carpels replacing sepals in whorl 1 and stamens replacing petals in whorl 2.





Wild type flower, the individual and cooperative expressions of class A, B, & C genes are in the formation of sepals, petals, stamens and in whorls 1,2,3 & 4 respectively.

- **Class A mutant, *apetala 1*.** this homeotic mutant contains loss –of – function A genes. **class C genes** expresses alone in whorl 1 in addition to whorl 4. Class C genes & class B genes together expresses in whorls 2 & 3, as a result stamens are formed in both whorls 2 & 3.

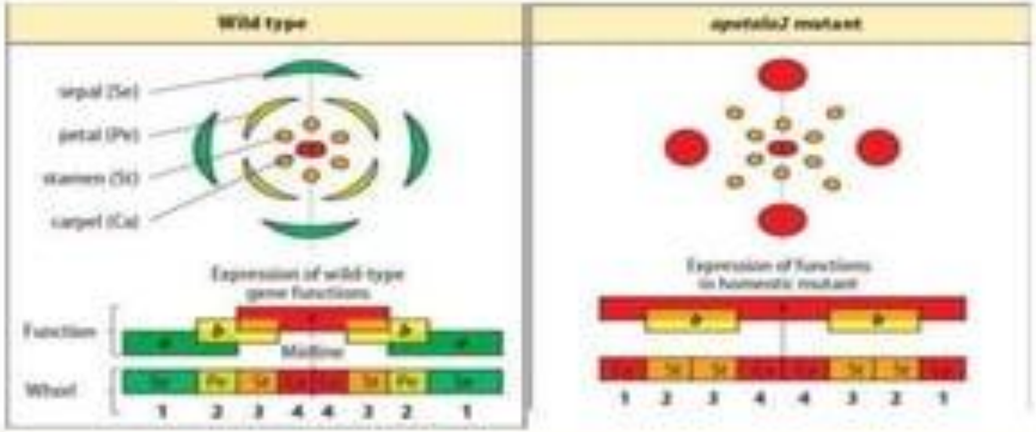


apetala2

apetala2

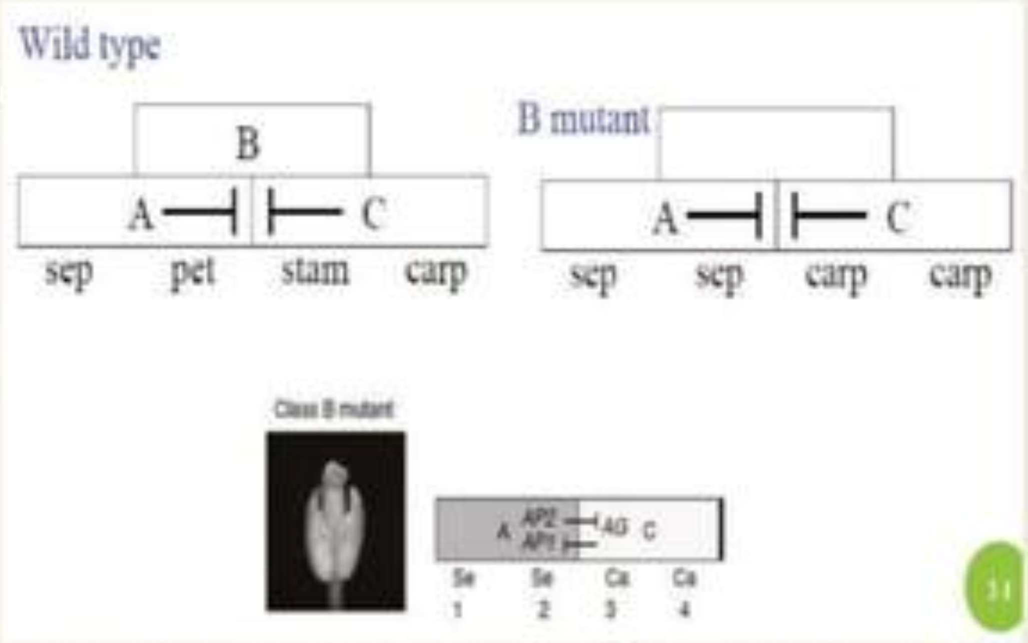
Wild-type

Sepals → carpelloid organs
petals → Absent or stamenoid
stamens → normal
carpels → normal

