ALAGAPPA UNIVERSITY

[Accredited with 'A+' Grade by NAAC (CGPA:3.64) in the Third Cycle
and Graded as Category–I University by MHRD-UGC]

KARAIKUDI – 630 003

DIRECTORATE OF DISTANCE EDUCATION

M.Sc. [Botany]

346 22

PLANT ANATOMY AND EMBRYOLOGY

II - Semester

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PLANT ANATOMY AND EMBRYOLOGY

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SYLLABI-BOOK MAPPING TABLE

Plant Anatomy and Embryology

Syllabi	Mapping in Book
BLOCK-I: MERISTEM, CONNECTIVE TISSUES	
Unit-1: General Account and Theories of Organization of Meristems.	**Unit 1:** General Account and Theories of Organization of Meristems **(Pages 1-20);**
Unit-2: Light and Electron Microscopic Structure of Cell Walls.	**Unit 2:** Light and Electron Microscopic Structure of Cell Walls **(Pages 21-36);**
Unit-3: Structural Diversity and Phylogenetic Specialization of Xylem and Phloem.	**Unit 3:** Structural Diversity and Phylogenetic Specialization of Xylem and Phloem **(Pages 37-53);**
Unit-4: Distribution, Structure and Significance of Transfer Cells, Vascular Cambium - Storied, Non-Storied and the Mode of Activity.	**Unit 4:** Transfer Cells and Vascular Cambium **(Pages 54-63)**
BLOCK-2: VASCULAR TISSUES	
Unit-5: Vascular Differentiation in the Primary Body of Stem, Root and Leaf.	**Unit 5:** Vascular Differentiation in Stem, Root and Leaf **(Pages 64-84);**
Unit-6: Root Stem Transition- Molecular Aspects of Developing Vegetative Organs.	**Unit 6:** Root Stem Transition **(Pages 85-96);**
Unit-7: Cambial Variants and Floral Vasculature.	**Unit 7:** Cambial Variants and Floral Vasculature **(Pages 97-132)**
BLOCK-3: THE WOOD	
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Unit-9: Physical, Chemical and Mechanical Properties of Wood.	**Unit 9:** Physical, Chemical and Mechanical Properties of Wood **(Pages 165-176);**
Unit-10: Natural Defects, Knots, Reaction Wood, Compression Wood Tension Wood.	**Unit 10:** Natural Defects, Knots and Wood Types **(Pages 176-188);**
Unit-11: Molecular Aspects on Wood Differentiation, Commercial Woods of South India.	**Unit 11:** Molecular Aspects on Wood Differentiation and Commercial Wood of South India **(Pages 189-205)**

BLOCK-4: THE DEVELOPMENTAL BIOLOGY

Unit-12: Anther Development- Pollen Morphology, Pollen Stigma Compatibility.

Unit-13: Megasporogenesis Female Gametopohyte- Nutrition of Embryo sac-Endosperm Types.

Unit-14: Apomixis- Vegetative Reproduction- Agamospermy and Apospory- Exploitation of Polyembryony and Apomixis in Plant Improvement Progrmmes- Molecular Aspects of Higher Plant Reproduction.

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INTRODUCTION

Plant anatomy or phytotomy is the general term for the study of the internal structure of plants. Originally it included plant morphology, the description of the physical form and external structure of plants, but since the mid-20th century plant anatomy has been considered a separate field referring only to internal plant structure. Plant anatomy is now frequently investigated at the cellular level, and often involves the sectioning of tissues and microscopy.

The plant bodies are made up of a variety of cell types that are organized into tissues. Tissues are organized into organs, and organs function together within systems. Within this hierarchy of structure, embryonic properties are studied which is a characteristic or function of the specific plant. Basically, the plants are made up of two organ systems: the shoot system and the root system. For terrestrial plants the shoot system is above ground and consists of a number of organs. These include stems, leaves, and flowers. On the other hand, the root system is most often underground and consists of organs, such as roots, underground stems (tubers), and rhizomes. Each of these organs performs a different function. Stems are support structures and mediate the growth of the plant. Shoot tips contain actively dividing regions called meristems, which produce auxin, a hormone that regulates the growth and shape of the plant. Leaves are the primary sites of photosynthesis, so they are the food production centers of the plant. Flowers are reproductive structures, where eggs and sperm (pollen) are produced and where pollination and fertilization occur. Roots, tubers, and rhizomes are the main system for nutrient and water acquisition and storage. All of these organs are made up of cells that can be categorized into three major tissue types - dermal, ground, and vascular tissue.

This book, *Plant Anatomy and Embryology*, is divided into four blocks, which is further divided into fourteen units which will help you understand the internal structures of various plant parts, their significance and various stages of development of new plant, i.e., male and female gametes, pollination and fertilization. The topics discussed includes, meristem, connective tissues, general account and theories of organization of meristems, light and electron microscopic structure of cell walls, structural diversity and phylogenetic specialization of xylem and phloem, distribution, structure and significance of transfer cells, vascular cambium, vascular tissues, vascular differentiation in the primary body of stem, root and leaf, root stem transition, molecular aspects of developing vegetative organs, cambial variants and floral vasculature, the wood, structure, identification, classification and uses of woods, natural defects, knots, the developmental biology, anther development - pollen morphology and pollen stigma compatibility, megasporogenesis of female gametopohyte, nutrition of embryo sac, endosperm types, apomixes, vegetative reproduction, agamospermy and apospory.

The book follows the self-instruction mode or the SIM format wherein each unit begins with an 'Introduction' to the topic followed by an outline of the 'Objectives'. The content is presented in a simple and structured form interspersed with 'Check Your Progress' questions and answers for better understanding. A list of 'Key Words' along with a 'Summary' and a set of 'Self Assessment Questions and Exercises' is provided at the end of the each unit for effective recapitulation.

NOTES

BLOCK - I
MERISTEM, CONNECTIVE TISSUES

UNIT 1 GENERAL ACCOUNT AND THEORIES OF ORGANIZATION OF MERISTEMS

Structure

1.0 INTRODUTION

Meristematic tissue or meristems, as they are also called are tissues that have the ability to enlarge, stretch and differentiate into other types of cells as they mature. The cells of this tissue are generally young and immature, with the power of continuous division. Meristematic cells are all living cells. The meristematic cells can be oval or rounded or polygonal in shape. They have a large nucleus with no vacuoles. Intercellular space between cells is absent. The cells are also small in size but have a high capacity of cell division.

Depending on the occurrence of the meristematic tissue on the plant body, we can classify the meristems into three types. They are: Apical Meristems: These meristems are located on the tip of the root, stem, etc. They help in the growth of the root system as well as the shoot system. The various cell divisions along with the cellular enlargement help in the growth of the stem above the ground and the growth of the root below the ground. Intercalary Meristems: The intercalary meristems are located at the internodes or the base of the leaves. The intercalary meristems help in increasing the length of the internode. This is usually seen in monocotyledonous plants. Lateral Meristems: The lateral meristems are present on the lateral side of the stem and root of a plant. These meristems help in increasing the thickness of the plants. The vascular cambium and the cork cambium are good examples of a lateral meristematic tissue.

NOTES

In this unit, you will study about general account and theories of organization of meristems in detail.

1.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand about meristems
- Explain the theories of organization of meristems

1.2 GENERAL ACCOUNT AND THEORIES OF ORGANIZATION OF MERISTEMS

A meristem is the tissue in most plants containing undifferentiated cells (meristematic cells), found in zones of the plant where growth can take place. Meristematic cells give rise to various organs of a plant and are responsible for growth.

Differentiated plant cells generally cannot divide or produce cells of a different type. Meristematic cells are incompletely or not at all differentiated, and are capable of continued cellular division. Therefore, cell division in the meristem is required to provide new cells for expansion and differentiation of tissues and initiation of new organs, providing the basic structure of the plant body. Furthermore, the cells are small and protoplasm fills the cell completely. The vacuoles are extremely small. The cytoplasm does not contain differentiated plastids (chloroplasts or chromoplasts), although they are present in rudimentary form (proplastids). Meristematic cells are packed closely together without intercellular cavities. The cell wall is a very thin primary cell wall as well as some are thick in some plants. Maintenance of the cells requires a balance between two antagonistic processes: organ initiation and stem cell population renewal.

There are three types of meristematic tissues: apical (at the tips), intercalary (in the middle) and lateral (at the sides). At the meristem summit, there is a small group of slowly dividing cells, which is commonly called the central zone. Cells of this zone have a stem cell function and are essential for meristem maintenance. The proliferation and growth rates at the meristem summit usually differ considerably from those at the periphery.

The term meristem was first used in 1858 by Carl Wilhelm von Nägeli (1817–1891) in his book *(Beiträge zur Wissenschaftlichen Botanik)* ('Contributions to Scientific Botany'). It is derived from the Greek word merizein, meaning to divide, in recognition of its inherent function.

Plants have meristematic tissue in several locations. Both roots and shoots have meristematic tissue at their tips called apical meristems that are responsible for the lengthening of roots and shoots. The shoot apical meristem is formed during embryonic development, but after germination gives rise to the stem, leaves, and flowers. The root apical meristem is also formed during development, but during germination gives rise to the root system. Cell division and cell elongation in the apical meristem is called primary growth and results in an increase in plant height and root length. Increasing root length enables the plant to tap into the water and mineral resources of a new region or layer of soil. Increasing shoot length makes the plant taller, thus allowing it better access to sunlight for photosynthesis.

Many types of plants also increase the diameter of their roots and stems throughout their lifetime. This type of growth is called secondary growth and is the product of lateral meristem. Lateral meristem is called the vascular cambium in many of the plants in which it is found. Secondary growth gives a plant added stability that allows for the plant to grow taller. Lastly, some plants have intercalary meristem. These are areas of plants that help in the regeneration of parts of the plant that have been damaged by predators or the environment. Intercalary meristems produce growth at the base of grass blades, for instance.

Meristem tissue is not autonomous. Throughout the life of the plant, the rate of cell division and cell elongation in the meristems is regulated by plant hormones. For example, giberellins stimulate cell division in shoot apical meristem, causing the plant to grow taller. These hormones also cause cell elongation in intercalary meristem of grasses. Cytokinin and auxin are also important growth regulators. Auxin stimulates growth by inducing cell elongation, while cytokinins are thought to stimulate both cell division and cell elongation.

Meristematic tissues are cells or group of cells that have the ability to divide. These tissues in a plant consist of small, densely packed cells that can keep dividing to form new cells. Meristematic tissue is characterized by small cells, thin cell walls, large cell nuclei, absent or small vacuoles, and no intercellular spaces.

Meristematic tissues are found in many locations, including near the tips of roots and stems (apical meristems), in the buds and nodes of stems, in the cambium between the xylem and phloem in dicotyledonous trees and shrubs, under the epidermis of dicotyledonous trees and shrubs (cork cambium), and in the pericycle of roots, producing branch roots. The two types of meristems are primary meristems and secondary meristems.

On the basis of the development, tissues have been classified into two groups:

- Meristematic Tissue
- Permanent Tissue

Meristematic Tissue: It consists of a group of cells that divide continuously and the daughter cells differentiate into the permanent tissue. The cells of the meristematic tissue have the capability to divide indefinitely. The cells are isodiametric in shape. They have thin cellulosic wall with dense cytoplasm and large nucleus. Vacuoles are either absent or if present are very few in number except the cambial cells which show vacuolation. They are tightly packed without any intercellular spaces. Plastids occur in the form of proplastids. Mitochondria and endoplasmic reticulum are not well developed. They have very high metabolic rate.

Permanent Tissue: The cells of this tissue have lost their ability of division. They are thin or thick walled, living or dead, with well-developed intercellular spaces and cell organelles.

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Classification of Meristem

The meristem can be classified on the basis of origin, plane of division, function and position in the plant body (Refer Figure 1.1).

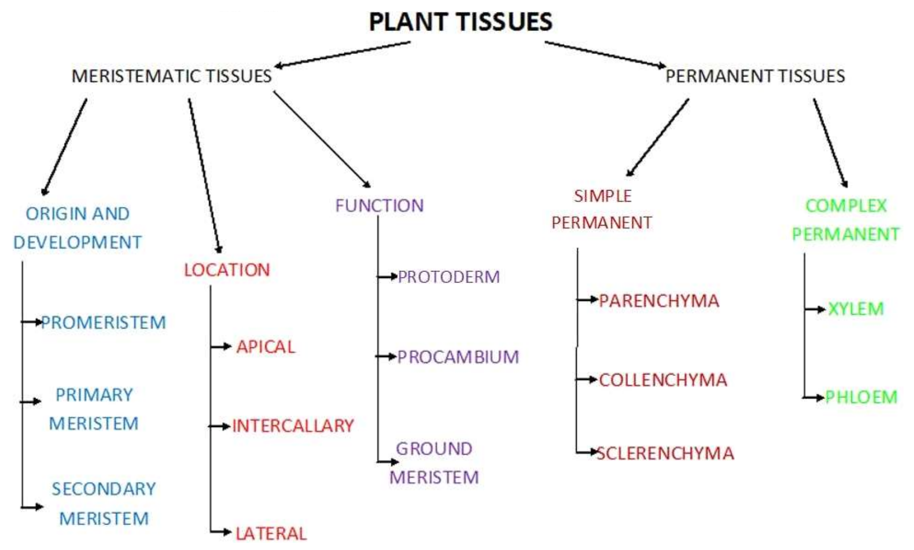

Fig. 1.1 *Chart Showing the Different Types of Tissues in Plants*

Meristem on the Basis of Origin

Following are the meristems based on the origin:

- Primordial Meristem
- Primary Meristem
- Secondary Meristem

Primordial Meristem: The undifferentiated group of cells is termed as promeristem. It is also known as primordial meristem or embryonic meristem. The cells are thin walled isodiametric cells with dense cytoplasm and large nuclei. Promeristem differentiates into primary meristem.

Primary Meristem: Primary meristem originates from the promeristem and differentiates into the permanent tissue. It forms the fundamental parts of the plant and persists throughout the life of plant. The main primary meristems are root apical and shoot apical meristem. It also occurs at the tip of the leaf and forms the abaxial and adaxial surface of the leaf which encloses mesophyll and vascular tissues. The primary tissue of the plant such as epidermis, cortex, xylem, phloem, pith all are the derivatives of primary meristem. After the differentiation some permanent cells regain the capability of division and this is known as dedifferentiation.

Secondary Meristem: This meristem develops from the permanent tissue which has undergone the dedifferentiation. New tissues are added to dermal and epidermal tissue system. It is usually developed either at the time of emergency or to effect secondary growth. Cork cambium and vascular cambium are the examples of secondary meristem. Vascular cambium produces secondary xylem towards inner side and secondary phloem towards outer side. Cork cambium also known as phellogen, produces cork (phellem) towards outer side and secondary cortex (phelloderm) towards inner side. Phellem, Phellogen and Phelloderm constitutes the periderm which is protective in nature.

Meristem Based on the Function

Following are the meristems based on the function:

- Protoderm
- Procambium
- Ground Meristem

Protoderm: It is the outermost layer of young growing regions which develops into the epidermis. It is protective in nature and forms the part of dermal tissue system. Stomata, trichomes and all glandular hairs develop from the protoderm.

Procambium: It consists of narrow, elongated meristematic cells which develop into primary vascular tissue. The cells are densely cytoplasmic and consist of large nucleus. In stem, the cells of procambium develop primary xylem towards inner side and primary phloem towards outer side. In dicotyledons stem, a portion of procambium remains between primary xylem and primary phloem and later differentiates into cambium, which forms open collateral vascular bundles.

Ground Meristem: It consists of large thin walled cells which later on differentiate into hypodermis, cortex, pericycle, pith and medullary rays. Mesophyll cells of leaf and additional procambial bundles also derive from the ground meristem.

Meristem Based on the Position

Following are the meristems based on the position (Refer Figure 1.2):

- Apical Meristem
- Intercalary Meristem
- Lateral Meristem

Apical Meristem: It is present at the apex of root and apex of main and lateral shoots. Apical meristem is the growing point of shoot and forms leaves and branches. Flowers also differentiate from apical meristem. It is responsible for increasing the length of root and shoot.

Intercalary Meristem: The meristem which is present between the regions of permanent tissues is known as intercalary meristem. It is present at the base of internode of grasses.

Lateral Meristem: It is located parallel to the long axis of root and shoot and predominantly divide periclinally. They are responsible for increasing the diameter and form secondary permanent tissue. Vascular cambium and cork cambium are the examples of lateral meristem.

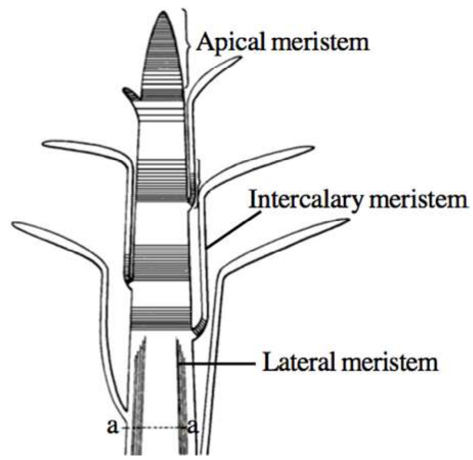

Fig. 1.2 *Different Types of Meristems on the Basis of Position in Plant*

Meristem Based on the Division

Following are the meristems based on the division:

- Rib or File Meristem
- Plate Meristem
- Mass Meristem

Rib or File Meristem: This meristem divide at the right angles to the longitudinal axis of the plant organ, and therefore parallel files of cells are formed. For example, cortex and pith of root and stem.

Plate Meristem: It consists of parallel layer of cells which divide anti-clinally and bring intercalary growth. This meristem is present in leaf and increases the surface area without increasing the number of mesophyll layers.

Mass Meristem: The cells of this meristem divide in all possible planes therefore, the tissue increases in volume. For example, embryo and endosperm.

1.2.1 Theories of Root Apical Meristem

The cells forming the apical meristem of primary root are densely cytoplasmic with large nuclei. They undergo active division and all the permanent tissues of the root are derived from the root apical meristem. The position of root apical meristem is sub-terminal as terminal position is occupied by a root-cap. The meristem that generates root cap is known as calyptrogen.

There are mainly three theories to explain the root apex of vascular plants, i.e., as follows:

- Apical Cell Theory
- Histogen Theory
- Korper–Kappe Theory

I. Apical Cell Theory: This theory was proposed by Nageli. According to this theory, there is a single apical tetrahedral cell which gives rise to all the tissues of the root (Refer Figure 1.3). The root cap is derived from the base of the apical cell and all other tissues like epidermis, cortex and vascular cylinder originate from the upper three sides of apical cell. This theory is restricted to the vascular cryptogams only because in flowering plants a group of the initial cells has been observed in the root apical meristem.

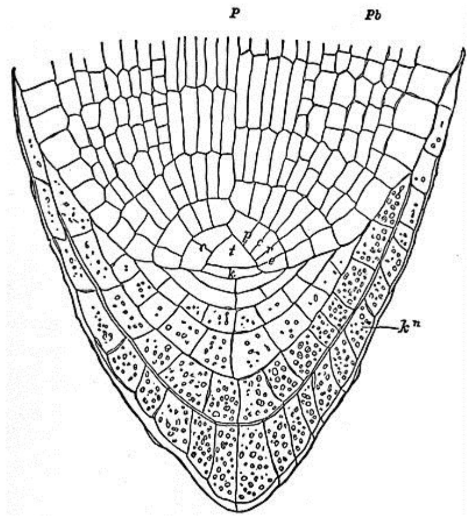

Fig. 1.3 *Median Longitudinal Section through Root Apical Meristem*

II. Histogen Theory: This theory was advocated by Hanstein. According to this theory, there are three distinct meristematic zones termed as histogens. These three zones are known as dermatogen, periblem and plerome which form epidermis, cortex and vascular cylinder respectively (Refer Figure 1.4). Haberlandt suggested protoderm, ground meristem and procambium for these three histogens.