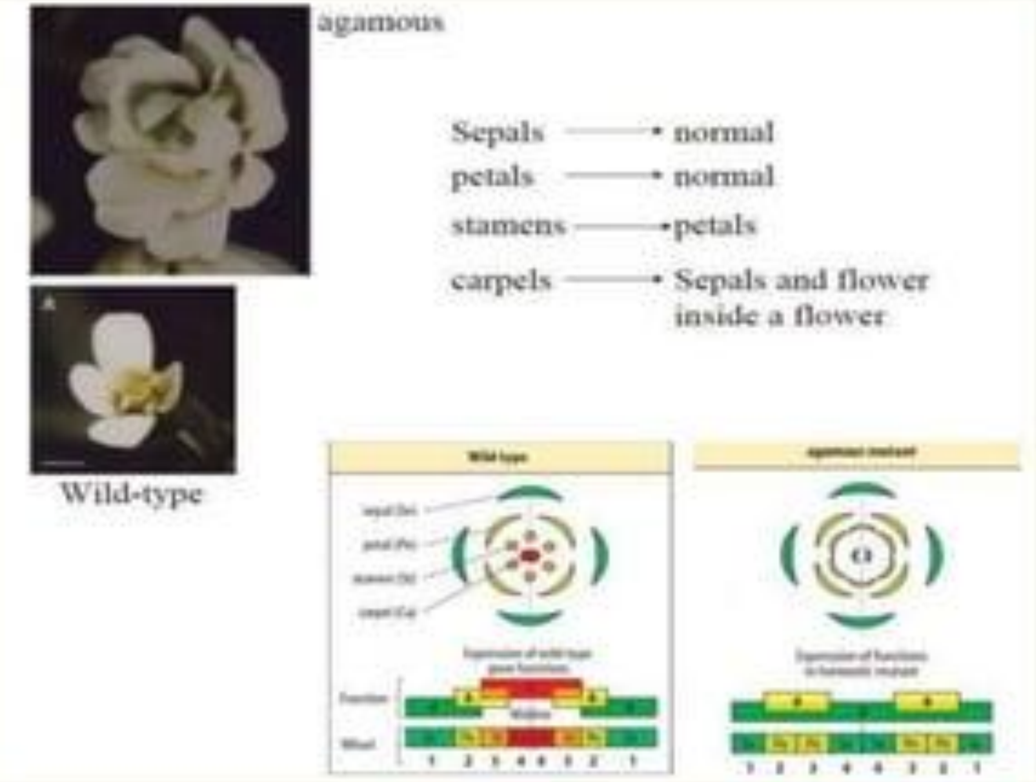


- **Mutations** in the class **B genes** result in flowers with sepals in the outer 2 whorls and carpels in the inner 2 whorls.

- **Class B mutant (*apetala 3*),** contains loss-of-functions B genes. Class A genes express in whorls 1 & 2. As a result sepals are formed in both whorls 1 & 2.
  Class C genes expresses in whorls 3 & 4, so carpels are formed in both whorls 3 & 4.



- **i.e.** Flower of Arabidopsis withc class B mutant , such as apetala (ap3), the flower shows sepals only both in whorls 1 & 2, while the whorls 3 & 4 shows the carpel only.
- **Class B mutant** contains loss-of-function genes and as a result class A genes express in whorls 1 and 2; and class C genes alone expresses in whorls 3 & 4.
- In ap3 mutants in whorls 2, sepal are formed instead of petals and in whorl 3, carpel is formed instead of stamens.



- **Mutations** in the class **C gene AG** result in class A activity in all four whorls.

- The **ag mutants** produced indeterminate flowers repeating the organs **(Se Pe Pe)n**

- In **Arabidopsis** the class C genes contains the sole genes **agamous (ag).**

- **Arabidopsis** flower with agamous (ag) mutant consist of many sepals and petals.

- The reproductive organs – stamens and carpel are not formed in the whorls 3 & 4.

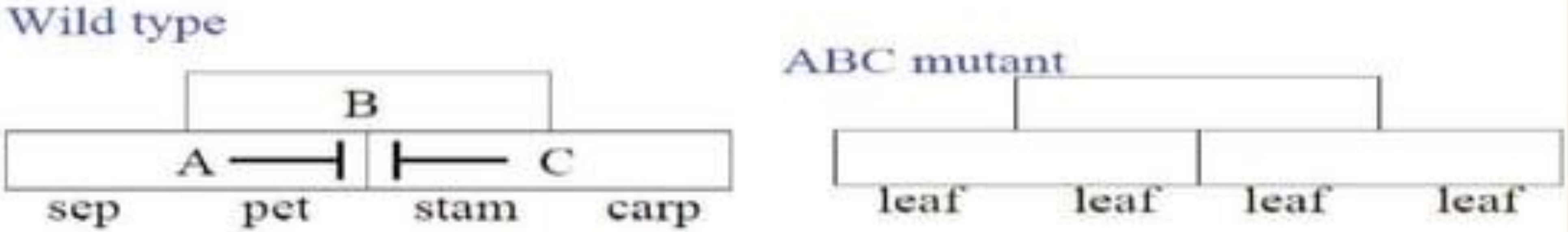
- **Class C genes** with ag mutant contains loss-of-function gene. As a result class A genes express in whorls 3 & 4 in addition to 1 & 2.

- In ag mutant sepals and petals are formed in whorls 3 & 4 instead of stamens and carpel.

- In **Arabidopsis**, however, it was observed that in all mutants one homeotic gene remains functional in each whorl. The flower with class ABC triple mutant shows sepals in each whorl.

- In **ABC triple mutant** the gene required for floral organ formation become non functional. As a result sepals or leaves are formed in each whorl , as homeotic mutants specify no floral organs.

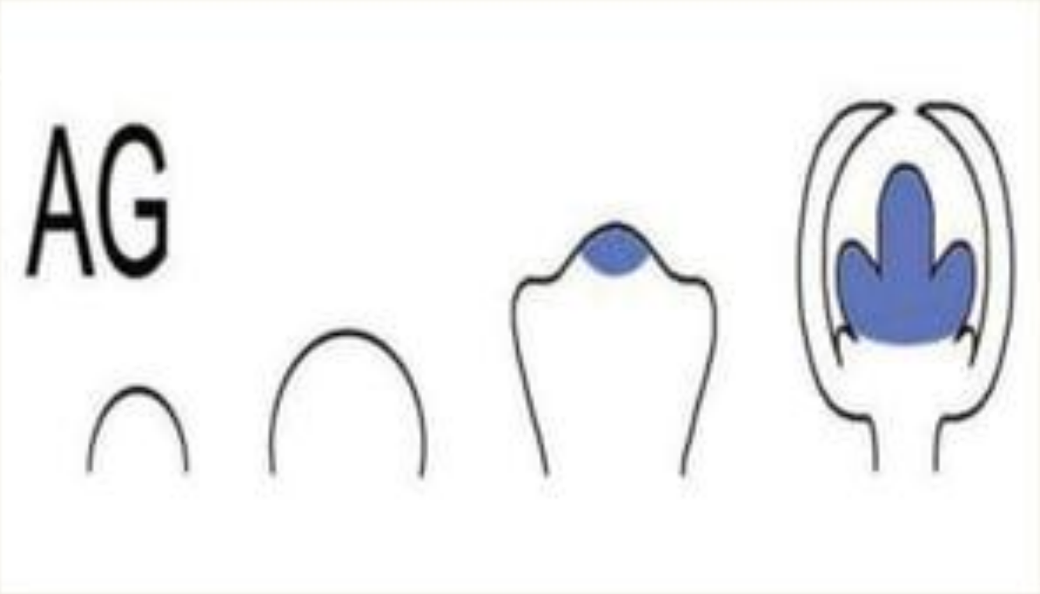
- The **ABC triple mutant** produce indeterminate flowers consisting only of leaf-like organs.

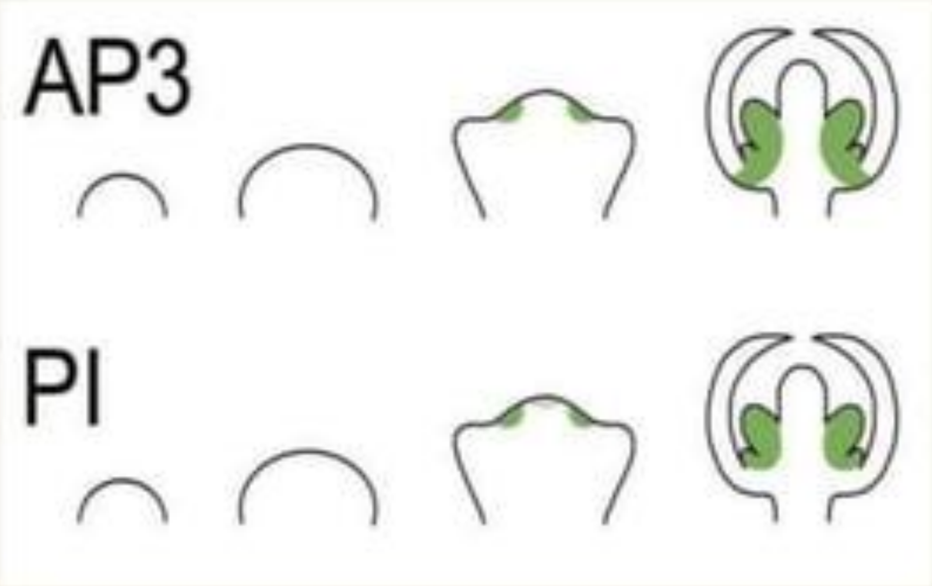


ap2 pi ag triple mutant / loss of ABC function

All whorls leaf like

- The organ identity genes are expressed at the RNA level in spatially restricted regions of a FM consistent with the activities of these genes as proposed in the ABC model.
- Gene **ag** is expressed in cells that will give rise to the 3rd & 4th whorls of a flower and subsequently in developing stamen and carpel primordial.





B genes are expressed in largely overlapping domains that correspond to 2nd & 3rd whorl cells and later in petal and stamen primordial.

- The important feature of ABC model is that it can predict the type of floral organ to be induced to develop in any whorl.
- **Krizek et al., (1996),** was successful to induce any of the 4 different floral parts in whorl 1 of Arabidopsis flower.
- This became possible by genetic manipulations of right combination of homeotic selector genes.
- The ABC model appears to be simple but a completely different picture is obtained when it is analyzed on the basis of molecular genetics and in molecular terms.
- The analysis includes the structure of different classes of homeotic genes, the homeotic mutants, the co-operative function between homeotic genes, mutual exclusion in expression of class A and C genes in the same whorl, the identification of floral homeotic genes and their isolation by cloning, the production of MADS box protein by homeotic mutants, and others.

- As for **Arabidopsis thaliana**, it belongs to the family Brassicaceae and has become the model organism for understanding the genetics and molecular biology of the flowering plants like that of **mice** and **Drosophila** in animal researches due to the following reasons:

- 1. it has 5 chromosome (n=5) and so this small-size-genome is advantageous in gene mapping and sequencing.

- 2. the size of plant is small and so can be cultivated in a small space and requires modest indoor facilities.

- 3. it has rapid life cycle and take about 6 weeks from germination to mature seeds.

- 4. an individual plant produces several thousands seeds.

- 5. the **Arabidopsis** genome is among the smallest in higher plants, with a haploid size of about 100 megabases (mb) of DNA. With a small genome size it was expected that 3 would be fewer with gene duplication.

- 6. it is easily transformable wit T-DNA mediated transformation.

- Such that, all of the class **A, B, C & E** genes except for AP2 code for members of the **MADS-** domain family od dimeric transcription factors.

- **MADS** is an acronym for the first 4 identified members of the family:

- **MCMI =** yeast
- **AG =** Arabidopsis
- **DEFCIENS (DEF) =** Antirrhinum
- **SRF** = humans

- The proteins share a 56 amino acids DNA – binding domain called the MADS domain and bind to CArG box [CC(A/T) 6GG] sequence.