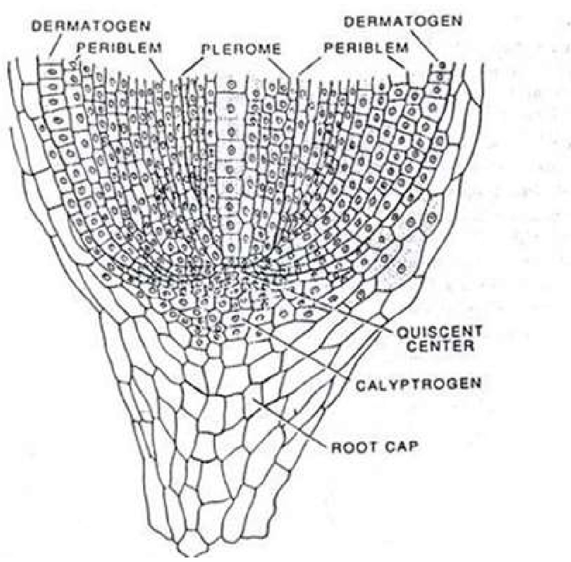

Fig. 1.4 *Diagram Showing the Root Apex in Terms of Hanstein's Histogen Concept*

On the basis of cellular configuration, Schuepp divided the root apical meristem into four types (Refer Figure 1.5):

- **Type A:** All the permanent tissues of root are derived from a single apical cell. It is present in all vascular cryptogams.
- **Type B:** There are two separate groups of initials. Vascular cylinder is derived from one group and epidermis, cortex and root cap originates from other group. It is common in gymnosperms.
- **Type C:** There are poorly individualized initials which give rise to root cap, cortex and vascular cylinder. It is present in dicotyledons.
- **Type D:** In this type, there are three separate groups of initials. One group forms root cap, epidermis and cortex derive from other group and vascular cylinder originates from separate group. This type is common in monocotyledons.

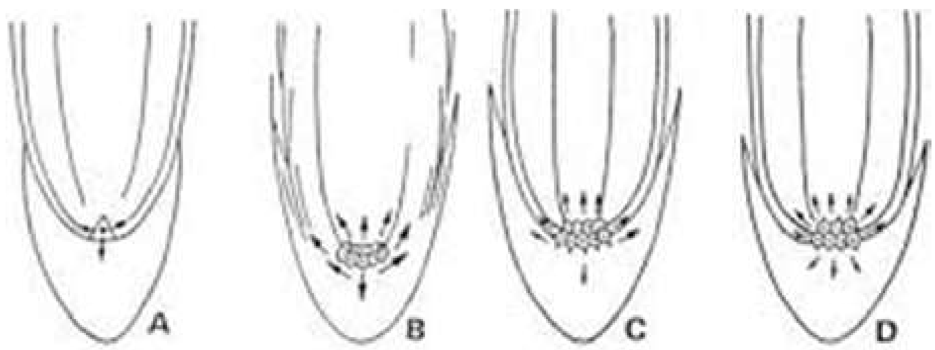

Fig. 1.5 *Organization of Root Apical Meristem*

Guttenberg also divided the root apical meristem into two types:

- Enclosed Type
- Open Type

Enclosed Type: The initials of the various tissues lie closer to the central cells. Cortex and vascular cylinder have separate initials. Root cap and protoderm may have common or separate initials.

Open Type: In this type, the initials of various tissues are at some distance from the cemtral cells. Only vascular cylinder originates from separate initial and all other tissues have common origin.

III. Korper–Kappe Theory: This theory was proposed by Schuepp (1917). According to this theory, the cells at the root apex divide in two planes. First, a cell divides into two by a transverse division and then one of the daughter cells divides by a longitudinal division and therefore, a T shaped structure is formed. It is also known as T division. On this basis, root apical meristem has been divided into two distinct zones, Korper (cap) and Kappe (body). In the inner region, the second division occurs in upper daughter cell and therefore, inverted T shaped structure is formed and it is known as Korper (cap). In the outer region, the second division occurs in lower daughter cell and straight T shaped structure is formed, known as Kappe (body) (Refer Figure 1.6).

The central region of root cap is known as columella where the cells are arranged in longitudinal files. These cells divide rarely. The korper-kappe theory of root apex is similar with tunica-corpus theory of shoot apical meristem as both are based on the plane of cell division.

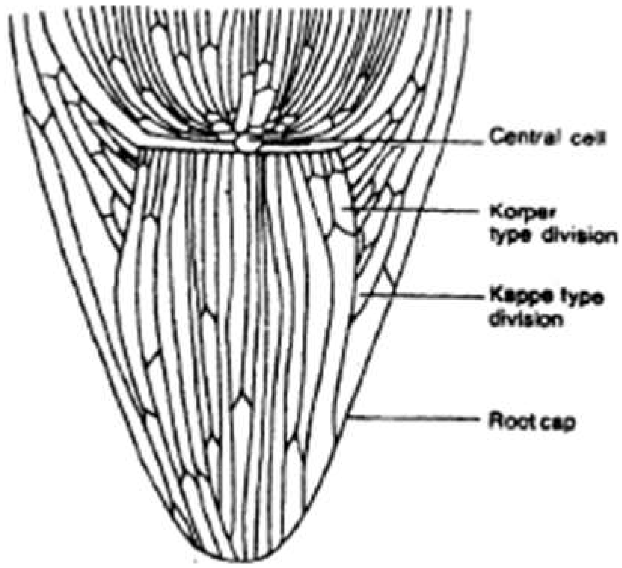

Fig. 1.6 *Diagrammatic Representation Showing the Root Apical Merisetm in Terms of Korper Kappe Theory*

Quiescent Centre

In the root tip of *Zea*, Clowes observed a central cup like hemispherical region between the root cap and active meristematic zone. The cells of this zone have less amount of DNA, RNA and protein and these cells also show very low mitotic activity. They do not actively synthesize DNA. The cell organelles are also less in numbers. They have few mitochondria, less endoplasmic reticulum, small dictyosomes, nuclei and nucleoli. This zone was termed as quiescent centre (Refer Figure 1.7). Later on, the existence of quiescent zone has been observed in the root tips of many plants.

When the cells of this zone are exposed to X-rays, the meristematic cells stop dividing and the cells of quiescent centre become active. It is because the cells of quiescent centre are more resistant to the radiations than actively dividing cells.

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Therefore, quiescent centre is regarded as central mother cells that form promeristem of the apex. It provides a reservoir of diploid cells when the root tip is damaged. It is also considered the site of hormone synthesis.

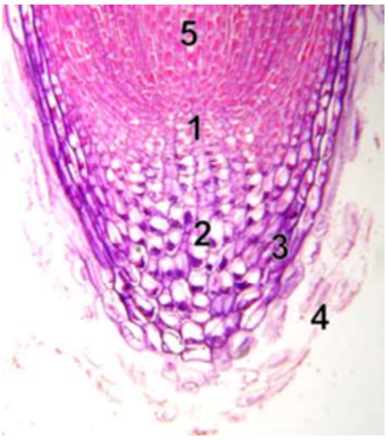

Fig. 1.7 *Root Apical Meristem Showing; 1. Quiescent Centre; 2. Calyptrogens; 3. Root Cap; 4. Sloughed Off Dead Root Cap Cells; 5. Procambium*

1.2.2 Theories of Shoot Apical Meristem

Shoot apical meristem is more complicated than root apical meristem and it shows the differences in the following aspect:

- Shoot apical meristem is terminal in position whereas root apical meristem is sub-terminal as root cap occupies the terminal position.
- Shoot apical meristem produces cells toward the axis but root apical meristem produces cells toward the axis as well as away from the axis to initiate the root cap.
- Shoot apex shows the rhythmic changes in shape and size before and after the initiation of leaf primordium. It widens considerably before leaf initiation and again becomes narrow after leaf initiation. Root apical meristem does not show any kind of rhythmic changes in shape and size.
- Shoot apical meristem is associated with the formation of lateral appendages (branches), but in root the lateral organs (lateral roots) are formed behind the root apical meristem.

Theories of Shoot Apical Meristem

Several theories have been proposed to describe the organization of shoot apical meristem:

- Apical Cell Theory
- Histogen Theory
- Tunica-Corpus Theory
- Tunica-Corpus Theory

NOTES

Apical Cell Theory: This theory was proposed by Nageli. According to this theory, there is a single apical tetrahedral cell in the shoot apex and it is considered the 'structural and functional unit' of apical meristem. The single apical cell divides to give rise to all the tissues of the shoot (Refer Figure 1.8). This theory is restricted to the vascular cryptogams only. In flowering plants a group of the initial cells has been observed in the root apical meristem and therefore this theory was discarded.

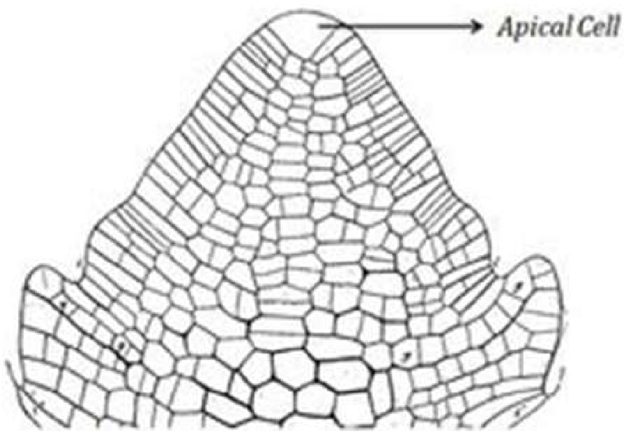

Fig. 1.8 *Diagram Showing the Shoot Apex with a Single Apical Cell*

Histogen Theory: This theory was advocated by Hanstein. According to this theory, there are three distinct meristematic zones which arise from the independent initial of the apical mersitem. These layers are termed as histogens. The outermost histogen is known as dermatogen, middle one periblem and the inner most plerome (Refer Figure 1.9). Epidermis originates from dermatogen, cortex from periblem and vascular cylinder from plerome. This theory was not accepted as these layers are not specific in their functions. In gymnosperms and angiosperms, it was not possible to make clear distinction between periblem and plerome. Haberlandt suggested protoderm, ground meristem and procambium for these three histogens.

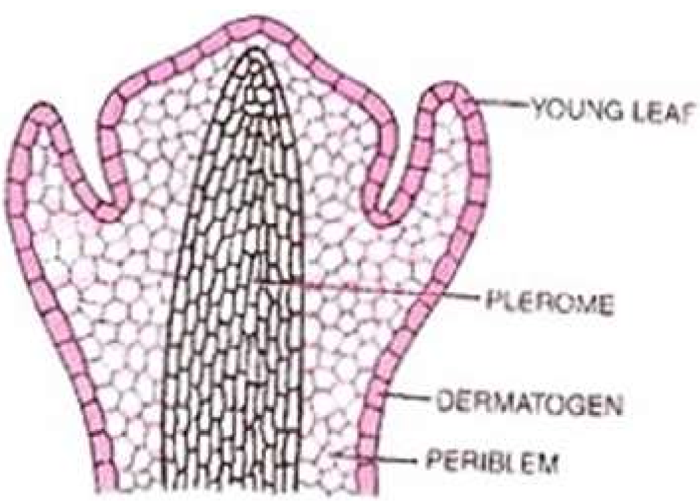

Fig. 1.9 *L.S. of Vegetative Shoot Apex Showing Histogens*

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Tunica-Corpus Theory: Tunica-corpus theory was proposed by Schmidt (1924). This theory was based on the plane of cell division in the apex. According to this theory, there are two distinct layers in the shoot apex of angiosperms. These two distinct zones were termed as tunica and corpus. The outer zone consisting of one or more layers of regularly arranged cells known as tunica in which only anticlinal division (perpendicular to the surface) occurs. Therefore, tunica develops as a layer but does not increase in thickness. In a same species, variations in the number of tunica layers have been observed in the different stages of development of shoot apex. These variations may be due to the plastochron periodicity. Usually tunica gives rise to epidermis. The inner zone of shoot apex is known as corpus, which is covered by tunica. Here, the cells divide in all possible planes. Therefore, shoot apex increases in volume. Corpus gives rise to cortex and vascular tissue.

In some grasses like maize, periclinal divisions have also been observed. Therefore, some scientists consider that tunica should include only those layers in which only anticlinal divisions occur. The other layers of tunica in which cells divide by periclinal division, they should be termed as corpus. To accommodate these fluctuations in tunica and corpus, Popham and Chan (1950) suggested mantle-core hypothesis. They divided shoot apex into two zones but not on the basis of cell division. Mantle included all the outer layers of the apex and tunica was restricted only to those layers which divide anticlinally. The inner mass of cells covered by mantle termed as core.

Both of these layers have separate set of initials which are adjacent with one another at the tip of the apex. These cells can be easily identified by their larger size and more vacuolation. The shoot apex of most of the gymnosperms does not exhibit tunica-corpus organization as their shoot apex does not have a surface layer which divides anticlinally.

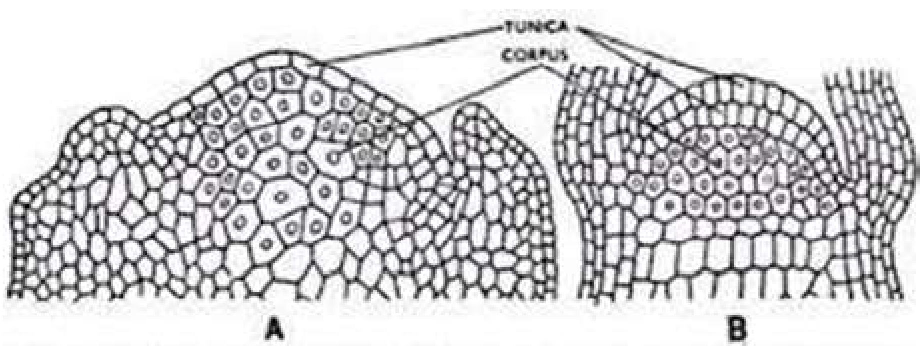

Fig. 1.10 Longitudinal Section of Shoot Apex Showing; A). One Tunica Layer in a and Two Layers in; B). Corpus

Anneau Initial and Meristem D'attente: This theory was put forwarded by Buvat. According to this theory, peripheral and subterminal regions are active initiating zones whereas the cells of central apical zone are inactive during the development of shoot apex. The cells of central zone become active when the vegetative shoot converts into reproductive phase. The central apical zone is called meristem d'attente (waiting meristem). The peripheral active zone is called anneau initial and the central pith region is called meristem medullaire (Refer Figure 1.11). This theory became controversial as it considered the central apical zone as a waiting meristem which was earlier regarded as apical initials.

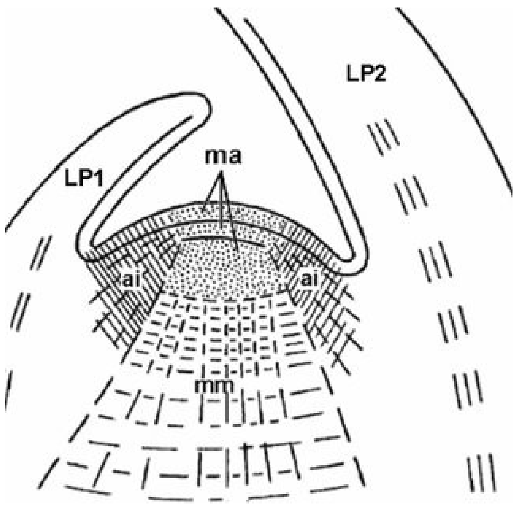

***Fig. 1.11** Shoot Apical Meristem of a Dicotyledon in Terms of Anneau Initial and Meristem D' Attente Concept*

Cytohistological Zonation: On the basis of cytological characters and staining shoot apex have been classified in the five zones (ReferFigure 1.12).

- **Apical Initial Group**: It includes a group of initials along the apical surface and their lateral derivatives.
- **Central Mother Cell Zone**: This cell is present below the apical initial group and it originates from it only. The cells of the distal zone are highly vacuolated and therefore take lighter stain. The cells also show low mitotic activity.
- **Rib Meristem**: It consists of centrally situated derivatives of central mother cells which divide transversely to form vertical files. Pith is formed from this zone and therefore this region is also known as file meristem or pith meristem.
- **Peripheral Zone**: It originates partly from the lateral derivatives of the apical initial and partly from the central mother cells. The cells of this zone are densely cytoplasmic and mitotically active, therefore these cells are darkly stained. Periclinal divisions result the elongation of shoot and anticlinal divisions increases the width.
- **Cambium Like Zone**: It is cup shaped zone and present between the central mother cell and rib and flank meristem. It occurs below the youngest leaf primordium.

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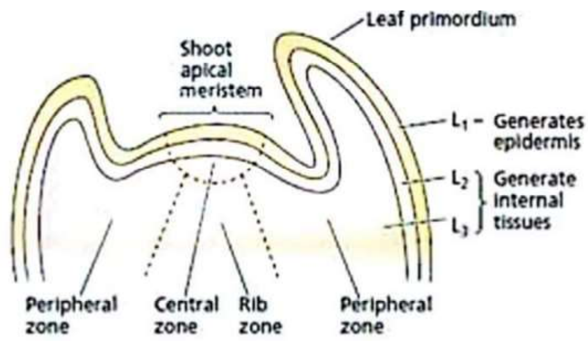

Fig. 1.12 *Shoot Apical Meristem Showing Cytohistological Zones*

Types of Shoot Apex

Newman (1965) gave this concept, and according to this there is nothing like a group of permanent initial cells in the shoot apex, instead there is a sequence of meristematic cells and it is known as continuing meristematic residue. He classified shoot apex into three types (Refer Figure 1.13):

- **Monoplex Type**: It is found in vascular cryptogams and ferns; here the shoot apex is denoted by one or more cells which divide by walls parallel to the inclined walls in the stem.
- **Simplex Type**: It is found in gymnosperms; it consists of one or more initial cells arranged in a single layer; these cells divide anticlinally and periclinally.
- **Duplex Type**: It is found in the shoot apex of angiosperms; it consists of atleast two successive layers of cells; the cells of surface layer divide anticlinally and that of inner layer divide in more than one plane.