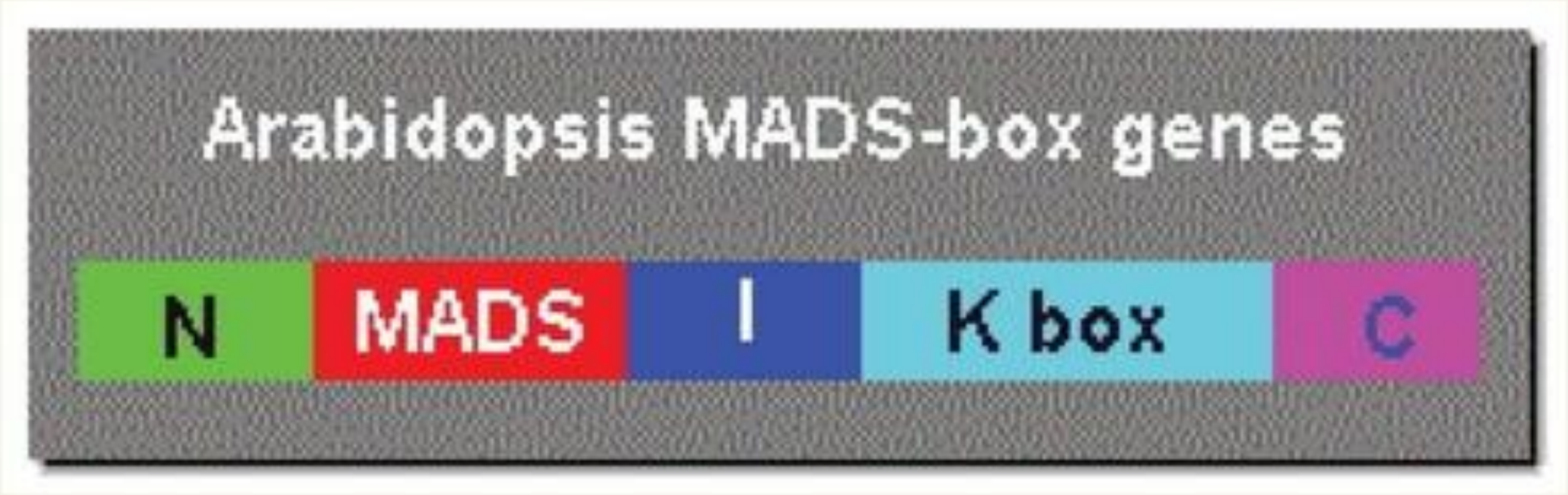
- The floral homeotic MADS box gene in:
  - ***Arabidopsis*** is AGAMOUS
  - ***Antirrhinum*** is DEFCIENS

- The length of the MADS- box are in the range of 168 to 180 base pairs

Types of Genes

- House Keeping Genes
- Non-constitutive Genes
- Structural Genes (Cistrons)
- Pseudogenes
- Transposons (Jumping Genes)
- Single Copy genes
- Processed genes
- Overlapping genes.

- In plants, MADS-box genes are involved in controlling all major aspects of development, including male & female gametophyte development, embryo and seed development, as well as root, flower, fruit development, floral organ identity and flowering time determination.



Structure of plant MADS box transcription factors

- MADS transcription factor

- MADS - DNA binding
- I - Intervening region : contributes to dimerization specificity
- K - Protein- protein interactions : form a coiled-coil structure and is also involved in dimerization of these proteins
- C - Carboxy – terminal domain: acts as a transcriptional activation domain in some family members

- Bind DNA through a conserved DNA sequence called CArG Box – CC(A/T)6GG

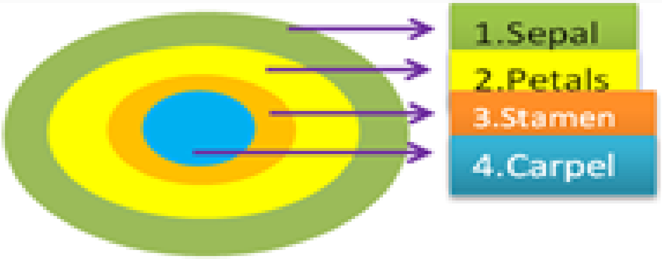
ABC Model of Flower Development

Whorl 1: Sepal A alone	Whorl 2: Petal (A+B)	Whorl 3: Stamen(B+C)	Whorl 4: Carpel C alone

A

C

B



ABC Model

Case 1: mutation in A gene

Whorl 1: Carpel C alone	Whorl 2: stamen (C+B)	Whorl 2: stamen (C+B)	Whorl 4: Carpel C alone

C

C

B

apetala 2

Case 2: mutation in B gene

Whorl 1: Sepal A alone	Whorl 2: Sepal A alone	Whorl 3: Carpel C alone	Whorl 4: Carpel C alone

A

C

apetala 3

Case 3: mutation in C gene

Whorl 1: Sepal A alone	Whorl 2: Petal (A+B)	Whorl 3: Petal (A+B)	Whorl 4: Sepal A alone