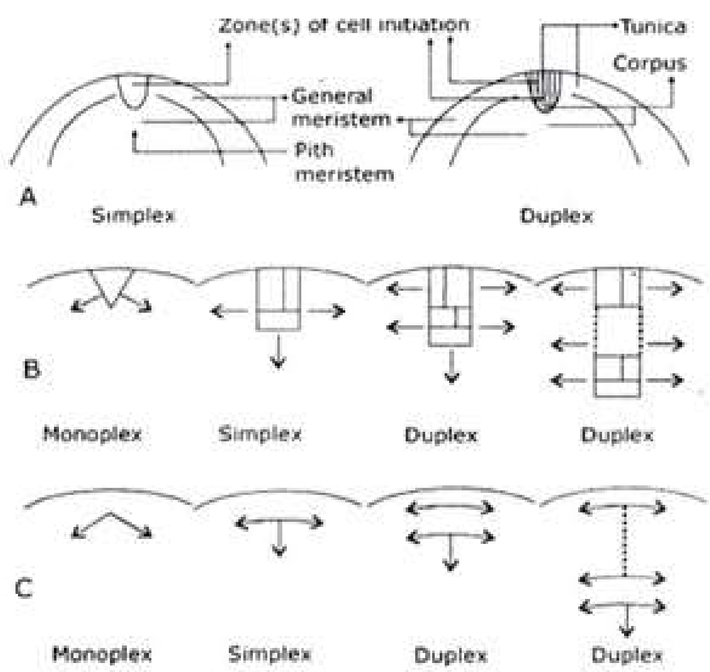

Fig. 1.13 *Different Types of Shoot Apex*

Check Your Progress

1. Define meristem.
2. How many types of meristematic tissues are there?
3. What are meristematic tissues?
4. Where are meristematic tissues found?
5. How many types tissues are classified on basis of the development?
6. How many types tissues are classified meristem on the basis of origin?
7. How many types tissues are classified meristem on the basis of function?
8. What does ground meristem consists of?
9. How many types tissues are classified meristem on the basis of divison?

1.3 ANSWERS TO CHECK YOUR POGRESS QUESTIONS

1. A meristem is the tissue in most plants containing undifferentiated cells (meristematic cells), found in zones of the plant where growth can take place. Meristematic cells give rise to various organs of a plant and are responsible for growth.
2. There are three types of meristematic tissues: apical (at the tips), intercalary (in the middle) and lateral (at the sides).
3. Meristematic tissues are cells or group of cells that have the ability to divide. These tissues in a plant consist of small, densely packed cells that can keep dividing to form new cells. Meristematic tissue is characterized by small cells, thin cell walls, large cell nuclei, absent or small vacuoles, and no intercellular spaces.
4. Meristematic tissues are found in many locations, including near the tips of roots and stems (apical meristems), in the buds and nodes of stems, in the cambium between the xylem and phloem in dicotyledonous trees and shrubs, under the epidermis of dicotyledonous trees and shrubs (cork cambium), and in the pericycle of roots, producing branch roots. The two types of meristems are primary meristems and secondary meristems.
5. On the basis of the development, tissues have been classified into two groups:
   - Meristematic Tissue
   - Permanent Tissue
6. Following are the meristems based on the Origin:
   - Primordial Meristem
   - Primary Meristem
   - Secondary Meristem

7. Following are the meristems based on the function:
   - Protoderm
   - Procambium
   - Ground Meristem
8. Ground meristem consists of large thin walled cells which later on differentiate into hypodermis, cortex, pericycle, pith and medullary rays. Mesophyll cells of leaf and additional procambial bundles also derive from the ground meristem.
9. Following are the meristems based on the division:
   - Rib or File Meristem
   - Plate Meristem
   - Mass Meristem

1.4 SUMMARY

- A meristem is the tissue in most plants containing undifferentiated cells, found in zones of the plant where growth can take place.
- Meristematic cells give rise to various organs of a plant and are responsible for growth.
- Meristematic cells are incompletely or not at all differentiated, and are capable of continued cellular division.
- Cell expansion and differentiation of tissues and initiation of new organs, providing the basic structure of the plant body.
- Meristematic cells are packed closely together without intercellular cavities. The cell wall is a very thin primary cell wall as well as some are thick in some plants.
- There are three types of meristematic tissues: apical (at the tips), intercalary (in the middle) and lateral (at the sides).
- At the meristem summit, there is a small group of slowly dividing cells, which is commonly called the central zone.
- The proliferation and growth rates at the meristem summit usually differ considerably from those at the periphery.
- Plants have meristematic tissue in several locations. Both roots and shoots have meristematic tissue at their tips called apical meristems that are responsible for the lengthening of roots and shoots.
- The shoot apical meristem is formed during embryonic development, but after germination gives rise to the stem, leaves, and flowers.

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- The root apical meristem is also formed during development, but during germination gives rise to the root system.
- Cell division and cell elongation in the apical meristem is called primary growth and results in an increase in plant height and root length.
- Increasing root length enables the plant to tap into the water and mineral resources of a new region or layer of soil.
- Increasing shoot length makes the plant taller, thus allowing it better access to sunlight for photosynthesis.
- Many types of plants also increase the diameter of their roots and stems throughout their lifetime. This type of growth is called secondary growth and is the product of lateral meristem.
- Lateral meristem is called the vascular cambium in many of the plants in which it is found.
- Secondary growth gives a plant added stability that allows for the plant to grow taller.
- Auxin stimulates growth by inducing cell elongation, while cytokinins are thought to stimulate both cell division and cell elongation.
- Meristematic tissue is characterized by small cells, thin cell walls, large cell nuclei, absent or small vacuoles, and no intercellular spaces.
- Meristematic tissue consists of a group of cells that divide continuously and the daughter cells differentiate into the permanent tissue.
- Vacuoles are either absent or if present are very few in number except the cambial cells which show vacuolation.
- Permanent tissue cells of this tissue have lost their ability of division. They are thin or thick walled, living or dead, with well-developed intercellular spaces and cell organelles.
- Primordial meristem are undifferentiated group of cells is termed as promeristem. It is also known as primordial meristem or embryonic meristem.
- Primary meristem originates from the promeristem and differentiates into the permanent tissue.
- Secondary meristem develops from the permanent tissue which has undergone the dedifferentiation.
- Vascular cambium produces secondary xylem towards inner side and secondary phloem towards outer side.
- Cork cambium also known as phellogen, produces cork (phellem) towards outer side and secondary cortex (phelloderm) towards inner side.

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- Protoderm is the outermost layer of young growing regions which develops into the epidermis. It is protective in nature and forms the part of dermal tissue system.
- Procambium consists of narrow, elongated meristematic cells which develop into primary vascular tissue.
- Ground meristem consists of large thin walled cells which later on differentiate into hypodermis, cortex, pericycle, pith and medullary rays.
- Mesophyll cells of leaf and additional procambial bundles also derive from the ground meristem.
- Lateral meristem is located parallel to the long axis of root and shoot and predominantly divide periclinally.
- Plate meristem consists of parallel layer of cells which divide anti-clinally and bring intercalary growth.
- Histogen theory was advocated by Hanstein. According to this theory, there are three distinct meristematic zones termed as histogens.
- Korper–Kappe theory was proposed by Schuepp (1917). According to this theory, the cells at the root apex divide in two planes.
- Shoot apical meristem is terminal in position whereas root apical meristem is sub-terminal as root cap occupies the terminal position.
- Shoot apical meristem produces cells toward the axis but root apical meristem produces cells toward the axis as well as away from the axis to initiate the root cap.
- Apical cell theory was proposed by Nageli. According to this theory, there is a single apical tetrahedral cell in the shoot apex and it is considered the 'structural and functional unit' of apical meristem.
- Epidermis originates from dermatogen, cortex from periblem and vascular cylinder from plerome.
- Tunica-corpus theory was proposed by Schmidt (1924). This theory was based on the plane of cell division in the apex.
- Apical initial group includes a group of initials along the apical surface and their lateral derivatives.
- Central mother cell zone is present below the apical initial group and it originates from it only.
- Rib meristem consists of centrally situated derivatives of central mother cells which divide transversely to form vertical files.
- Pith is formed from this zone and therefore this region is also known as file meristem or pith meristem.

- Peripheral zone originates partly from the lateral derivatives of the apical initial and partly from the central mother cells.
- Cambium like zone is cup shaped zone and present between the central mother cell and rib and flank meristem.

NOTES

1.5 KEY WORDS

- **Meristem:** A meristem is the tissue in most plants containing undifferentiated cells, found in zones of the plant where growth can take place.
- **Apical Meristem:** Apical meristem is the growing point of shoot and forms leaves and branches.
- **Intercalary Meristem:** The meristem which is present between the regions of permanent tissues is known as intercalary meristem.
- **Protoderm:** Protoderm is the outermost layer of young growing regions which develops into the epidermis.

1.6 SELF ASSESSEENT QUESTIONS AND EXERCISES

Short Answer Questions

1. What is meristem?
2. What is meristem tissue and how many types of meristem tissue are there?
3. What is permanent tissue?
4. Draw a systematic diagram to showing different types of tissues in plants.
5. What is primary meristem?
6. Distinguish between plate meristem and mass meristem.
7. In how many types did Guttenberg divided the root apical meristem?

Long Answer Questions

1. What is meristem? Explain types of meristem tissue.
2. Give the classification of meristem tissue.
3. Explain the types of meristem on the basis of origin.
4. Write in detail about meristem based on the function.
5. What are the theories of root apical meristem?
6. Write a note on quiescent centre.
7. Discuss about theories of shoot apical meristem.

NOTES

1.7 FURTHER READINGS

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NOTES

UNIT 2 LIGHT AND ELECTRON MICROSCOPIC STRUCTURE OF CELL WALLS

Structure

2.0 INTRODUCTION

Cell walls are important features of plant cells that perform a number of essential functions, including providing shape to the many different cell types needed to form the tissues and organs of a plant. Forming the interface between adjacent cells, plant cell walls often play important roles in intercellular communication. Because of their surface location, plant cell walls play an important role in plant-microbe interactions, including defense responses against potential pathogens. The desire to understand these and other plant functions help explain the strong interest in wall structure and biosynthesis.

Cell wall composition varies depending on the organism. In plants, the cell wall is composed mainly of strong fibers of the carbohydrate polymer cellulose. Cellulose is the major component of cotton fiber and wood, and it is used in paper production. Bacterial cell walls are composed of a sugar and amino acid polymer called peptidoglycan. The main components of fungal cell walls are chitin, glucans, and proteins.

The plant cell wall is multi-layered and consists of up to three sections. From the outermost layer of the cell wall, these layers are identified as the middle lamella, primary cell wall, and secondary cell wall. While all plant cells have a middle lamella and primary cell wall, not all have a secondary cell wall. Middle lamella is outer cell wall layer contains polysaccharides called pectins. Pectins aid in cell adhesion by helping the cell walls of adjacent cells to bind to one another. Primary cell wall is formed between the middle lamella and plasma membrane in growing plant cells. It is primarily composed of cellulose microfibrils contained within a gel-like matrix of hemicellulose fibers and pectin polysaccharides. The primary cell wall provides the strength and flexibility needed to allow for cell growth. Secondary cell wall is formed between the primary cell wall and plasma membrane in some plant cells. Once the primary cell wall has stopped dividing and growing, it may thicken to form a secondary cell wall. This rigid layer strengthens and supports the cell. In addition to cellulose and hemicellulose, some secondary cell walls contain lignin. Lignin strengthens the cell wall and aids in water conductivity in plant vascular tissue cells.

In this unit, you will study about light and electron microscopic structure of cell walls in detail.

2.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand about cell wall
- Explain the light and electron microscopic structure of cell walls

2.2 STRUCTURE OF CELL WALLS: IN LIGHT AND ELECTRON MICROSCOPIC

A cell wall is a structural layer surrounding some types of cells, just outside the cell membrane. It can be tough, flexible, and sometimes rigid. It provides the cell with both structural support and protection, and also acts as a filtering mechanism. Cell walls are present in most prokaryotes (except mycoplasma bacteria), in algae, plants and fungi but rarely in other eukaryotes including animals. A major function is to act as pressure vessels, preventing over-expansion of the cell when water enters.

The composition of cell walls varies between species and may depend on cell type and developmental stage. The primary cell wall of land plants is composed of the polysaccharides cellulose, hemicelluloses and pectin. Often, other polymers such as lignin, suberin or cutin are anchored to or embedded in plant cell walls. Algae possess cell walls made of glycoproteins and polysaccharides such as carrageenan and agar that are absent from land plants. In bacteria, the cell wall is composed of peptidoglycan. The cell walls of archaea have various compositions, and may be formed of glycoprotein S-layers, pseudopeptidoglycan, or polysaccharides. Fungi possess cell walls made of the N-acetylglucosamine polymer chitin. Unusually, diatoms have a cell wall composed of biogenic silica.

A plant cell wall was first observed and named (simply as a wall) by Robert Hooke in 1665. However, ‘the dead excrusion product of the living protoplast’ was forgotten, for almost three centuries, being the subject of scientific interest mainly as a resource for industrial processing or in relation to animal or human health.

In 1804, Karl Rudolphi and J.H.F. Link proved that cells had independent cell walls. Before, it had been thought that cells shared walls and that fluid passed between them this way.

The mode of formation of the cell wall was controversial in the 19th century. Hugo von Mohl (1853, 1858) advocated the idea that the cell wall grows by apposition. Carl Nägeli (1858, 1862, 1863) believed that the growth of the wall in thickness and in area was due to a process termed intussusception. Each theory was improved in the following decades: the apposition (or lamination) theory by Eduard Strasburger (1882, 1889), and the intussusception theory by Julius Wiesner (1886).

In 1930, Ernst Münch coined the term apoplast in order to separate the 'living' symplast from the 'dead' plant region, the latter of which included the cell wall.

By the 1980s, some authors suggested replacing the term cell wall, particularly as it was used for plants, with the more precise term extracellular matrix, as used for animal cells; 168 but others preferred the older term.

Cell walls serve similar purposes in those organisms that possess them. They may give cells rigidity and strength, offering protection against mechanical stress. In multicellular organisms, they permit the organism to build and hold a definite shape (morphogenesis). Cell walls also limit the entry of large molecules that may be toxic to the cell. They further permit the creation of stable osmotic environments by preventing osmotic lysis and helping to retain water. Their composition, properties, and form may change during the cell cycle and depend on growth conditions.

In most cells, the cell wall is flexible, meaning that it will bend rather than holding a fixed shape, but has considerable tensile strength. The apparent rigidity of primary plant tissues is enabled by cell walls, but is not due to the walls' stiffness. Hydraulic turgor pressure creates this rigidity, along with the wall structure. The flexibility of the cell walls is seen when plants wilt, so that the stems and leaves begin to droop, or in seaweeds that bend in water currents.

Think of the cell wall as a wicker basket in which a balloon has been inflated so that it exerts pressure from the inside. Such a basket is very rigid and resistant to mechanical damage. Thus does the prokaryote cell (and eukaryotic cell that possesses a cell wall) gain strength from a flexible plasma membrane pressing against a rigid cell wall.

The apparent rigidity of the cell wall thus results from inflation of the cell contained within. This inflation is a result of the passive uptake of water.

In plants, a secondary cell wall is a thicker additional layer of cellulose which increases wall rigidity. Additional layers may be formed by lignin in xylem cell walls, or suberin in cork cell walls. These compounds are rigid and waterproof, making the secondary wall stiff. Both wood and bark cells of trees have secondary walls.

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Other parts of plants such as the leaf stalk may acquire similar reinforcement to resist the strain of physical forces.

The primary cell wall of most plant cells is freely permeable to small molecules including small proteins, with size exclusion estimated to be 30-60 kDa. The pH is an important factor governing the transport of molecules through cell walls.

The walls of plant cells must have sufficient tensile strength to withstand internal osmotic pressures of several times atmospheric pressure that result from the difference in solute concentration between the cell interior and external solutions. Plant cell walls vary from 0.1 to several μm in thickness.

Up to three strata or layers may be found in plant cell walls:

- The primary cell wall, is generally a thin, flexible and extensible layer formed while the cell is growing.
- The secondary cell wall, a thick layer formed inside the primary cell wall after the cell is fully grown. It is not found in all cell types. Some cells, such as the conducting cells in xylem, possess a secondary wall containing lignin, which strengthens and waterproofs the wall. The middle lamella, a layer rich in pectins. This outermost layer forms the interface between adjacent plant cells and glues them together.
- The middle lamella is laid down first, formed from the cell plate during cytokinesis, and the primary cell wall is then deposited inside the middle lamella. The actual structure of the cell wall is not clearly defined and several models exist - the covalently linked cross model, the tether model, the diffuse layer model and the stratified layer model. However, the primary cell wall, can be defined as composed of cellulose microfibrils aligned at all angles. Cellulose microfibrils are produced at the plasma membrane by the cellulose synthase complex, which is proposed to be made of a hexameric rosette that contains three cellulose synthase catalytic subunits for each of the six units. Microfibrils are held together by hydrogen bonds to provide a high tensile strength. The cells are held together and share the gelatinous membrane called the middle lamella, which contains magnesium and calcium pectates (salts of pectic acid). Cells interact though plasmodesmata, which are inter-connecting channels of cytoplasm that connect to the protoplasts of adjacent cells across the cell wall.

In some plants and cell types, after a maximum size or point in development has been reached, a secondary wall is constructed between the plasma membrane and primary wall. Unlike the primary wall, the cellulose microfibrils are aligned parallel in layers, the orientation changing slightly with each additional layer so that the structure becomes helicoidal. Cells with secondary cell walls can be rigid, as in the gritty sclereid cells in pear and quince fruit. Cell to cell communication is possible through pits in the secondary cell wall that allow plasmodesmata to connect cells through the secondary cell walls.

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The presence of a cell wall in a plant cell distinguishes them from animal cell. It is the outermost layer of the cell which covers the plasma membrane. In the young cell, the cell wall is thin, elastic, soft, about 1-3μ thick whereas in mature cell, it is rigid, strong, and 5-10μ thick. The cell wall of parenchyma is thinner than those of collenchyma, sclerenchyma and xylem vessels. Cell wall formation begins at the telophase stage of the cell division. Fine granular structures known as phragmoplasts appear at the equatorial plane which condenses to form cell-plate or middle lamella. A plant cell may consist of either primary wall or the cell may contain both primary and secondary walls.

The structure of the cell wall is highly differentiated in some tissues. They possess a special sequence of their arrangements. The wall of a cell can be differentiated into following layers:

- Primary Cell Wall
- Secondary Cell Wall
- Middle Lamella

Primary Cell Wall: The first formed wall which develops on the new cell is called primary wall (Refer Figure 2.1). It develops in the young growing or meristematic and parenchymatous cells. The primary wall is comparatively thin and permeable. Certain epidermal cells of leaf and the stem also possess the cutin and cutin-waxes that makes the primary cell wall impermeable. It chiefly consists of cellulose which is strongly hydrophilic in nature. At first the primary wall is rather elastic and able to extend as the cell grows, but when more and more cellulose is deposited, it becomes more rigid. The meristem, cambial cell, parenchyma, collenchyma, root hairs, etc., possess primary walls. In fungi, the cell wall is composed of chitin.

Secondary Cell Wall: Next to the primary cell wall is another layer known as secondary cell wall. It is comparatively thicker than the primary wall (Refer Figure 2.1). The secondary cell wall is commonly found in the mature, permanent or non-growing cells. Secondary walls are more prominent in dead cell such as tracheids and sclerenchyma. In addition to primary wall, secondary wall is composed of lignin, hemicelluloses, pectic substances and a phenolic polymer which imparts hardness and mechanical rigidity. In the majority of tracheids and fibres secondary cell wall is differentiated into three layers-the outer layer (S_1), the central layer (S_2) and the inner layer (S_3). Of these layers, the central layer is usually the thickest. The S_1 and S_3 layers lie adjacent to the primary wall and cell lumen respectively.

Middle Lamella: This layer lies in between the two primary walls of adjacent cell. During the development of cell wall, the middle lamella is formed first. Middle lamella binds the adjoining cells firmly. It originates at the end of nuclear division and creates a new boundary between the two nuclei which had previously shared a common cytoplasm. As growth continues the primary wall materials are laid on either side of middle lamella. It is composed of calcium and magnesium pectate. In mature and aged cells, the middle lamella is dissolved and therefore the cells are

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loosened. The ripe fruits are soft and sweet in taste because the pectic substances of the middle lamella get dissolved due to the action of pectolytic enzymes.

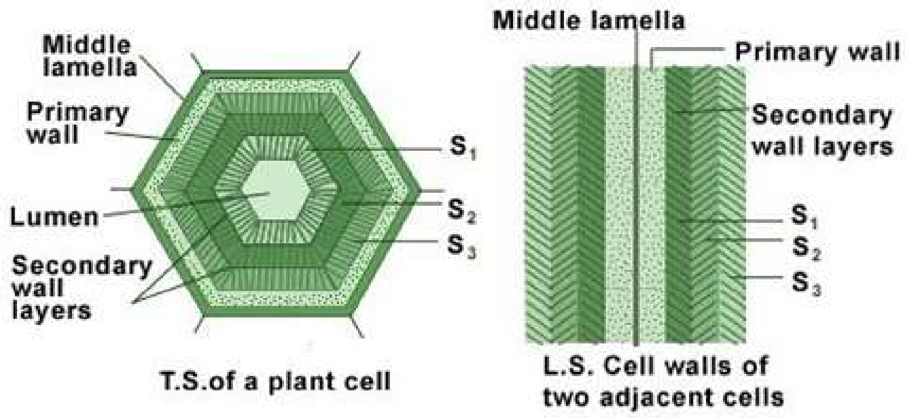

Fig. 2.1 *(A) T.S. of a Plant Cell (B) L.S. Cell Walls of Two Adjacent Walls*

Chemical Composition of Cell Wall

The primary cell wall consists of interwined cellulose fibres. It also consists of the depositions of pectin, lignin, hemicelluloses, etc. Cellulose is a long chain polysaccharide in which β D-glucose units are joined together by glycosidic linkages. Many chains of cellulose molecules lie parallel to each other to form the bundles. A bundle of 100 cellulose molecular chains forms the elementary fibril known as micelle. The 20 parallely arranged micelles form another bundle known as microfibril. It is bout 250A thick. Similarly, 250 microfibril form the large-sized bundle known as macrofibril. The macrofibrils ultimately form the main framework of the cell wall.

The hemicelluloses are the polysaccharides of pentose as well as hexose sugars like arabinose, xylose, mannose and galactose.

Pectins are group of polysaccharides which are rich in galacturonic acid, rhamnose, arabinose and galactose. The other pectin polysaccharides are arabinan, galactan, arabinogalactan I. Pectic polysaccharides are linked covalently to cellulose, proteins and phenols. Pectins are present in more amounts in middle lamella where they serve the function of cementing adjacent cells together.

Lignin is a phenolic polymer and the cell wall component of sclerenchyma tissue which includes fibres and sclereids. It is also present in the tracheids and vessels of xylem. In some cells, lignin deposits in response to attack of microorganisms. It is usually absent from growing walls or may be present in a very little amount. Initially, it is deposited over the middle lamella and gradually extends to primary walls that have developed secondary walls. Lignified walls form a waterproof system of xylem and resist the pathogens. It provides the mechanical strength to the plants. Besides lignin, other phenolic substances cutin and suberin are also present as a component of the cell wall.

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Functions of Cell Wall

- It protects the cell from adverse environmental conditions.
- It maintains a definite shape of the cell.
- It provides strength to the cell
- It also controls the cell expansion
- It permits the entry of molecules of different sizes.
- It determines the manner of cell division and growth.
- It possesses plasmodesmata through which cells remain connected with adjacent cells.
- It also protects the plants against pathogens.
- It separates one cell from the other.
- It also plays some important role in secretion, transpiration, absorption and translocation, etc.

Ultrastructure of Cell wall

The cell wall consisting of cellulose microfibrils embedded in a gel like non-cellulosic matrix. The microfibrillar phase is composed of microfibrils which are long, thin structure with oval or circular in cross section and having the width of 10nm in higher plants. Cellulose , a kind of polysaccharide composed of purely glucose molecule linked to each other by β1-4 bond and are unbranched 1,4 glucan. The glucose residues are linked together with oxygen atoms (Refer Figure 2.2). There are at least 8000 to 15,000 glucose monomers per cellulose molecules and 0.25ìm to 0.5 μm long. The molecules are flat and ribbon like, and lie parallel to each other. Hydrogen bonding occurs between the molecules, thus crystallizing and producing aggregates. These aggregates are called microfibrillar. Each microfibril contains 40 to 70 chains, which lie side by side. The cellulose molecules form chains, which are at some regions of microfibrils, are arranged in parallel into 3-dimensional crystalline lattices termed micelles. The lattices are connected with each other by intra and inter molecular hydrogen bonds. The spaces between microfibrils are filled up with lignin, cutin, pectin, hemicelluloses, etc. Thus, the microfibrils have good mechanical strength.

The microfibrils are arranged to from macrofibrils which are composed of 5,00,000 cellulose molecules in transection. Several macrofibrils are aggregated to form cell wall.

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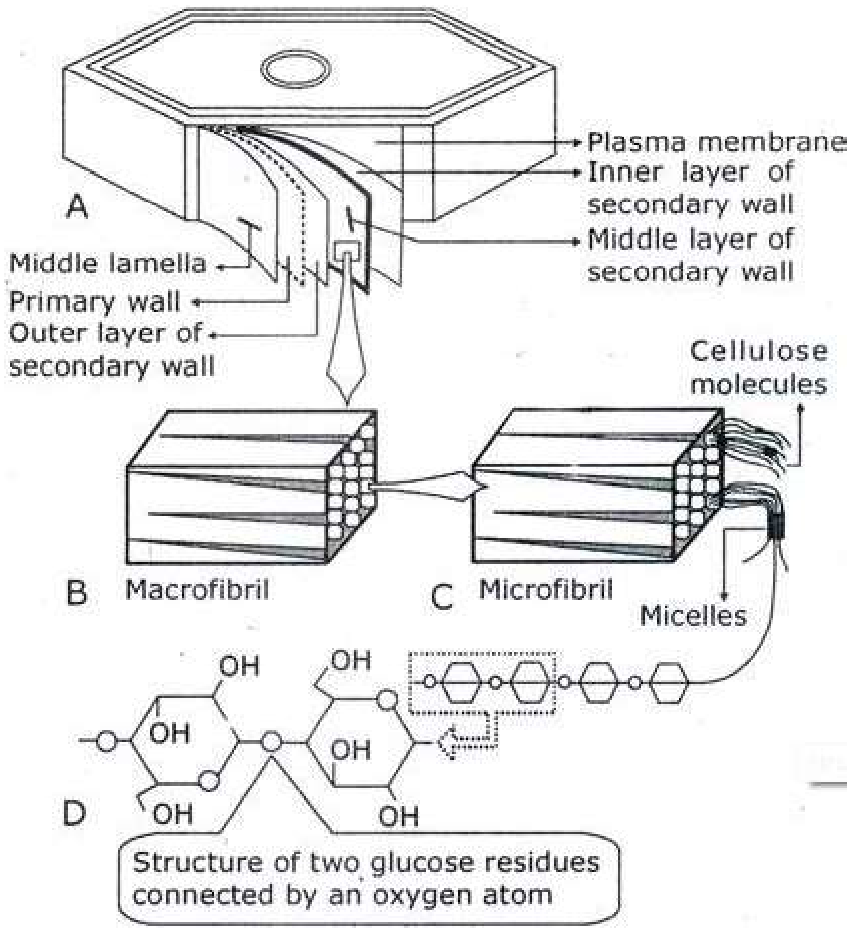

Fig. 2.2 *Ultrastructure of Cell Wall*

Thickening of Cell Wall

The cell wall of some cells like xylem, etc. during secondary growth becomes very thick and hard. It is because that lignin and other materials are deposited upon it. As soon as the lignin starts depositing on the primary wall, the protoplasm of the cell starts decreasing. After deposition, the protoplasm of the cell is lost and cell becomes dead. The deposition of lignin takes place in a definite sequence, first it is deposited on middle lamella, then on primary wall and finally on secondary wall. Due to the deposition of lignin, cell wall becomes very thick and it may be of the following shapes (Refer Figure 2.3):

- **Annular**: When the lignin is deposited in the form of rings.
- **Spiral**: When the lignin is deposited in the form of helices.
- **Scalariform**: When the lignin is deposited in the form of ladder.
- **Reticulate**: When the lignin is deposited in the form of a net.
- **Pitted**: When the thickening is present on the entire cell wall except at certain places.

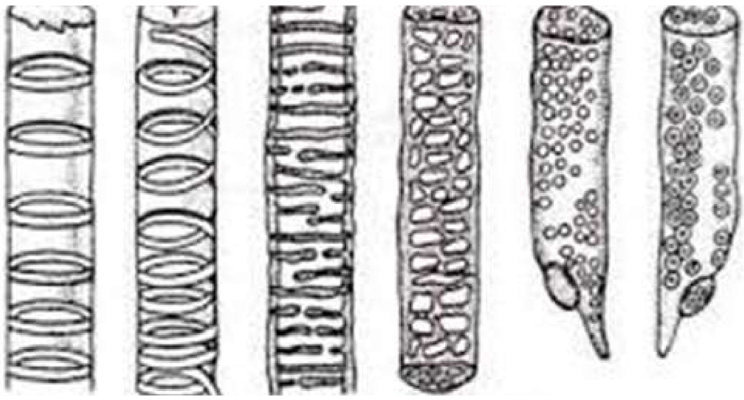

Fig. 2.3 *Lignified Thickenings in Xylem Tracheids*

Plasmodesmata

These are thread like structures which form a connection between the cytoplasm of adjacent cells (Refer Figure 2.4). They are present in higher plants and fluctuate widely in distribution. These are commonly present in primary pit fields and pit membranes of young and mature living cells respectively. In a young dividing cell, the number of plasmodesmata varies from 1000 to 10,000 and their distribution is not uniform. Plasmodesma originates during cytokinesis when cell plate is formed. It is formed at those regions of the cell plate where the ER is present and prevents the fusion of vesicles. At this area, cellulose microfibrils and pectic substances are not accumulated and therefore intercellular canal is formed. It has also been observed that desmotubules are continuous with the ER of adjoining cells through intercellular canals. Plasmodesmata occurs in thick cell walls also, for example endosperms of seeds of date palm and coffee.

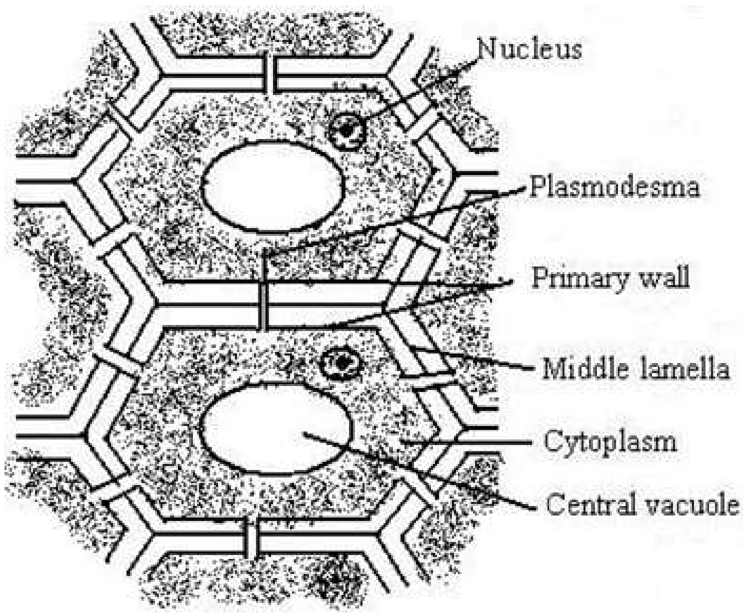

Fig. 2.4 *T.S. of a Cell Showing Plasmodesmata between two Adjacent Cells*

Functions of Plasmodesmata

- It helps in the short distance transport of materials.
- Viruses can pass through the plasmodesmata.
- Plant hormones can pass through plasmodesmata.
- The movement through plasmodesmata is bidirectional.
- Small ions and molecules can easily pass through plasmodesmata.

Chemical Changes in the Cell Wall

Following chemical changes may occur during the growth of cell wall:

- **Lignification**: It is the deposition of lignin.
- **Cutinization**: It is the conversion of cellulose into cutin in the cell wall.
- **Suberization**: It is the deposition of suberin on the cork cell wall.
- **Mucilaginous**: It is the conversion of cellulose into mucilage in the cell wall.
- **Mineralization**: It is the deposition of mineral substances like silica, calcium carbonate and calcium oxalate on the cell wall.

Pits

There are certain areas where the cell wall remains thin even after the formation of secondary cell wall. These areas consist of primary wall material only and when viewed under the electron microscope, it appears as a beaded structure because of the presence of depressions. These structures in primary wall are known as primary pit fields, primary pits or primordial pits. The important feature of primary pit field is the presence of large number of plasmodesmata through which substances can easily pass from one cell to another. Plasmodesmata play an important role in the transport of materials and the relay of stimuli.

In addition to the primary pits on the primary wall, secondary cell wall is also provided with cavities or depressions which are known as pits. The cytoplasmic continuity is maintained with the help of these pits. Generally each pit has a complementary pit exactly opposite to it in the wall of neighbouring cell. These two pits of adjacent wall are known as pit-pair and the plasma membrane separating the two pit cavities of the pit-pair is called pit membrane or closing membrane. The opening of the pit on the side facing the lumen of the cell is called pit aperture.

Morphologically, there are two types of pits:

- Simple Pits
- Bordered Pits

In the bordered pits, secondary wall forms a dome shape structure (overarching) over the pit cavity. This arching takes place on both sides of the pit (Refer Figure 2.5). When there is no as such dome shaped structure or overarching the pits are called simple pits. Simple pits are present in parenchyma cells with thickened walls in libriform fibres and in sclereids. If both the pits of a pair are simple, it is known as simple pit-pair and if both are bordered, it is called bordered pit-pair. If one of the pits is simple and the other bordered it is called half bordered pit-pair. If the pit has no complementary pit in the neighbouring cell it is termed as blind pit.

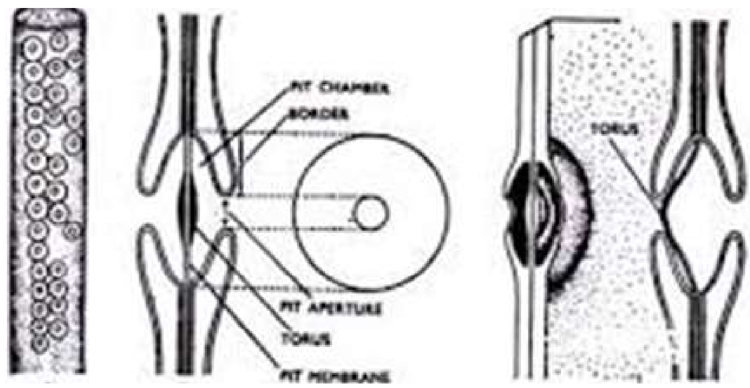

Fig. 2.5 *Bordered Pits*

In bordered pits, plasma membrane or closing membrane is thickened in its central portion and it is disc shaped. This thickening is known as torus (Refer Figure 2.6). The diameter of the torus is wider than pit aperture. Torus is well developed in the bordered pits of Gymnosperms especially of Coniferales and it is surrounded by bundles of microfibrils, known as margo. When the torus is in the middle, water can easily pass from one tracheid to another. When the torus is in lateral position, the channel for the water is prevented. The pit membrane loses flexibility and therefore pit becomes nonfunctional. This pit is called aspirated pit and are present in heartwood of *Pinus*.

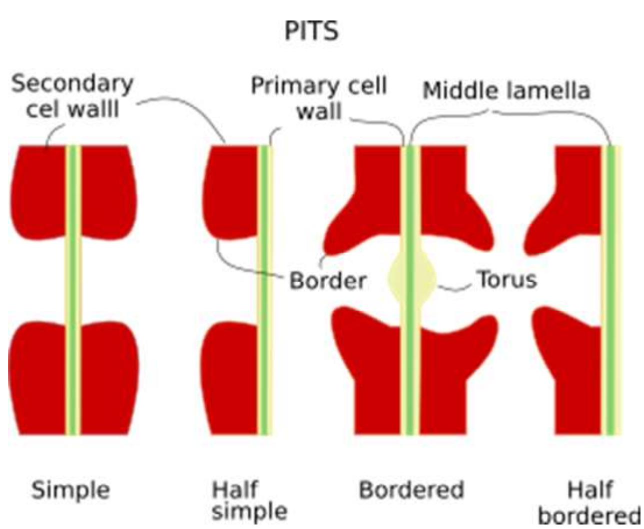

Fig. 2.6 *Diagram Showing Simple Pit and Bordered Pit*

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Check Your Progress

1. What is a cell wall?
2. In how many parts wall of a cell is differentiated?
3. Give the functions of cell wall.
4. Distinguish between scalariform, reticulate and pitted.
5. Give few functions of plasmodesmata.
6. How many types of pits are there?

2.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. A cell wall is a structural layer surrounding some types of cells, just outside the cell membrane. It can be tough, flexible, and sometimes rigid. It provides the cell with both structural support and protection, and also acts as a filtering mechanism.
2. The wall of a cell can be differentiated into following layers:
   - Primary Cell-Wall
   - Secondary Cell-Wall
   - Middle Lamella
3. Following are the functions of cell wall:
   - It protects the cell from adverse environmental conditions.
   - It maintains a definite shape of the cell.
   - It provides strength to the cell
   - It also controls the cell expansion
   - It permits the entry of molecules of different sizes.
   - It determines the manner of cell division and growth.
   - It possesses plasmodesmata through which cells remain connected with adjacent cells.
4. Scalariform: When the lignin is deposited in the form of ladder.

   Reticulate: When the lignin is deposited in the form of a net.

   Pitted: When the thickening is present on the entire cell wall except at certain places.
5. Following are the functions of plasmodesmata:
   - It helps in the short distance transport of materials.
   - Viruses can pass through the plasmodesmata.
   - Plant hormones can pass through plasmodesmata.

- The movement through plasmodesmata is bidirectional.
- Small ions and molecules can easily pass through plasmodesmata.