A

A

B

agamous

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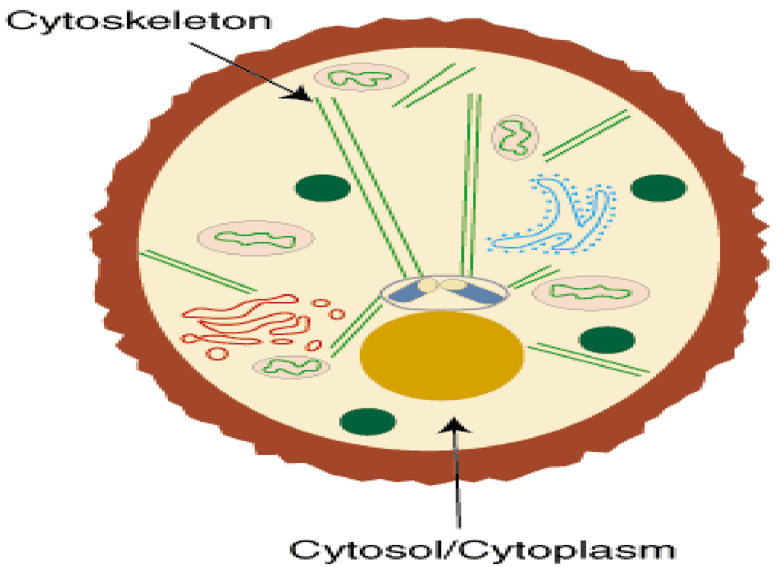
- Early studies showed that although all of the class A, B, & C MADS domain proteins could interact with each other.
- Only certain combinations (API homodimers, AP3/PI heterodimers and AG homodimers in Arabidopsis) could bind DNA in vitro.
- Hence, the ABC classes of genes act alone, or with combination to specify the 4 four types of floral organs.
- The ABC genes are sufficient to convert vegetative meristem to floral meristem and finally flowers are generated.
- The ABC model is applicable to all flowering plants.

The Cytosol

- In this section we will discuss the intracellular components that are not organelles. The cytoskeleton and cytosol are structural elements that help provide the cell with its structure.
- The cytoskeleton is composed of protein filaments and is found throughout the inside of a eukaryotic cell. The cytosol is the main component of the cytoplasm, the fluid that fills the inside of the cell.
- The cytoplasm is everything in the cell except for the cytoskeleton and membrane-bound organelles. Both structures, the cytoskeleton and cytosol, are "filler" structures that do not contain essential biological molecules but perform structural functions within a cell.



- The interior of a cell is composed of organelles, the cytoskeleton, and the cytosol. The cytosol often comprises more than 50% of a cell's volume.
- Beyond providing structural support, the cytosol is the site wherein protein synthesis takes place, and the provides a home for the centrosomes and centrioles. These organelles will be discussed more with the cytoskeleton.

The Cytoskeleton

- The cytoskeleton is similar to the lipid bilayer in that it helps provide the interior structure of the cell the way the lipid bilayer provides the structure of the cell membrane.
- The cytoskeleton also allows the cell to adapt. Often, a cell will reorganize its intracellular components, leading to a change in its shape.

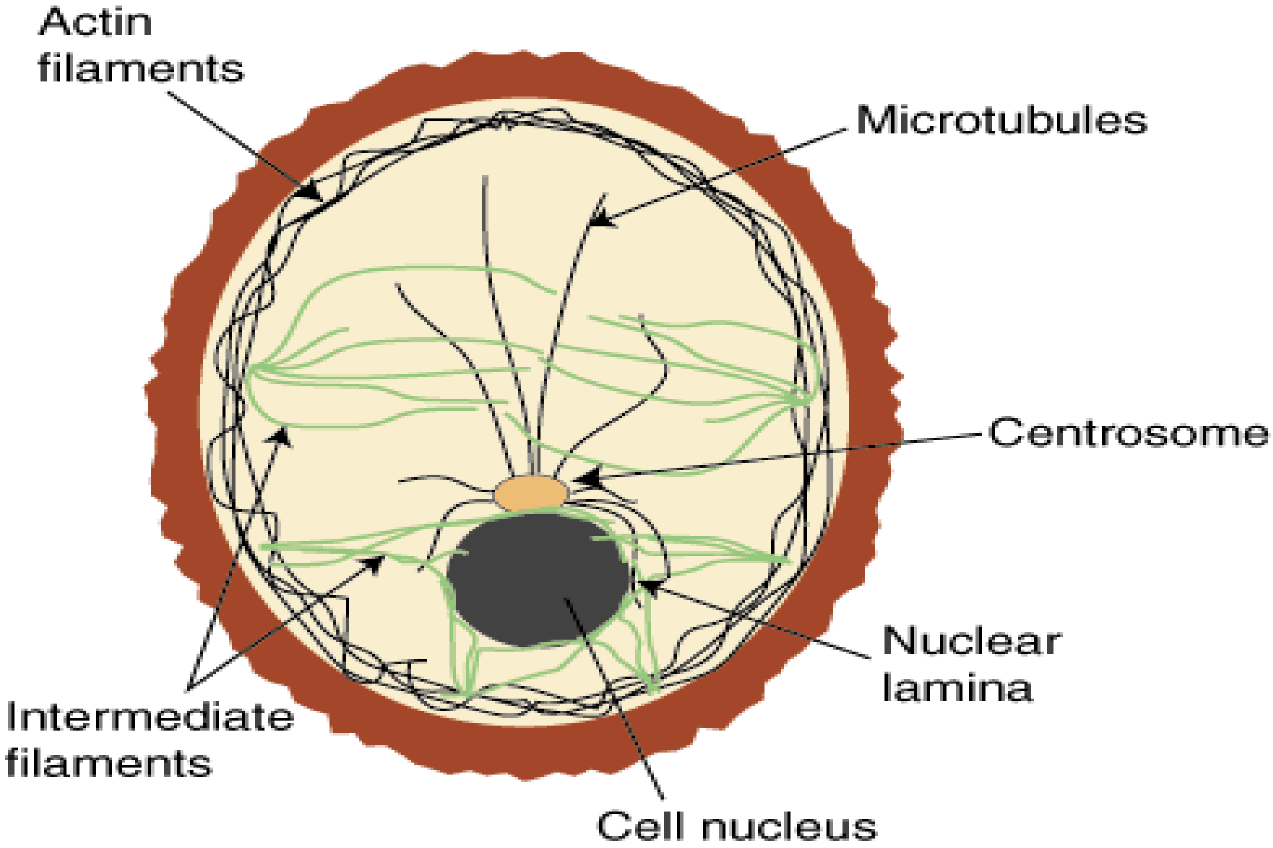
- The cytoskeleton is responsible for mediating these changes. By providing "tracks" with its protein filaments, the cytoskeleton allows organelles to move around within the cell.
- In addition to facilitating intracellular organelle movement, by moving itself the cytoskeleton can move the entire cells in multi-cellular organisms. In this way, the cytoskeleton is involved in intercellular communication.
- The cytoskeleton is composed of three different types of protein filaments: actin, microtubules, and intermediate filaments.