6. Morphologically, there are two types of pits, i.e., as follows:
   - Simple pits
   - Bordered pits

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2.4 SUMMARY

- A cell wall is a structural layer surrounding some types of cells, just outside the cell membrane.
- Cell wall can be tough, flexible, and sometimes rigid. It provides the cell with both structural support and protection, and also acts as a filtering mechanism.
- Cell walls are present in most prokaryotes (except mycoplasma bacteria), in algae, plants and fungi but rarely in other eukaryotes including animals.
- A major function of cell wall is to act as pressure vessels, preventing over-expansion of the cell when water enters.
- The composition of cell walls varies between species and may depend on cell type and developmental stage.
- The primary cell wall of land plants is composed of the polysaccharides cellulose, hemicelluloses and pectin.
- Algae possess cell walls made of glycoproteins and polysaccharides such as carrageenan and agar that are absent from land plants.
- In bacteria, the cell wall is composed of peptidoglycan. The cell walls of archaea have various compositions, and may be formed of glycoprotein S-layers, pseudopeptidoglycan, or polysaccharides.
- Fungi possess cell walls made of the N-acetylglucosamine polymer chitin. Unusually, diatoms have a cell wall composed of biogenic silica.
- A plant cell wall was first observed and named (simply as a wall) by Robert Hooke in 1665.
- Each theory was improved in the following decades: the apposition (or lamination) theory by Eduard Strasburger (1882, 1889), and the intussusception theory by Julius Wiesner (1886).
- In 1930, Ernst Münch coined the term apoplast in order to separate the 'living' symplast from the 'dead' plant region, the latter of which included the cell wall.
- Cell walls also limit the entry of large molecules that may be toxic to the cell. They further permit the creation of stable osmotic environments by preventing osmotic lysis and helping to retain water.
- In most cells, the cell wall is flexible, meaning that it will bend rather than holding a fixed shape, but has considerable tensile strength.

- The apparent rigidity of primary plant tissues is enabled by cell walls, but is not due to the walls' stiffness.
- Hydraulic turgor pressure creates this rigidity, along with the wall structure. The flexibility of the cell walls is seen when plants wilt, so that the stems and leaves begin to droop, or in seaweeds that bend in water currents.
- In plants, a secondary cell wall is a thicker additional layer of cellulose which increases wall rigidity.
- The pH is an important factor governing the transport of molecules through cell walls.
- The actual structure of the cell wall is not clearly defined and several models exist - the covalently linked cross model, the tether model, the diffuse layer model and the stratified layer model.
- Microfibrils are held together by hydrogen bonds to provide a high tensile strength.
- The cells are held together and share the gelatinous membrane called the middle lamella, which contains magnesium and calcium pectates (salts of pectic acid).
- Cells interact though plasmodesmata, which are inter-connecting channels of cytoplasm that connect to the protoplasts of adjacent cells across the cell wall.
- The cell wall of parenchyma is thinner than those of collenchyma, sclerenchyma and xylem vessels.
- A plant cell may consist of either primary wall or the cell may contain both primary and secondary walls.
- The structure of the cell wall is highly differentiated in some tissues. They possess a special sequence of their arrangements.
- Primary cell wall is the first formed wall which develops on the new cell is called primary wall. It develops in the young growing or meristematic and parenchymatous cells.
- The meristem, cambial cell, parenchyma, collenchyma, root hairs, etc., possess primary walls.
- Secondary walls are more prominent in dead cell such as tracheids and sclerenchyma.
- Middle lamella layer lies in between the two primary walls of adjacent cell. During the development of cell wall, the middle lamella is formed first.
- The hemicelluloses are the polysaccharides of pentose as well as hexose sugars like arabinose, xylose, mannose and galactose.
- Pectins are group of polysaccharides which are rich in galacturonic acid, rhamnose, arabinose and galactose.
- Lignin is a phenolic polymer and the cell wall component of sclerenchyma tissue which includes fibres and sclereids.

- Lignified walls form a waterproof system of xylem and resist the pathogens. It provides the mechanical strength to the plants.
- The cell wall consisting of cellulose microfibrils embedded in a gel like non-cellulosic matrix.
- The microfibrillar phase is composed of microfibrils which are long, thin structure with oval or circular in cross section and having the width of 10nm in higher plants.
- Cellulose , a kind of polysaccharide composed of purely glucose molecule linked to each other by â1-4 bond and are unbranched 1,4 glucan.
- The deposition of lignin takes place in a definite sequence, first it is deposited on middle lamella, then on primary wall and finally on secondary wall.
- These are thread like structures which form a connection between the cytoplasm of adjacent cells.
- In a young dividing cell, the number of plasmodesmata varies from 1000 to 10,000 and their distribution is not uniform.
- Pits are certain areas where the cell wall remains thin even after the formation of secondary cell wall.
- Plasmodesmata play an important role in the transport of materials and the relay of stimuli.
- Torus is well developed in the bordered pits of Gymnosperms especially of Coniferales and it is surrounded by bundles of microfibrils, known as margo.
- The pit membrane loses flexibility and therefore pit becomes nonfunctional. This pit is called aspirated pit and are present in heartwood of *Pinus*.

2.5 KEY WORDS

- **Cell wall:** A cell wall is a structural layer surrounding some types of cells, just outside the cell membrane.
- **Primary cell wall**: Primary cell wall is the first formed wall which develops on the new cell is called primary wall.
- **Lignification:** Lignification is the deposition of lignin.
- **Cutinization:** Cutinization is the conversion of cellulose into cutin in the cell wall.
- **Suberization:** Suberization is the deposition of suberin on the cork cell wall.
- **Mucilaginous:** Mucilaginous is the conversion of cellulose into mucilage in the cell wall.
- **Mineralization:** Mineralization is the deposition of mineral substances like silica, calcium carbonate and calcium oxalate on the cell wall.

2.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

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Short Answer Questions

1. What is cell wall?
2. What is middle lamella?
3. What is primary cell wall?
4. Give chemical composition of cell wall.
5. What are pectins?
6. Give some functions of cell wall.
7. List some functions of Plasmodesmata.

Long Answer Questions

1. Discuss about cell wall in detail.
2. Distinguish between primary and secondary cell wall.
3. Write a note on chemical composition of cell wall.
4. Elaborate a note on ultrastructure of cell wall.
5. Write a note on thickening of cell wall.
6. Write a note on plasmodesmata.
7. Discuss about chemical changes in the cell wall.
8. Distinguish between simple pits and bordered pits.

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UNIT 3 STRUCTURAL DIVERSITY AND PHYLOGENETIC SPECIALIZATION OF XYLEM AND PHLOEM

Structure

3.0 INTRODUCTION

Xylem is a type of tissue in vascular plants that transports water and some nutrients from the roots to the leaves. Phloem is the other type of transport tissue; it transports sucrose and other nutrients throughout the plant. Xylem and phloem give vascular plants their classification; they are the vascular tissues that transport substances throughout the plant.

The main function of xylem is to transport water, and some soluble nutrients including minerals and inorganic ions, upwards from the roots to the rest of the plant. Xylem cells form long tubes that transport materials, and the mixture of water and nutrients that flows through the xylem cells is called xylem sap. These substances are transported through passive transport, so the process doesn't require energy. The phenomenon that allows xylem sap to flow upwards against gravity is called capillary action. This occurs when surface tension makes liquid move upward. Water is also aided in moving up through the xylem by adhering to the xylem cells. However, it gets harder to work against gravity to transport materials as a plant grows taller, so xylem sets an upper limit on the growth of tall trees.

In vascular plants, phloem is the living tissue that transports the soluble organic compounds made during photosynthesis and known as photosynthates, in particular the sugar sucrose, to parts of the plant where needed. This transport process is called translocation. In trees, the phloem is the innermost layer of the bark, hence the name, derived from the Greek word phloios meaning 'bark'. The term was introduced by Nägeli in 1858.

Phloem, also called bast, tissues in plants that conduct foods made in the leaves to all other parts of the plant. Phloem is composed of various specialized cells called sieve tubes, companion cells, phloem fibres, and phloem parenchyma cells. Primary phloem is formed by the apical meristems of root and shoot tips; it may be either protophloem, the cells of which are matured before elongation of the area in which it lies, or metaphloem, the cells of which mature after elongation. Sieve tubes of protophloem are unable to stretch with the elongating tissues and are torn and destroyed as the plant ages. The other cell types in the phloem may be converted to fibres. The later maturing metaphloem is not destroyed and may function during the rest of the plant's life in plants such as palms but is replaced by secondary phloem in plants that have a cambium.

Sieve tubes, which are columns of sieve-tube cells having perforated, sieve like areas in their lateral or end walls, provide the channels in which food substances travel. Phloem parenchyma cells, called transfer cells and border parenchyma cells, are located near the finest branches and terminations of sieve tubes in leaf veinlets, where they also function in the transport of foods. Phloem fibres are flexible long cells that make up the soft fibres of commerce.

In this unit, you will study about structural diversity and phylogenetic specialization of xylem and phloem in detail.

3.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the structural diversity of xylem and phloem
- Explain phylogenetic specialization of xylem and phloem

3.2 STRUCTURAL DIVERSITY AND PHYLOGENETIC SPECIALIZATION OF XYLEM AND PHLOEM

In biology, tissue is a cellular organisational level between cells and a complete organ. A tissue is an ensemble of similar cells and their extracellular matrix from the same origin that together carry out a specific function. Organs are then formed by the functional grouping together of multiple tissues.

The study of human and animal tissues is known as histology or, in connection with disease, histopathology. For plants, the discipline is called plant anatomy. The classical tools for studying tissues are the paraffin block in which tissue is embedded and then sectioned, the histological stain, and the optical microscope. In the last couple of decades, developments in electron microscopy, immuno-fluorescence, and the use of frozen tissue sections have enhanced the detail that can be observed in tissues. With these tools, the classical appearances of tissues

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can be examined in health and disease, enabling considerable refinement of medical diagnosis and prognosis.

The complex tissues are heterogeneous in nature, being com-posed of different types of cell elements. The latter remain contiguous and form a struc-tural part of the plant, adapted to carry on a specialised function.

Xylem and phloem are the complex tissues which constitute the component parts of the vascular bundle. They are also called vascular tissues. The vascular system occupies a unique position in the plant body, both from the point of view of prominence and physiological importance. The term 'vascular plants' has been in use since a long time.

In recent years a new phylum Tracheophyta has been introduced to include all vascular plants; it covers pteridophyta and spermatophyta of old classifications. Vascular bundles form a continuous and inter-connected system in the different organs of the plants. They are primarily responsible for transport of water and solutes and elaborated food matters. Complex tissue is composed of more than one type of cell. Xylem and phloem which are known as vascular tissue are the examples of complex tissue. Xylem and phloem together constitute the conducting tissue in the plants.

3.2.1 Xylem

It is the water conducting tissue which is made up of four different types of cells (tracheids, vessels, xylem fibre and xylem parenchyma) associated with each other. Xylem occurs in both primary and secondary vascular tissues. The procambium develops into primary xylem and vascular cambium gives rise to secondary xylem.

Tracheids: Tracheid is a single-celled, imperforate, elongated structure with tapering ends. The cell is characterized by the presence of lignified secondary walls having pits on their walls (Refer Figure 3.1). Tracheids are situated one above the other and their end walls are in contact with others. Water diffuses through pits. Pits may be simple, bordered or half bordered.

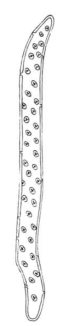

Fig. 3.1 *Tracheid Showing Pits*

Secondary wall thickenings in the primitive formed xylem (protoxylem) are present in the form of rings (annular), or helices (spiral), whereas in later formed xylem (metaxylem) thickenings are in the form of ladder (scalariform) and network

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shape (reticulate) and pit shape (pitted). Ontogenetically pitted thickening is the most advanced type of thickening. Tracheids occur in all groups of vascular plants (Refer Figure 3.2).

The function of tracheids is the conduction of water and minerals in solution. It also provided the mechanical strength.

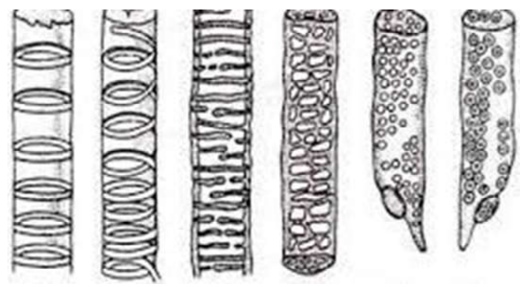

Fig. 3.2 *Lignified Thickenings in Xylem Tracheids*

Phylogeny of Tracheids: Vascular cryptogams have very long tracheids, gymnosperms consists the tracheids of intermediate length. There are different types of secondary wall thickeneings (annular, helical, scalariform, reticulate and bordered pit) in which pitted thickening is considered to be the most advanced type. Tracheids with annular thickening are the most primitive type as it has been reported from one of the oldest fossils, *Cooksonia,* a leafless vascular plant. The scalariform thickening has been originated from helical as the helical bands joined at certain areas.

Vessels

Vessels are also non-living lignified secondary cell wall. Vessels members are joined into long continuous tubes of varying length. Vessels are characterized by the presence of perforated ends. The part of the cell wall which bears perorations is known as perforation plates (Refer Figure 3.3). If the perforation plate consists of one large perforation it is called simple perforation plate, or if it consists of more than one it is known as multiple perforation plate. In multiple perforation plate, when perforations are arranged in a parallel series, it is scalariform perforation plate, when they are arranged in the form of network, it is reticulate perforation plate and when the perforations are in a circular manner it is termed as foraminate perforation plate (Refer Figure 3.4).

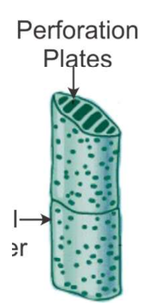

Fig. 3.3 *Vessel Showing Perforation Plate at their End Wall*

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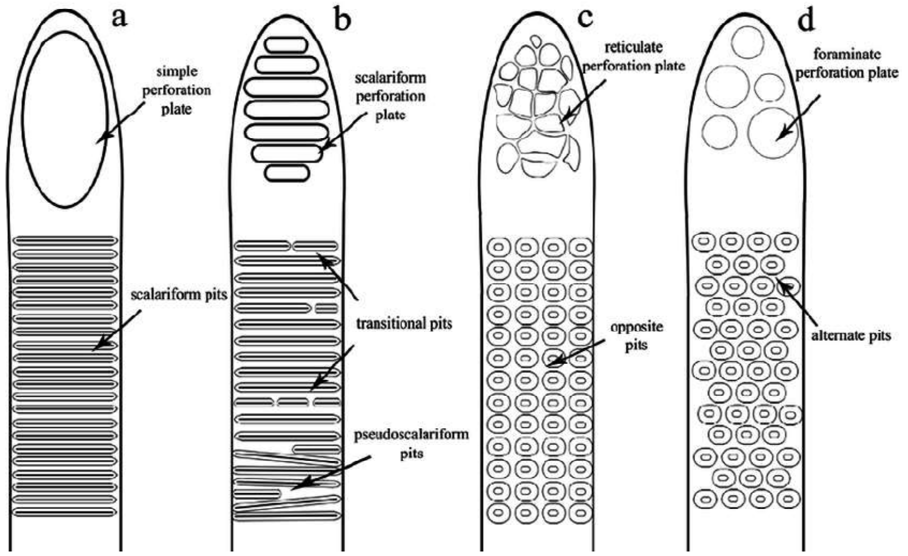

Fig. 3.4 *Diagram showing Simple and Multiple Perforation Plates in Vessels*

Vessels help in the conduction of water and dissolved mineral nutrients and also provide mechanical strength.

Phylogeny of Vessel

The following characters are used to trace the trends of evolutionary specialization.

Phylogeny of Tracheary Elements: The tracheary elements have developed during the evolution of land plants. In the lower vascular plants the func-tion of conduction and support were combined in the tracheids.

With increasing specialisation woods evolved with conducting elements—the vessel members being more efficient in conduction that in providing mechanical support. On the other hand fibres evolved as principal supporting tissue.

Thus from the primitive tracheids two lines of specialisa-tion diverged—one toward the vessel and the other toward the fibre.

The following structural features may be taken as the basis in support of the evolu-tion of the tracheary elements from primitive tracheids which are usually long imper-forate cells with small diameter, angular in cross-section, having lignified scalariformly pitted walls.

The primitive vessels are also elongate bodies like the tracheids with rather small diameter and tapering ends. Similar condition is still noticed in lower dicotyle-dons. With evolutionary advance they gradually become shorter and wider, often be-coming drum-shaped in appearance.

The wall of the primitive tracheid is rather thin, more or less of equal thickness, and it is angular in cross-section. Same condition prevails in primitive vessels. With progressive advance considerable thickening appeared and the vessels became circular or nearly so in cross-section.

In the primitive vessels the perforation plates are multiple, usually scalariform with numerous bars, and oblique end-walls. Progressive increase in specialisation led to gradual decrease in the number of bars and their ultimate disappearance, so that the perforation plates become simple with transverse end-walls. These are positively advanced characters.

The pitting of the vessel wall also changed from early scalariform arrangement, characteristic of tracheids, to small bordered pit pairs, first in opposite (arranged in transverse rows) and ultimately in alternate (arranged spirally or irregularly) pattern. Moreover the pit pairs between vessels and parenchyma changed from bordered to half-bordered and then to simple.

In the specialisation of the xylem fibres adapted for more efficient support there has been steady increase in thickness of the wall leading to decrease in cell-lumen. The pits changed from elongate to circular, the borders becoming reduced and functionless, and ultimately disappeared. Thus the evolutionary sequence was from tracheids, through fibre-tracheids to libiriform fibres.

Length: Vessels have been originated from the tracheids which are long and elongated cells. Therefore, long vessel is considered to be primitive whereas the advanced form is wide, short and narrow. In the phylogenetic evolution of the tracheids the diameter of the cell has increased and the wall has become perforated by large openings. Because of these specializations water can move from cell to cell without any resistance.

End Wall: Vessel with transverse end wall is an advanced feature whereas vessel with long slanted end is a primitive feature.

Perforation Plate: The primitive long vessels have scalariform perforation plate (parallel series) with many bars. During the evolution, number of bars and number of pores both have been reduced and therefore, the advanced form is simple perforation plate with no bars. In scalariform perforation plate, the bars may offer resistance to the flow of water. Simple perforation with circular rim is more advanced than long oval rim. The simple perforation plate with circular rim in a transverse end-wall is a characteristic feature of an advanced vessel which is beneficial for the conduction of water (Refer Figure 3.5). In these vessels, adhesive interaction between water molecules and cellulosic cell wall is greatly reduced and this reduction helps in the easy flowing of water.

Lateral Wall Pitting: Scalariform pitting is considered to be the primitive type as it is associated with long vessels. The short vessel having alternate pitting is an advanced character. Vessels with medium length are associated with transitional and opposite pitting.

Thickening: Spiral thickening on the secondary wall is an advanced feature.

Grouping: Vessels may be present in groups or single. In a group the vessel may be arranged in radial, oblique or tangential lines. The presence of a single vessel represents the primitive character whereas the grouping of vessels is an advanced character.

Vessels are polyphyletic in origin. Vessels are confined only to the angiosperms except in Pteridophytes (*Selaginella, Equisetum*), four ferns (*Pteridium*, *Marsilea*, *Actiniopteris* and *Regnellidium*) and Gymnosperms (*Ephedra*, *Gnetum* and *Welwitschia*). The presence of vessels in the above mentioned genera except in angiosperms is considered as anomalies. However in some angiospermic families vessels are absent such as Winteraceae, Trochodendraceae and Tetracentraceae. In some monocotyledons (for example, *Yucca*, *Dracaena*) vessels are absent from the stems and leaves.

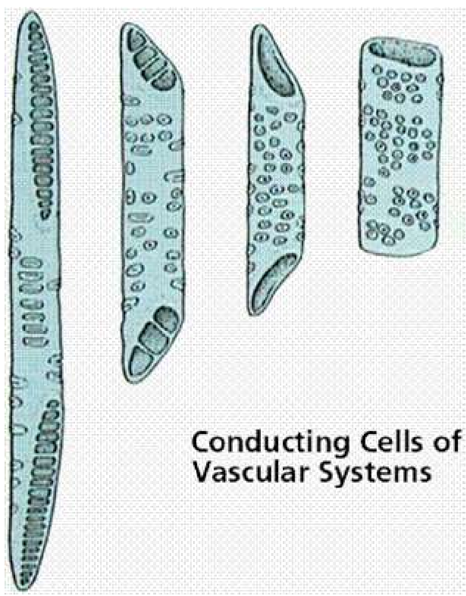

Fig. 3.5 *Perforation Plate from Multiple to Simple*

Xylem Fibre: Fibres are long cells present in both primary and secondary xylem but predominantly in secondary xylem. In primary xylem it originates from procambium and in secondary xylem it originates from fusiform initials of vascular cambium. They have thick walls with the presence of simple and bordered both types of pits on their walls (Refer Figure 3.6). Due to the deposition of lignin, lumen of fibre becomes narrow. They are also known as xylary fibre and wood fibre. Fibres may be sepate or aseptate.

There are basically two types of xylary fibres:

- **Libriform Fibre**: These fibres are having thick walls with simple pits with a very small lumen.
- **Fibre-Tracheid**: These fibres are shorter than libriform fibre, having thin walls with bordered pits with a very small lumen.

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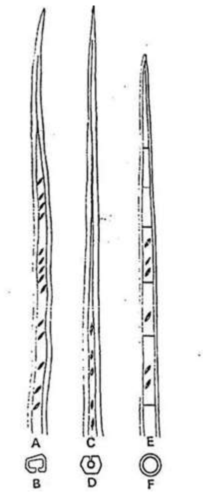

Fig. 3.6 Libriform Fibre and Fibre Tracheid

In addition to these two, there is another third type of fibre which is present in reaction wood of angiosperms. It is known as gelatinous or mucilaginous fibre. This fibre does not have the deposition of lignin instead of this secondary wall has cellulose in its innermost layer termed G layer. This layer is hygroscopic in nature.

Phylogeny of Fibres: Fibres have been originated from tracheids (Refer Figure 3.7). In the course of evolution, length of fibre and size of bordered pits both are reduced and thickness of cell wall has been increased. In secondary xylem of dicots, libriform fibres are evolved from tracheids, then fibre tracheids and last libriform fibre. Prominent bordered pits are present on the common wall of tracheid, in fibre traceids bordered pits have less developed border and in libriform fibre only simple pits are present. In libriform fibre cell wall is thicker than fibre-tracheid.

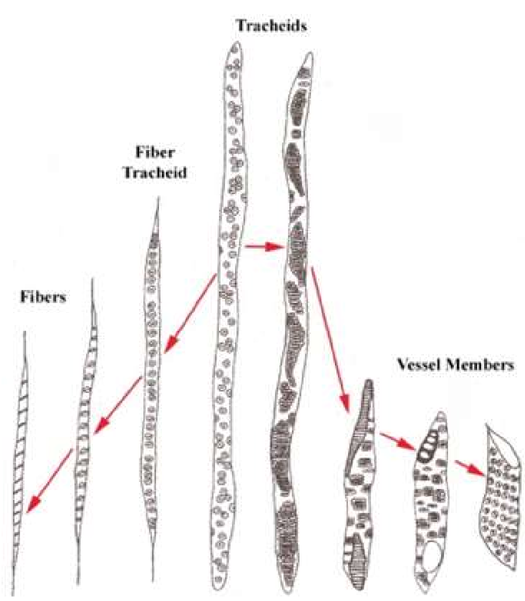

Fig. 3.7 Evolution of Fibres and Vessels from Tracheids

Xylem Parenchyma: Xylem parenchyma is present in both primary and secondary xylem. In primary xylem the cells of parenchyma are thin walled and made up of cellulose. Parenchyma forms a major part of primary xylem. It originates from procambium whereas in secondary xylem it develops from vascular cambium. In secondary xylem parenchyma is thick walled, lignified and it may consist of simple and bordered pits. In secondary xylem parenchyma is of two types:

- Axial Parenchyma or Wood Parenchyma
- Ray Parenchyma

Axial parenchyma originates from fusiform initial and arranged in vertical series whereas ray parenchyma originates from ray initials and arranged in a radial transverse series.

The main function of parenchyma is to store food material such as starch, oil fat and other ergastic substances. The ray parenchyma of secondary xylem is associated with radial conduction of water.

3.2.1 Phloem

Phloem is the principal food conducting tissue which is associated with xylem in the vascular system. Phloem occurs in both primary and secondary vascular tissues. The procambium develops into primary phloem and vascular cambium gives rise to secondary phloem. Primary and secondary phloem consists of same type of tissues. In primary phloem there is axial system but in secondary phloem there are axial and radial systems. In root, phloem occurs in the form of patches alternating with xylem (Radial condition). In stem, xylem and phloem is present on the same radius (conjoint), and phloem is external to the xylem (collateral). In Cucurbitaceae, bicollateral condition is present where xylem is surrounded by inner and outer phloem. Usually secondary phloem is present outside but in some plants, more amount of secondary phloem is produced which gets intruded in the secondary xylem. This is known as included phloem or interxylary phloem. Phloem is composed of four types of cells:

Sieve Elements: Sieve elements are characterized by the presence of sieve areas and absence of nuclei in the mature cells. There are two kinds of sieve elements sieve cells and sieve tube elements.

Sieve cells are present in Gymnosperms and Pteridophytes. They have a similar degree of specialization and there are no regions that can be distinguished as sieve plates.

Sieve tube elements are present in Angiosperms. There are certain sieve areas which are highly specialized than others and these sieve areas occur on the transverse end walls to form sieve plates (Refer Figure 3.8). Sieve tube consists of longitudinal files of cells that are connected with each other through sieve areas present at their end walls. Sieve areas appear as depressed area in the wall where sieve pores occur. Through these sieve pores the protoplast of one sieve tube member is connected to the other neighbouring tube and therefore continuity is maintained and a long sieve tube is formed. When there is only one sieve area it is known as simple sieve plate (for example *Cucurbita*) (Refer Figure 3.9) and if more than one sieve area is present it is known as compound sieve pate (for example, *Vitis*, *Pyrus*). There may be variation in the size of pores of sieve areas. They may be less than one micron and may be more than ten microns in diameter. The cell wall of sieve tube is composed of mainly cellulose and pectin. The thickness of sieve elements varies but usually they are thicker than the neighbouring parenchyma cells. The inner wall layers have glistening properties and therefore they are known as nacreous thickenings. These thickenings have glistening properties and are composed of microfibrils. Nacreous wall is absent from the region of sieve plate.

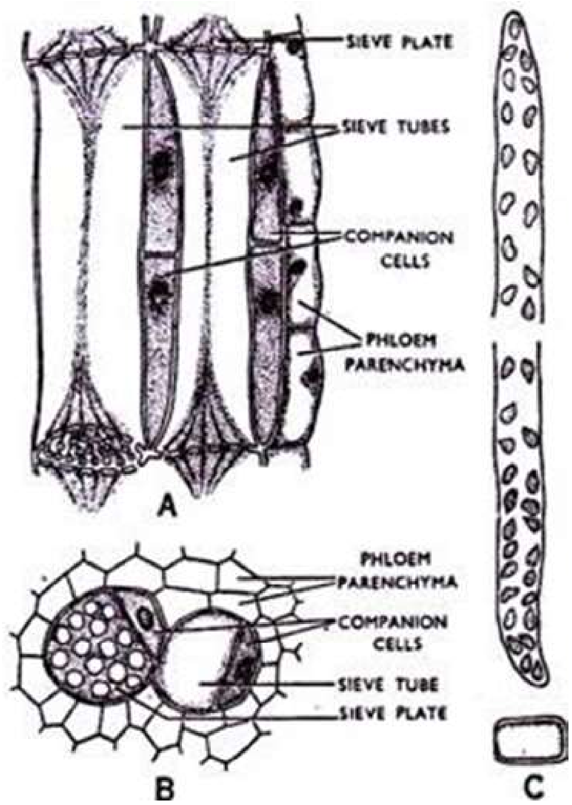

Fig. 3.8 *A. Sieve Tube in L.S.; B. same in T.S.; C. Sieve Cell in L.S. and T.S*

Sieve tubes are the only living cells in which the nuclei are absent from the mature protoplast. The mature protoplast is also devoid of ribosomes and dictysomes. The young sieve tube contains nucleus, dictyosomes, ribosomes, endoplasmic reticulum, plastids, mitochondria and other cell organelles. Degeneration of nucleus starts during the differentiation of sieve elements.

A large central vacuole and a thin layer of parietal cytoplasm are present in mature sieve elements. In dicotyledons, a slimy substance of proteinaceous nature has been observed in the vacuole along with the sap. The slime originates in the cytoplasm and is termed as p-proteins. These proteins are present only in dicotyledons and rare in monocotyledons. These are absent in Gymnosperms (except *Ephedra*) and Pteridophytes. In young sieve elements, these bodies consist of aggregates of tubules, designated as P_1-protein whereas in mature sieve elements these tubules are dispersed in the cytoplasm to form groups known as P_2-proteins. If sieve element is injured, P-proteins plug the pore of sieve plate and therefore eliminate the leaking of substances when plant is wounded. This plug is known as slime plug.

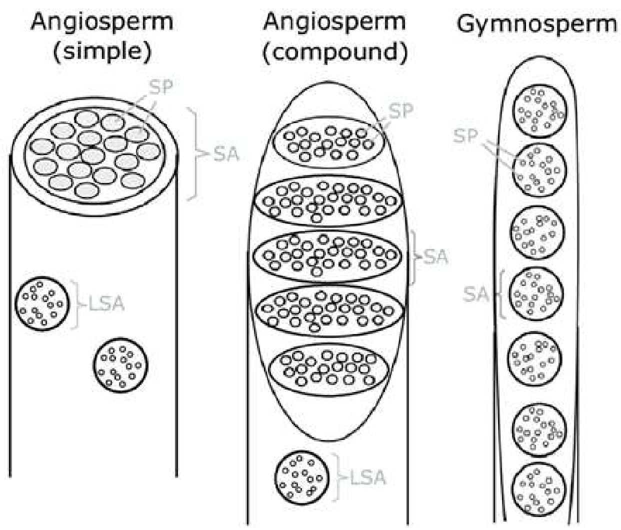

***Fig. 3.9** Schematic drawing of Phloem Sieve Element End Wall Types*

Around each sieve pore, a sheath is formed which is made up of callose. Callose is a carbohydrate and is composed of β1, 3-linked glucan. As more and more callose deposit the connecting strands in the sieve pore gradually become thin and ultimately disappear. The callose masses of the neighbouring sieve areas may coalesce to form a single mass which forms callose pad. When sieve tubes become non-functional, sieve pores are plugged with callose. This callose deposition is known as callose platelets. Deposition of callose may be seasonally or permanently. When the callose deposition is seasonal it is known as dormancy callose. Permanent deposition of callose on the sieve pores causes the sieve tubes nonfunctional and known as definitive callose. In some plants during autumn callose deposits around the pore and sieve tubes become non-functional but during spring callose gets dissolved and sieve tubes again becomes functional (for example, *Vitis*).

Phylogeny of Sieve Tube: Long sieve tubes are considered as primitive feature whereas the short sieve tubes indicate the advanced character. During the evolution, cambial initials become shortened and therefore results in the formation of short sieve tubes. The primitive sieve tubes are having long end wall, numerous sieve areas and small pores. Compound sieve plate with oblique position is a primitive character whereas in advanced forms simple sieve tube with horizontal position is present.

NOTES

Companion Cells: The sieve tube elements and companion cells are related ontogenetically as both of them originate from a single mother cell. A meristematic cell divides longitudinally, one of the daughter cell usually larger one differentiates into sieve tube element and other differentiates as companion cell (Refer Figure 3.10). They remain strongly associated with each other. In the primary phloem of herbaceous plants, one companion cell is associated with a single sieve tube but in carrot more than one companion cell is associated with a single sieve tube. Many short companion cells are associated with a sieve tube in the secondary phloem of woody plants. The companion cells are vertically elongated, and angular in cross-section. They may be as long as sieve tube or may be shorter.

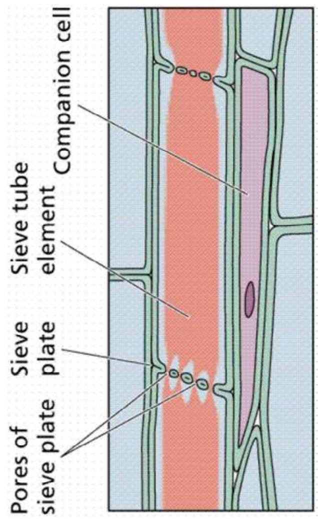

Fig. 3.10 *Part of Phloem Tissue Showing the Companion Cell Associated with Sieve Tube*

Companion cells are living, with a prominent nucleus and numerous small vacuoles. The nucleus may be elongated or lobed and bounded by a normal double membrane. The cytoplasm is dense due to the presence of various cell organelles such as dictyosomes, endoplasmic reticulum, mitochondria with well-developed cristae, ribosomes and plastids. In some companion cells P-proteins are also present. Companion cell with phloem parenchyma plays an important role in maintaining a pressure gradient in the sieve tubes and also helps in controlling the passage of materials.

Companion cells are confined to the Angiosperms. In Pteridophytes and Gymnosperms, another kind of cell is present known as albuminous cell (Refer Figure 3.11). They may be as long as sieve tube or may be shorter. Their end walls may be oblique or tapered. They also have a well developed nucleus and protein rich cytoplasm. When the phloem is active albuminous cells do not contain starch but it may store during the rest period. In fully differentiated sieve cells, associated with companion cells, high respiratory and phosphatase activity has been observed. They are also known as Strasburger cell after they name of their discoverer.

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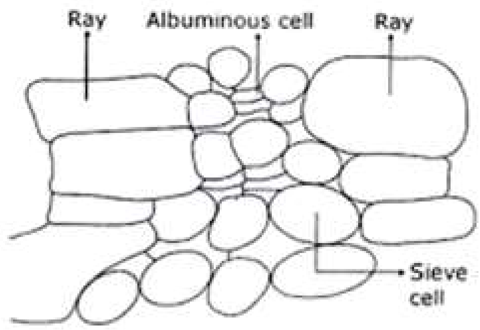

Fig. 3.11 *Albuminous Cell of Gymnosperms*

Check Your Progress

1. What is a tissue?
2. What is the nature of complex tissue?
3. What is the composition of complex tissue?
4. Define xylem.
5. What is the function of tracheids?
6. Give the functions of vessels.
7. How are sieve elements characterized?
8. Where are sieve cells present?

3.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Tissue is a cellular organisational level between cells and a complete organ.
2. The complex tissues are heterogeneous in nature, being com-posed of different types of cell elements. The latter remain contiguous and form a struc-tural part of the plant, adapted to carry on a specialised function.
3. Complex tissue is composed of more than one type of cell. Xylem and phloem which are known as vascular tissue are the examples of complex tissue. Xylem and phloem together constitute the conducting tissue in the plants.
4. Xylem is the water conducting tissue which is made up of four different types of cells (tracheids, vessels, xylem fibre and xylem parenchyma) associated with each other.
5. The function of tracheids is the conduction of water and minerals in solution. It also provided the mechanical strength.
6. Vessels help in the conduction of water and dissolved mineral nutrients and also provide mechanical strength.

7. Sieve elements are characterized by the presence of sieve areas and absence of nuclei in the mature cells. There are two kinds of sieve elements sieve cells and sieve tube elements.
8. Sieve cells are present in gymnosperms and pteridophytes. They have a similar degree of specialization and there are no regions that can be distinguished as sieve plates.

3.4 SUMMARY

- In biology, tissue is a cellular organisational level between cells and a complete organ.
- A tissue is an ensemble of similar cells and their extracellular matrix from the same origin that together carry out a specific function.
- Organs are then formed by the functional grouping together of multiple tissues.
- The study of human and animal tissues is known as histology or, in connection with disease, histopathology.
- The latter remain contiguous and form a struc-tural part of the plant, adapted to carry on a specialised function.
- Xylem and phloem are the complex tissues which constitute the component parts of the vascular bundle.
- The vascular system occupies a unique position in the plant body, both from the point of view of prominence and physiological importance.
- In recent years a new phylum Tracheophyta has been introduced to include all vascular plants; it covers pteridophyta and spermatophyta of old classifications.
- Vascular bundles form a continuous and inter-connected system in the different organs of the plants.
- Complex tissue is composed of more than one type of cell. Xylem and phloem which are known as vascular tissue are the examples of complex tissue.
- Xylem occurs in both primary and secondary vascular tissues. The procambium develops into primary xylem and vascular cambium gives rise to secondary xylem.
- Tracheid is a single-celled, imperforate, elongated structure with tapering ends.
- Tracheids are situated one above the other and their end walls are in contact with others.
- Tracheids with annular thickening are the most primitive type as it has been reported from one of the oldest fossils, *Cooksonia,* a leafless vascular plant.
- The scalariform thickening has been originated from helical as the helical bands joined at certain areas.

- Vessels help in the conduction of water and dissolved mineral nutrients and also provide mechanical strength.
- The tracheary elements have developed during the evolution of land plants. In the lower vascular plants the func-tion of conduction and support were combined in the tracheids.
- Progressive increase in specialisation led to gradual decrease in the number of bars and their ultimate disappearance, so that the perforation plates become simple with transverse end-walls.
- The pitting of the vessel wall also changed from early scalariform arrangement, characteristic of tracheids, to small bordered pit pairs, first in opposite (arranged in transverse rows) and ultimately in alternate (arranged spirally or irregularly) pattern.
- The pits changed from elongate to circular, the borders becoming reduced and functionless, and ultimately disappeared. Thus the evolutionary sequence was from tracheids, through fibre-tracheids to libiriform fibres.
- Vessel with transverse end wall is an advanced feature whereas vessel with long slanted end is a primitive feature.
- The primitive long vessels have scalariform perforation plate (parallel series) with many bars.
- In scalariform perforation plate, the bars may offer resistance to the flow of water.
- The simple perforation plate with circular rim in a transverse end-wall is a characteristic feature of an advanced vessel which is beneficial for the conduction of water.
- Fibres are long cells present in both primary and secondary xylem but predominantly in secondary xylem. In primary xylem it originates from procambium and in secondary xylem it originates from fusiform initials of vascular cambium.
- Fibre-tracheid are shorter than libriform fibre, having thin walls with bordered pits with a very small lumen.
- Parenchyma forms a major part of primary xylem. It originates from procambium whereas in secondary xylem it develops from vascular cambium.
- In stem, xylem and phloem is present on the same radius (conjoint), and phloem is external to the xylem (collateral).
- Sieve elements are characterized by the presence of sieve areas and absence of nuclei in the mature cells.
- Sieve tube elements are present in Angiosperms. There are certain sieve areas which are highly specialized than others and these sieve areas occur on the transverse end walls to form sieve plates.
- The cell wall of sieve tube is composed of mainly cellulose and pectin. The thickness of sieve elements varies but usually they are thicker than the neighbouring parenchyma cells.