ACTIN

- Actin is the main component of actin filaments, which are double-stranded, thin, and flexible structures. They have a diameter of about 5 to 9 nanometers.
- Actin is the most abundant protein in most eukaryotic cells. Most actin molecules work together to give support and structure to the plasma membrane and are therefore found near the cell membrane.

Microtubules

- Microtubules are long, cylindrical structures composed of the protein tubulin and organized around a centrosome, an organelle usually found in the center of the cell near the cell nucleus. Unlike actin molecules, microtubules work separately to provide tracks on which organelles can travel from the center of the cell outward.



- Microtubules are much more rigid than actin molecules and have a larger diameter: 25 nanometers. One end of each microtubule is embedded in the centrosome; the microtubule grows outward from there. Microtubules are relatively unstable and go through a process of continuous growth and decay. Centrioles are small arrays of microtubules that are found in the center of a centrosome. Certain proteins will use microtubules as tracks for laying out organelles in a cell.

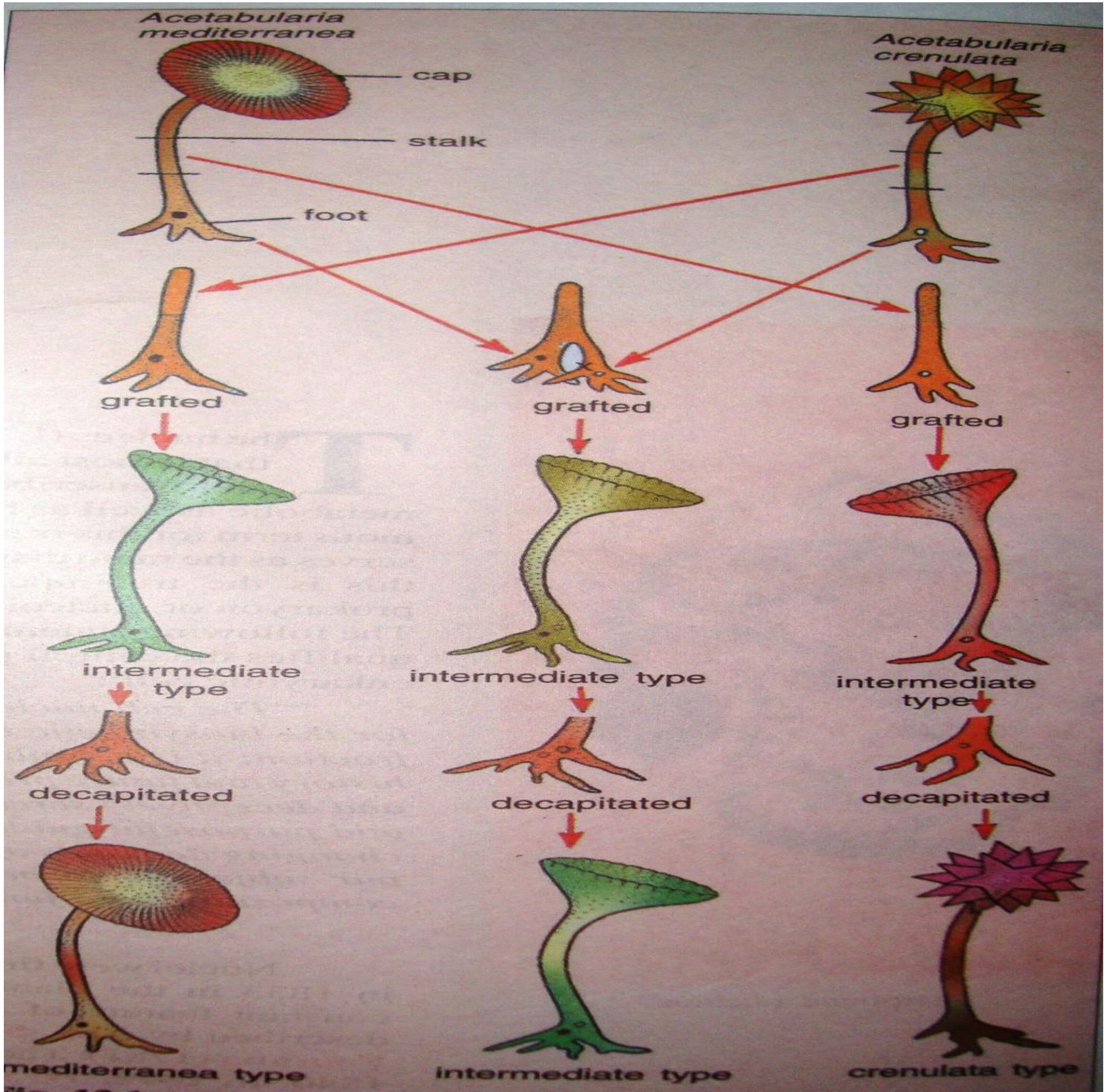
Intermediate filaments

- Intermediate filaments are the final class of proteins that compose the cytoskeleton. These structures are rope-like and fibrous, with a diameter of approximately 10 nanometers. They are not found in all animal cells, but in those in which they are present they form a network surrounding the nucleus often called the nuclear lamina. Other types of intermediate filaments extend through the cytosol. The filaments help to resist stress and increase cellular stability.