NOTES

- Sieve tubes are the only living cells in which the nuclei are absent from the mature protoplast. The mature protoplast is also devoid of ribosomes and dictysomes.
- The young sieve tube contains nucleus, dictyosomes, ribosomes, endoplasmic reticulum, plastids, mitochondria and other cell organelles.
- A large central vacuole and a thin layer of parietal cytoplasm are present in mature sieve elements.
- Around each sieve pore, a sheath is formed which is made up of callose. Callose is a carbohydrate and is composed of â1, 3-linked glucan.
- Deposition of callose may be seasonally or permanently. When the callose deposition is seasonal it is known as dormancy callose.
- Companion cells are confined to the Angiosperms. In Pteridophytes and Gymnosperms, another kind of cell is present known as albuminous cell.
- Companion cells originate from the individual mother cell and therefore sieve cells and companion cells are ontogenetically not associated with each other.
- Sieve tube and companion cell both originate from a single mother cell. It is present in both primary and secondary phloem.
- The mother cell divides by a longitudinal division, the smaller one gives rise to companion cell whereas the larger one develops into sieve tube.
- Short length of sieve tube is also considered as an advanced feature, it can be correlated with the increasing contact between companion cell and sieve tube.
- Fibres which are associated with phloem are known as phloic fibres which are present in both primary and secondary phloem.
- Fibres are long, elongated cells with their interlocked ends to form a strong strand which provide the mechanical strength.
- The cells of parenchyma are more or less rectangular or rounded.
- Parenchyma cells are living and concerned with storage of starch, fat, resins, tannins and other organic food materials, etc.

3.5 KEY WORDS

- **Tissue**: Tissue is a cellular organisational level between cells and a complete organ.
- **Xylem:** It is the water conducting tissue which is made up of four different types of cells associated with each other.
- **Phloem**: Phloem is the principal food conducting tissue which is associated with xylem in the vascular system.
- **Tracheids**: Tracheid is a single-celled, imperforate, elongated structure with tapering ends.

NOTES

3.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. What is vascular system?
2. What are complex tissues?
3. What is xylem?
4. Define tracheid.
5. What is phloem?
6. Write short note on vessels?

Long Answer Questions

1. Distinguish between xylem and phloem.
2. Write a note on phylogeny of vessel.
3. Draw a well-labelled diagram of perforation plate.
4. What are xylem fibers? Explain its types.
5. Elaborate a note on phloem.
6. What are companion cells.

3.7 FURTHER READINGS

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UNIT 4 TRANSFER CELLS AND VASCULAR CAMBIUM

NOTES

Structure

4.0 INTRODUCTION

Transfer Cells (TCs) are ubiquitous throughout the plant kingdom. Their unique ingrowth wall labyrinths, supporting a plasma membrane enriched in transporter proteins, provides these cells with an enhanced membrane transport capacity for resources. In certain plant species, TCs have been shown to function to facilitate phloem loading and/or unloading at cellular sites of intense resource exchange between symplasmic/apoplasmic compartments. Within the phloem, the key cellular locations of TCs are leaf minor veins of collection phloem and stem nodes of transport phloem. In these locations, companion and phloem parenchyma cells trans-differentiate to a TC morphology consistent with facilitating loading and re-distribution of resources, respectively. At a species level, occurrence of TCs is significantly higher in transport than in collection phloem. TCs are absent from release phloem, but occur within post-sieve element unloading pathways and particularly at interfaces between generations of developing Angiosperm seeds. Experimental accessibility of seed TCs has provided opportunities to investigate their inductive signaling, regulation of ingrowth wall formation and membrane transport function. This review uses this information base to explore current knowledge of phloem transport function and inductive signaling for phloem-associated TCs. The functional role of collection phloem and seed TCs is supported by definitive evidence, but no such information is available for stem node TCs that present an almost intractable experimental challenge. There is an emerging understanding of inductive signals and signaling pathways responsible for initiating trans-differentiation to a TC morphology in developing seeds. However, scant information is available to comment on a potential role for inductive signals that induce seed TCs, in regulating induction of phloem-associated TCs. Biotic phloem invaders have been used as a model to speculate on involvement of these signals.

NOTES

In stems the vascular cambium and the primary vascular tissues differentiate from procambium. Procambium develops from the derivative cells of apical meristem. Transverse sections of a growing vegetative shoot apex reveal the presence of a cylinder of cells that are highly cytoplasmic and more densely staining.

This ring of cells is regarded as a residuum of the meristematic tissue of apical meristem and so termed as residual meristem. Within the residua] meristem more densely staining regions are present and these regions have a topographic relationship with leaf primordia. This region constitutes procambium that develops as leaf trace.

The remainder of residual meristem forms the interfascicular parenchyma. In longitudinal section of vegetative apical shoot of angiosperm and gymnosperm it is observed that the procambial ring or strand is continuous and develops acropetally. Procambial strands exhibit two waves of differentiation, that is, differentiation of protophloem on the peripheral side and differentiation of protoxylem towards the inner edges in normal angiosperm.

In this unit, you will study about distribution, structure and significance of transfer cells, vascular cambium storied, non-storied and the mode of activity in detail.

4.1 OBJECTIVES

After going through this unit, you will be able to:

- Discuss the distribution, structure and significance of transfer cells
- Explain vascular cambium storied
- Discuss non-storied and the mode of activity

4.2 TRANSFER CELLS

Transfer cells are special kind of parenchymatous cells which are associated with the transport and secretion of substances. Therefore, these cells are present where there is a physiological demand for transport and secretion. These are characterized by the presence of wall ingrowths of unlignified secondary wall (Refer Figure 4.1). These ingrowths are formed by the deposition of wall materials on the inner side of the primary wall. The plasma membrane is in close association with these wall ingrowths and therefore, the surface area of plasma membrane in a transfer cell is increased several times. The numerous cytoplasmic projections are present between the neighbouring transfer cells. The cells consist of dense cytoplasm, large nucleus, numerous mitochondria, dictyosomes, ribosomes and endoplasmic reticulum. These cells are associated with xylem, phloem, nectaries, hydathodes, salt glands, synergids, and endosperm.

NOTES

In xylem, transfer cells are formed after the tracheary elements. Division in the procambial cell gives rise to two daughter cells. One becomes xylem parenchyma whereas the other one differentiates into transfer cell.

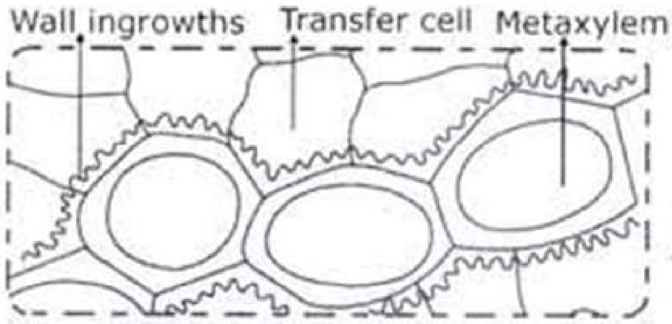

Fig. 4.1 Xylem Parenchyma Transfer Cells Showing Elaborate Wall Ingrowths

Vascular Cambium

The vascular cambium is a secondary/lateral meristem which develops after a certain stage of development. It produces secondary xylem and secondary phloem and surrounds the primary xylem of stem and root.

In plants where there is no secondary growth, all cells of the procambium differentiate into primary vascular tissue whereas in those plants where secondary growth occurs, a part of the procambium remains meristematic and develops into the cambium. Therefore, procambium and cambium represents two different stages of vascular meristem. The cambium present between the xylem and phloem is called fascicular cambium or intra fascicular cambium. The cambial strips present between two vascular bundles known as interfascicular cambium (Refer Figure 4.2). This interfascicular cambium develops from interfascicular parenchyma. Both inter and intra fascicular cambium combines to form a complete ring of cambium cylinder which divides predominantly divides periclinally and produces secondary phloem towards outer side (centrifugally) and secondary xylem towards inner side (centripetally).

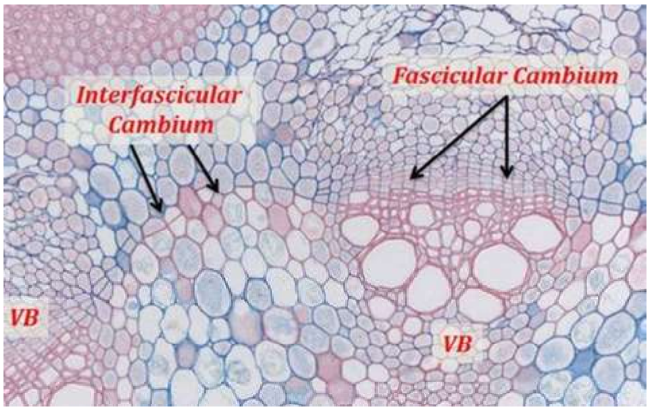

***Fig. 4.2** Portion of a Stem Showing Fascicular and Inter-Fascicular Cambium*

NOTES

Structure of Cambium

The cells of vascular cambium are highly vacuolated. They have thin, non-lignified walls with primary pit fields which give them as a beaded appearance. The cambial cells are connected each other with the help of plasmodesmata. The cytoplasm of cambial cells possesses nucleus, ribosomes, dictyosomes, Golgi bodies, endoplasmic reticulum and mitochondria. Cambial cells predominantly divide by the periclinal division and therefore their radial walls are usually thicker than tangential walls. In herbaceous forms, plastids of cambial cells form grana whereas these grana are absent in woody forms. The cambial cells also follow the law of Newman's concept of continuing meristematic residue. According to this concept, after each cell division, one of the daughter cells either differentiates into secondary xylem or secondary phloem and other daughter cell retains its meristematic activity. Therefore behaves as a permanent meristematic tissue. Cambial cells do not follow Errera's law, according to which a cell divides by a wall of minimal area.

Vascular cambium is made up of two types of cells (Refer Figure 4.3):

Fusiform Initial: These cells are single, long, spindle shaped with tapering ends and can be observed in tangential section. It is several times longer than wide. The components of secondary xylem and secondary phloem differentiate from fusiform initials. The fusiform initial compose the axial system of the cambium. A fusiform initial may be very long and it may attain a length of 8.7 mm in *Sequoia sempervirens*.

Ray Initials: These cells are isodiametric with flattened axis. Ray initials give rise to vascular parenchymatous rays. Ray initial compose the radial system of the cambium.

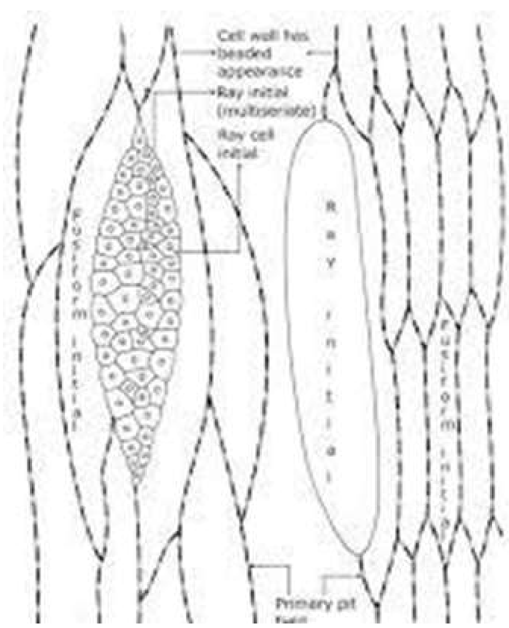

***Fig. 4.3** T.L.S Through Cambial Region Showing Fusiform Initial and Ray Initial*

NOTES

On the basis of the arrangement of fusiform initial, two types of the cambium have been indentified (Refer Figure 4.4):

- **Storied or Stratified Cambium**: The fusiform initials are arranged in horizontal row so that their ends are at the same level. It is present in *Dalbergia sisso*, *Robinia, Tamarix* and *Salvadora persica*. They represent a highest phylogenetic stage and developed by gradual reduction of the fusiform initials. The length of the fusiform initial sranges from 140μ to 520 μ.
- **Non-Storied and Non-Stratified Cambium**: Here, the fusiform initials overlap one another and give rise to non-storied cambium. It is more common and here the fusiform cells are longer than stratified type. The length of the fusiform cells ranges between 320μ to 2300μ and in vesselless dicotyledons it may be as long as 6200μ.

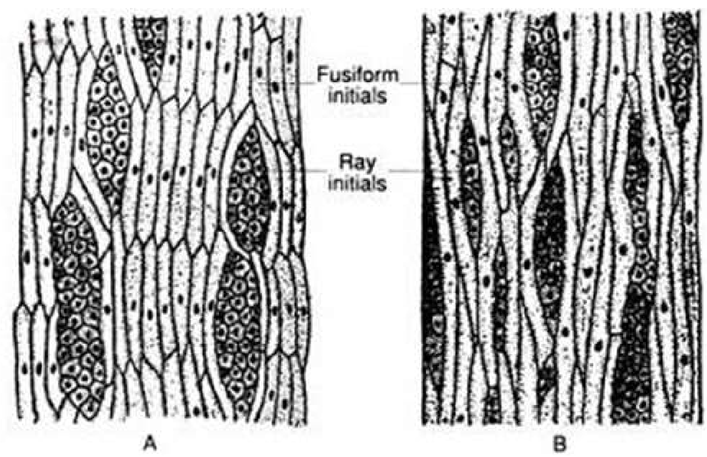

Fig. 4.4 *Fusiform Initial and Ray Initial in Longitudinal View; A. Storied Cambium; B. Non-Storied Cambium*

Activity of Vascular Cambium

The secondary growth of plants depends on the activity of the cambium and the activity of the cambium depends on the environmental conditions such as temperature, rain fall, relative humidity, etc. external and internal factors. In tropical region, cambium is active throughout its life because there is no such fluctuation in the temperature. Therefore, new secondary xylem and secondary phloem cells are added to the vascular tissue. The plants growing in the temperate zone, their cambium shows a significant variation in its activity in the different seasons. During spring season, when the vegetative phase is at its peak, there will more transpiring surface. At this time plant requires an elaborate system of water network and therefore vessels formed during this period will be broader and thin walled. Wood formed during spring is called spring wood or early wood.

In autumn, there is leaf fall and less vegetative growth, and therefore the plant does not require additional water channels. The vessels formed during this

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period have narrow and thick walled. Wood formed during autumn is called autumn wood or late wood. Spring wood and autumn wood also known as growth ring. Each growth ring denotes the growth of a single season so by counting the number of growth rings we can count the age of a tree (Refer Figure 4.5).

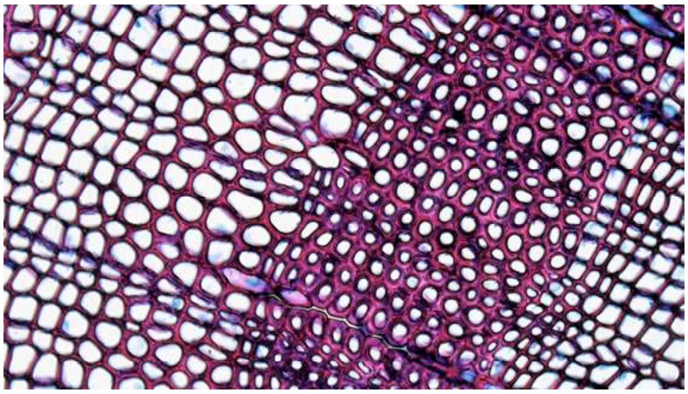

Fig. 4.5 *L.S. of a Wood showing Spring (thin walled) and Autumn Wood (thick walled)*

Sometimes due to the environmental fluctuations, there may be variations in the thickness of annual rings and sometimes more than one growth rings may be formed in one season. These variations arise due to any injury, infection, drought, flood, etc.

It has also been observed that besides the temperature, phytohormones (auxin, gibberellins and kinetin) also stimulate the activity of cambium. Auxin causes rapid cell differentiation whereas gibberellins causes rapid cell division. It has been demonstrated that cambial activity of *Robinia pseudoacacia* and *Pinus sylvestris* can be induced by exposing the plants under long day conditions. The cambial activity can also be stimulated by wounding, as a result of injury plant produces wound hormone.

Cambium Helps in Healing of Wounds and Grafting

Cambium produces callus over wounds. Callus is an undifferentiated mass of parenchyma which is formed on the damaged surface of stems and roots. Callus is also formed by the parenchymatous cells but usually it is formed by cambial cells. In case of deep wound where the cambium is damaged, normal callus is formed in the damaged area provided the uninjured tissues are protected from drying out immediately. In the callus, a new cambium develops and it unites with the uninjured cambium. Thus the cambium becomes continuous and the production of secondary tissue continues.

In horticultural practices grafting and budding are basically dependent on the activity of cambium of both stock and scion so that they can develop callus. These cambial cells also form a continuous layer at the junction of stock and scion to develop the normal conducting tissue. When both stock and scion are incompatible, their cambial cells do not get fuse. It is because of the abnormal arrangement of the xylem cells. Sometimes other physiological factors also affect the activity of cambium. Viral infection is also responsible for the failure of union.

NOTES

Check Your Progress

1. What are transfer cells and where are they present?
2. How transfer cells are characterized?
3. How are transfer cells ingrowths formed?
4. What does cells consist of?
5. How are transfer cells formed in xylem?
6. How cambial cells are connected with each other?

4.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Transfer cells are special kind of parenchymatous cells which are associated with the transport and secretion of substances. They are present where there is a physiological demand for transport and secretion.
2. Transfer cells are characterized by the presence of wall ingrowths of unlignified secondary wall.
3. Transfer cells ingrowths are formed by the deposition of wall materials on the inner side of the primary wall.
4. The cells consist of dense cytoplasm, large nucleus, numerous mitochondria, dictyosomes, ribosomes and endoplasmic reticulum. These cells are associated with xylem, phloem, nectaries, hydathodes, salt glands, synergids, and endosperm.
5. In xylem, transfer cells are formed after the tracheary elements. Division in the procambial cell gives rise to two daughter cells.
6. The cambial cells are connected with each other with the help of plasmodesmata. The cytoplasm of cambial cells possesses nucleus, ribosomes, dictyosomes, Golgi bodies, endoplasmic reticulum and mitochondria.

4.4 SUMMARY

- Transfer cells are special kind of parenchymatous cells which are associated with the transport and secretion of substances.
- Transfer cells are present where there is a physiological demand for transport and secretion.
- Transfer cells are characterized by the presence of wall ingrowths of unlignified secondary wall.