Nuclear transplantation experiments with *Acetabularia*

Hammerling’s Acetabularia grafting experiment

- Hammerling’s Acetabularia grafting experiment that established nucleus as the store house of hereditary material.
- Hammeling’s grafting experiment using Acetabularia cleared all speculations and confirmed the role of nucleus in heredity.
- His experimental material Acetabularia is a large single celled uni-nucleate alga.
- The algal body is 6cm long consists of a foot a stalk and a cap(largest unicelled organism).
- The upper cap or crown has a characteristic shape for each species. Cap has the regeneration potential if damaged or removed. The single nucleus is seen in the rhizoid region.
- He took two species for the experiment, *A.mediterranea* with a characteristic cap of 81 rays and rounded tips and *A.crenulate* with a cap of 31 rays and pointed tips. The algae are capable of regeneration from any part.


Acetabularia mediterranea
cap
stalk
foot
Acetabularia crenulata
grafted
grafted
grafted
intermediate type
intermediate type
intermediate type
decapitated
decapitated
decapitated
mediterranea type
intermediate type
crenulata type

Experiment:1

- *A.crenulate* (stalk) + *A.mediterranea* (rhizoid with nucleus) regenerated to intermediate type cap->stalk removed a regenerated from rhizoids into *A.mediterranea* type cap (rhizoid with 2 nucleus or nuclear donor).

Experiment:2

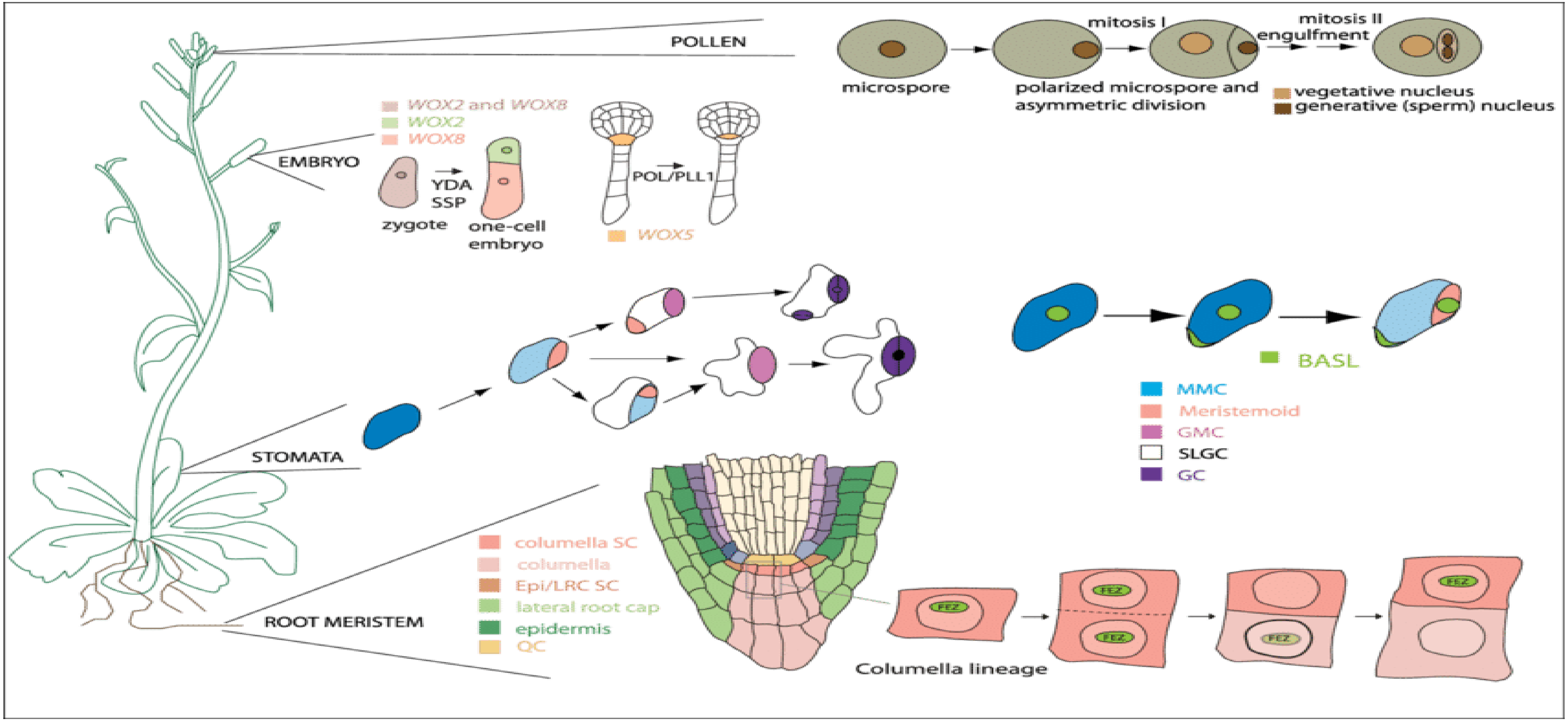
- *A.crenulata* (rhizoid with nucleus) + *A.mediterranea* (rhizoid with nucleus)->regenerated to intermediate type cap->stalk removed a regenerated from rhizoids into intermediate type cap (rhizoid with 2 nuclei from both species, charater of both the species as both nuclei are present in a common cytoplasm)

Experiment:3

- *A.Cerenulata* (rhizoid with nucleus) + *A.mediterranea* (stalk without nucleus) regenerated to intermediate from rhizoids into *A.Cerenulata* type cap(rhizoids with nucleus or nuclear donor).
- The type of the cap is determined by the nucleus present in the rhizoids. In both the nuclei(from two species) are present in the same cytoplasm, an intermediate type of cap develops.

Asymmetric division

- Asymmetric cell division is a fundamental mechanism that generates cell diversity while maintaining self-renewing stem cell populations in multicellular organisms.
- Both intrinsic and extrinsic mechanisms underpin symmetry breaking and differential daughter cell fate determination in animals and plants.
- Asymmetric divisions are universally used to create cellular diversity and allow stem cell self-renewal. Four well-studied plant developmental contexts – the embryo, root meristem, the epidermal stomatal lineage, and the male germline – exemplify key functions of asymmetric divisions.
- The creation of cellular diversity by asymmetric division begins during Arabidopsis embryogenesis when the first zygotic division generates a small apical cell (the



BASL, BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE; Epi, epidermis; GC, ground cell; GMC, guard mother cell; LRC, lateral root cap; MMC, meristemoid mother cell; PLL1, POLTERGEIST-LIKE 1; POL, POLTERGEIST; QC, quiescent center; SC, stem cell; SLGC, stomatal lineage ground cell; SSP, SHORT SUSPENSOR; WOX, WUSCHEL-related homeobox; YDA, YODA.

- progenitor of most of the embryo) and a large basal cell (the future extra-embryonic suspensor).
- Asymmetric or oriented divisions are associated with the generation of major tissue layers; they also create what will later become the stem cell niche of the root when an asymmetric division of the hypophyseal cell yields a large basal daughter cell that generates the columella stem cells and a small apical cell that will give rise to the quiescent center (QC).
- The QC consists of a group of mitotically inactive cells that maintain adjacent stem cells. Plants continue producing organs post-embryonically; much of this growth initiates from activities of the stem cell pools in the root and shoot; however, asymmetric divisions are also vital for de novo generation of cell lineages and patterns, as seen during stomatal development.

- Here, precursor cells of the stomatal lineage are generated by asymmetric divisions of meristemoid mother cells (MMCs) that are chosen, seemingly at random, from a field of equivalent protodermal cells. The daughters of the division include a stem cell-like meristemoid and a larger stomatal lineage ground cell (SLGC).
- The meristemoid, after completing a limited number of selfrenewing asymmetric divisions, will differentiate into a guard mother cell and then divide symmetrically to form a pair of stomatal guard cells.
- Although the SLGCs often differentiate into ‘default’ epidermal cells, they can also re-enter an asymmetric division phase, become MMCs, and produce satellite meristemoids whose positions are coordinated with neighbor cells through precise orientation of their asymmetric divisions.

- Plants again employ intrinsically asymmetric divisions during male germline formation; here, an asymmetric division of the haploid microspore generates two unequally sized daughter cells: a non-germline vegetative cell that exits the cell cycle and a germ cell that divides again to form twin sperm cells for each pollen grain.

What is a gall?

Gall induced by a wasp (*Andricus inflator*) on oak (*Quercus petraea*).

- A gall is an abnormal growth of tissue in a plant that is induced by another organism.
- Galls are induced in plants by insects, mites, fungi, bacteria and some viruses.
- Over 1,000 different types of plant galls have been recorded in Britain.
- The exact mechanism by which galls are induced in plants is still not fully understood.
- Galls come in a wide variety of shapes and growth forms, but each type is distinctive and its shape is always the same, thereby providing an opportunity to positively identify the causative agent.

The structure of galls

The robin's pincushion galls, induced by a wasp (*Diplolepis rosae*) here on dog rose (*Rosa canina*), can either be individual galls (above) or clusters of up to 60 galls grouped together (left).

Galls on oak

- These are the spangle galls induced by the sexual generation of the gall wasp (*Neuroterus quercusbaccarum*) on the underside of oak leaves (*Quercus petraea*), seen here in late summer on Dundreggan.
- The larvae in them lie dormant in the fallen leaves over the winter, and the all-female, agamic generation of wasps, which are able to reproduce without mating, emerge in spring.
- They lay eggs on the buds of oak, that then induce the currant galls, and so the cycle of galls continues.


THANK YOU