NOTES

- Transfer cells ingrowths are formed by the deposition of wall materials on the inner side of the primary wall.
- The plasma membrane is in close association with these wall ingrowths and therefore, the surface area of plasma membrane in a transfer cell is increased several times.
- The numerous cytoplasmic projections are present between the neighbouring transfer cells.
- The cells consist of dense cytoplasm, large nucleus, numerous mitochondria, dictyosomes, ribosomes and endoplasmic reticulum. These cells are associated with xylem, phloem, nectaries, hydathodes, salt glands, synergids, and endosperm.
- In xylem, transfer cells are formed after the tracheary elements. Division in the procambial cell gives rise to two daughter cells.
- The vascular cambium is a secondary/lateral meristem which develops after a certain stage of development. It produces secondary xylem and secondary phloem and surrounds the primary xylem of stem and root.
- In plants where there is no secondary growth, all cells of the procambium differentiate into primary vascular tissue whereas in those plants where secondary growth occurs, a part of the procambium remains meristematic and develops into the cambium.
- The cambial strips present between two vascular bundles known as interfascicular cambium.
- The cells of vascular cambium are highly vacuolated. They have thin, non-lignified walls with primary pit fields which give them as a beaded appearance.
- The cambial cells are connected with each other with the help of plasmodesmata. The cytoplasm of cambial cells possesses nucleus, ribosomes, dictyosomes, Golgi bodies, endoplasmic reticulum and mitochondria.
- Cambial cells predominantly divide by the periclinal division and therefore their radial walls are usually thicker than tangential walls. In herbaceous forms, plastids of cambial cells form grana whereas these grana are absent in woody forms.
- The cambial cells also follow the law of Newman's concept of continuing meristematic residue.
- Fusiform initial cells are single, long, spindle shaped with tapering ends and can be observed in tangential section. It is several times longer than wide. The components of secondary xylem and secondary phloem differentiate from fusiform initials.
- The fusiform initial compose the axial system of the cambium. A fusiform initial may be very long and it may attain a length of 8.7 mm in *Sequoia sempervirens*.

NOTES

- Ray initials cells are isodiametric with flattened axis. Ray initials give rise to vascular parenchymatous rays. Ray initial compose the radial system of the cambium.
- The fusiform initials are arranged in horizontal row so that their ends are at the same level. It is present in *Dalbergia sisso*, *Robinia, Tamarix* and *Salvadora persica*.
- Non-storied and non-stratified cambium fusiform initials overlap one another and give rise to non-storied cambium. It is more common and here the fusiform cells are longer than stratified type.
- The secondary growth of plants depends on the activity of the cambium and the activity of the cambium depends on the environmental conditions such as temperature, rain fall, relative humidity, etc., external and internal factors.
- In tropical region, cambium is active throughout its life because there is no such fluctuation in the temperature.
- The plants growing in the temperate zone, their cambium shows a significant variation in its activity in the different seasons.
- In autumn, there is leaf fall and less vegetative growth, and therefore the plant does not require additional water channels. The vessels formed during this period have narrow and thick walled. Wood formed during autumn is called autumn wood or late wood.
- Spring wood and autumn wood also known as growth ring. Each growth ring denotes the growth of a single season so by counting the number of growth rings we can count the age of a tree.
- Sometimes due to the environmental fluctuations, there may be variations in the thickness of annual rings and sometimes more than one growth rings may be formed in one season. These variations arise due to any injury, infection, drought, flood, etc.
- It has also been observed that besides the temperature, phytohormones (auxin, gibberellins and kinetin) also stimulate the activity of cambium.
- Auxin causes rapid cell differentiation whereas gibberellins causes rapid cell division.
- Cambium produces callus over wounds. Callus is an undifferentiated mass of parenchyma which is formed on the damaged surface of stems and roots.
- In case of deep wound where the cambium is damaged, normal callus is formed in the damaged area provided the uninjured tissues are protected from drying out immediately.

4.5 KEY WORDS

- **Transfer cells**: Transfer cells are special kind of parenchymatous cells which are associated with the transport and secretion of substances.

- **Spring wood:** Wood formed during spring is called spring wood or early wood.
- **Autumn wood:** Wood formed during autumn is called autumn wood or late wood.

4.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. Briefly describe about transfer cells.
2. What is vascular cambium?
3. What is fusiform initial?
4. Define stratified cambium.

Long Answer Questions

1. Discuss the distribution, structure and significance of transfer cells.
2. Explain the structure of vascular cambium.
3. Explain vascular cambium storied.
4. Discuss non-storied and the mode of activity.
5. Write a note on activity of vascular cambium.
6. 'Cambium helps in healing of wounds and grafting'. How?

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BLOCK - II
VASCULAR TISSUES

NOTES

UNIT 5 VASCULAR DIFFERENTIATION IN STEM, ROOT AND LEAF

Structure

5.0 INTRODUCTION

Vascular tissue is a complex conducting tissue, formed of more than one cell type, found in vascular plants. The primary components of vascular tissue are the xylem and phloem. These two tissues transport fluid and nutrients internally. There are also two meristems associated with vascular tissue: the vascular cambium and the cork cambium. All the vascular tissues within a particular plant together constitute the vascular tissue system of that plant.

The cells in vascular tissue are typically long and slender. Since the xylem and phloem function in the conduction of water, minerals, and nutrients throughout the plant, it is not surprising that their form should be similar to pipes. The individual cells of phloem are connected end-to-end, just as the sections of a pipe might be. As the plant grows, new vascular tissue differentiates in the growing tips of the plant. The new tissue is aligned with existing vascular tissue, maintaining its connection throughout the plant. The vascular tissue in plants is arranged in long, discrete strands called vascular bundles. These bundles include both xylem and phloem, as well as supporting and protective cells. In stems and roots, the xylem typically lies closer to the interior of the stem with phloem towards the exterior of the stem. In the stems of some Asterales dicots, there may be phloem located inwardly from the xylem as well.

Between the xylem and phloem is a meristem called the vascular cambium. This tissue divides off cells that will become additional xylem and phloem. This growth increases the girth of the plant, rather than its length. As long as the vascular cambium continues to produce new cells, the plant will continue to grow more stout. In trees and other plants that develop wood, the vascular cambium allows the expansion of vascular tissue that produces woody growth. Because this growth ruptures the epidermis of the stem, woody plants also have a cork cambium that develops among the phloem. The cork cambium gives rise to thickened cork cells to protect the surface of the plant and reduce water loss. Both the production of wood and the production of cork are forms of secondary growth.

In leaves, the vascular bundles are located among the spongy mesophyll. The xylem is oriented toward the adaxial surface of the leaf (usually the upper side), and phloem is oriented toward the abaxial surface of the leaf. This is why aphids are typically found on the undersides of the leaves rather than on the top, since the phloem transports sugars manufactured by the plant and they are closer to the lower surface.

In this unit, you will study about vascular differentiation in the primary body of stem, root and leaf in detail.

5.1 OBJECTIVES

After going through this unit, you will be able to:

- Discuss the vascular differentiation in the primary body of stem
- Understand the vascular differentiation in root and leaf

5.2 VASCULAR DIFFERENTIATION IN THE PRIMARY BODY OF STEM, ROOT AND LEAF

Plant vascular tissues evolved about 430 million years ago. This enabled long distance transport of water and food, and therefore, paved a way to land colonization by plants. In lower vascular plants, vascular tissues are organized in a simple manner- xylem at the center surrounded by phloem. This vascular arrangement is known as **protostele.** Along with the evolution of different vascular plants, vascular tissue also evolved into different vascular arrangements. The most common vascular organization within a vascular bundle is parallel placement of xylem and phloem tissue. This arrangement is known as **collateral** vascular bundles. In some families like Cucurbitaceae and Solanaceae, xylem is placed in parallel with external phloem and internal phloem, a pattern called bicollateral vascular bundles. Several uncommon type of vascular arrangements also involved in some angiosperms. In monocots, like *Dracaena* and *Acorus*, phloem is surrounded by a continuous ring of xylem. such pattern is called **amphivasal** vascular bundles. In contrast, some angiosperms and ferns possess no **amphicribral** vascular bundles, having xylem surrounded by a ring of phloem.

Vascular tissues consist of two basic types- **Xylem** and **phloem**. The xylem tissue, consisting of the tracheary elements (tracheids and vessels), xylem fibers and xylem parenchyma, transports water, minerals, phytohormones, and provides mechanical support. Phloem tissue, on the other hand, transports photosynthesis products (sugars), proteins and other solutes required for plant growth and development. Phloem consist of sieve elements, companion cells, phloem fibers and phloem parenchyma cells. Tracheary elements of xylem and sieve elements of phloem forms continuous columns- a **vascular system** throughout the plant body. There is a variation in arrangement of vascular tissues in different species of plant within a vascular bundle. The conducting elements of xylem and phloem maintain a continuous supply of water, nutrients phytohormones and food throughout the plant body.

Vascular Differentiation at Meristems

During growth and development of a plant body the two important processes involved are development and differentiation. The integrated process of growth, differentiation and morphogenesis is known as 'development'. On the other hand, differentiation of cells, tissues and organs achieve their distinctive morphological and physiological characteristics. Achievement of form during development is 'morphogenesis'.

The **primary** plant body is developed by division and differentiation of cells arising from the apical meristems at the root and shoot apices. At the meristematic regions, the meristematic cells give rise to the **progenitor** cells, which further differentiate to form the **primordial epidermal**, **ground** and **stellar** tissues. These primordial tissues further give rise to **permanent** epidermal tissue systems, ground tissue system and vascular tissue system as a result of morphogenesis. At the apical region, the meristematic tissues divide and give rise to the derivative cells. As the number of these cells increases, some of the cells start differentiating into different tissue types. As a result, **transitional tissue regions** or **zones** are formed near the proximal regions of apical meristems. These tissue regions- protoderm, ground meristem and provascular tissue, are located between the apical meristem and the mature tissues. Cell division continues in the upper part of these zones. Simultaneously, growth and differentiation of newly synthesized cells continues in these regions. As a result, the shoot apex undergoes extensive elongation. Steeves and Sussex characterised these activities as the '**expansion phase**' of shoot development. Ultimately, **protoderm** will develop into **epidermis**, **ground meristem** will give rise to **cortex** and **pith,** and the **provascular tissue** will form **primary vascular system** of the mature stem. The cells closest to the apical regions are produced recently and therefore are younger as compare to the cells at a distance from apices.

The primary vascular tissues arise from the **provascular** cells present as lateral meristems in the growing apical regions during the development of primary plant body. The provascular strands (provascular column or provascular cylinder in pteridophytes), often called **procambium,** surrounds the immature pith. In many taxa, the provascular strand differentiates in a cylindrical zone immediately below the apical meristem called **residual meristem.** The first strands of provascular tissue which differentiates within the residual meristem, become leaf traces. As development proceeds, additional provascular strands differentiate within the residual meristem. Some of these will become leaf traces and others will become axial bundles. The remaining residual meristem differentiate into interfascicular parenchyma (parenchyma between the vascular bundles). Later, the **cambial** cells keep on dividing and forming more and more xylem and phloem elements required to fulfill the growing supplies for developing plant. Some plants grow only for one season forming only the primary tissues, and at the commencement of unfavorable conditions, complete their life cycle and die off. Such plants are known as **annuals**. While other plants survive the unfavorable environment conditions, and regain cellular division and growth giving rise to secondary tissues. Such plants are known as **perennials**. Perennials may survive for a few years to thousands of years.

Primary Tissue Regions of Stem and Root

Generally, growth of the plant body initiates after fertilization of gametes, from the unicellular zygote which gradually develops into the embryo forming a seed. After germination the embryo gradually develops into the whole plant (Refer Figure 5.1). In spite of great diversities existing in the vascular plants regarding their size, structure and form, there is a fundamental consistency. Generally, the higher plant body has a polarity and forms along the axis. the lower part of this axis forms the underground root system and the continuous upper aerial part forms the shoot system. The root-stem axis bears different types of appendages, like leaves, branches, flowers and fruits. The entire plant body have continuous vascular tissues. The root, stem and leaves form the three fundamental organs of the plant body.

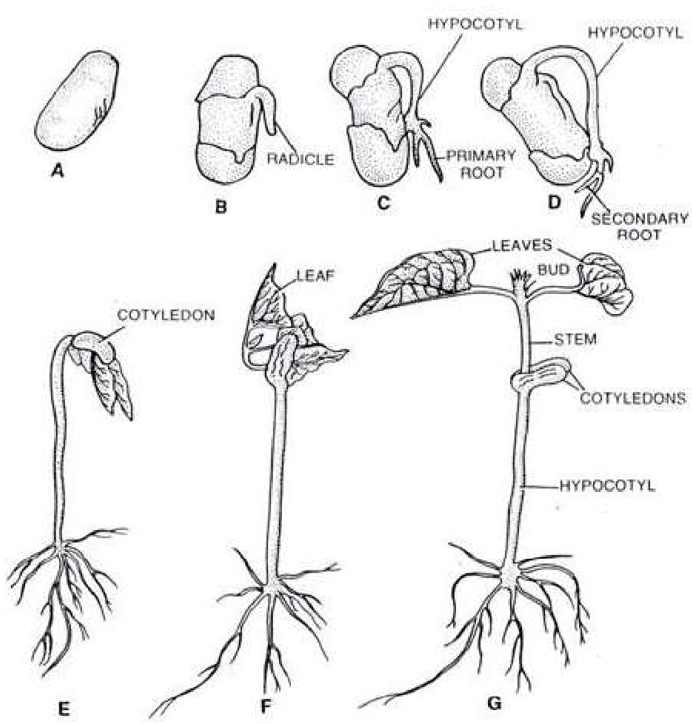

Fig. 5.1 Formation of Primary Plant Body; A. Seed; B. Emergence of Radicle; C-D. Development of Hypocotyl; E. Emergence of Leaves; F-G Young Seedling.

NOTES

The tissue organization of these fundamental organs is more or less similar consisting of all the basic tissue systems (Refer Figure 5.2). Starting from the periphery, the plant axis has three zones or regions – the epidermis, cortex and stele. The **epidermis** is the outermost layer forming the 'skin'. It is usually single-layered due to anticlinal (at right angles to the axis) division of the mother cells and provides protective covering to the plant body. The next internal zone to epidermis is the **cortex**. It is multi-layered and is composed of different types of tissues, like parenchyma, collenchyma and sclerenchyma. It provides mechanical support to the plant body, sometimes act as storage site, adds girth to the organs. The innermost layer of the cortex is the endodermis, it acts as a barrier between cortex and the vascular tissues. The central core zone is the stele or central cylinder of vascular tissues or vascular bundles. The vascular bundles perform the function of translocation of water and solutes as well as give mechanical support to the plant. A lateral meristem- **cambium**, may be present in between the xylem and phloem, as in the stems of dicotyledons and gymnosperms. Xylem and phloem tissues are arranged radially in the roots while occur on the same radius in other organs. Sometimes vascular stele encloses a central, soft parenchymatous pith or medulla, which is continuous in-between the vascular bundles looking like rays radiating from the pith — called **pith rays** or **medullary rays**. In between the vascular bundles and endodermis there occurs one or more layers of non-conducting cells known as **pericycle**.

The meristematic regions between the mature tissues are known as **intercalary meristem**. These tissues have been extensively studied in the stems of grasses. The initial internodes in the developing shoot in grasses are very short and entirely meristematic. As development proceeds, tissues in the distal regions with meristematic activity become progressively restricted to the basal regions of the internodes. With progressive growth and division in the intercalary meristems, the internodes elongate and the leaves arising at the nodes becomes more widely separated longitudinally. Differentiated vascular tissues within the elongating internodes are stretched and, in some species, disrupted. New xylem and phloem elements differentiate from adjoining parenchyma cells replacing the disrupted ones. Thus, maintaining the vascular tissue continuity. The basal meristems of many developing leaves, especially those with prominent petioles or that are needle-like, for example leaves of pine, are also considered to be intercalary meristems by many workers.

All the tissues forming the plant body are derived from the apical meristem present at the tips or apices of the axis. During primary growth, the axis grows in length, and leaves, axillary buds and other structures develop into the branch systems. The cambium prevailing between primary xylem and primary phloem in the vascular bundles of dicotyledons and gymnosperms divide and produce new tissues in the later stages of growth forming secondary xylem and secondary phloem. After formation of these secondary tissues a new meristem, called **phellogen** or cork cambium, arises in the peripheral portion of the stem. This lateral meristem cuts **phellem** or cork cells with suberised wall on the outer side and parenchymatous **phelloderm** or secondary cortex on the inner side. This three-tissue system forms the **periderm** which replaces the single layered epidermal tissue system of the primary plant body in stems and roots. As a result, the axis grows in girth or thickness. All these tissues, formed later by the lateral meristems, are known as secondary tissues, and the growth in thickness due to addition of secondary tissues is referred to as **secondary growth**.

Therefore, plant body is composed of morphologically distinct organs like stem, root and leaves, each performing specific functions. Every organ is a collection of tissue-systems which carry on controlled functions.

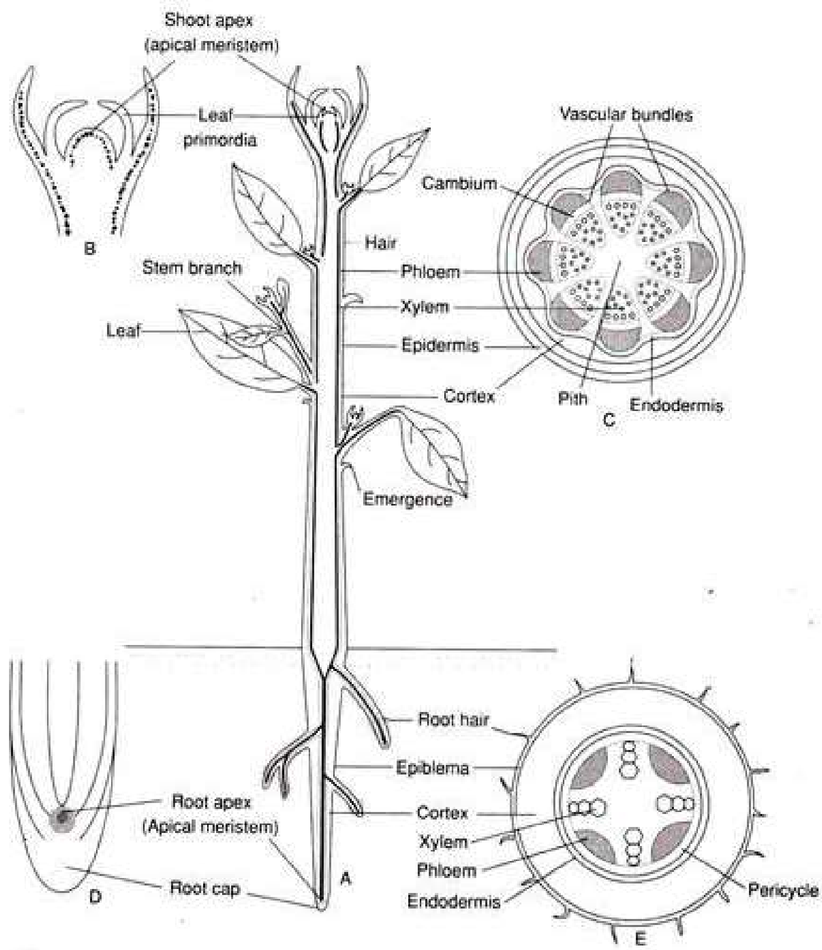

Fig. 5.2 *Tissue Organization Plan of a Vascular Plant Body*

The above Figure 5.2 shows tissue organization plan of a vascular plant body; a. polar axis of plant body showing different appendages an organ system; B. L.S. through shoot apex showing shoot apical meristem; C. T.S. through primary stem; D. L.S. through root apex showing root apical meristem; T.S. through primary root

NOTES

Primary Thickening Meristem

Increase in diameter of axis in the primary shoot system results partly from the diametric growth of individual cells and partly by production of additional cells in the ground tissue. In particular, in large plants consisting only of primary growth, such as some palms and monocots, new cells are added below the apical meristem by **primary peripheral thickening meristem**. This meristem is broadly located in the lateral regions of shoot apex. Anticlinal division of cells in the centre as well as peripheral regions results in several layers of cells around the meristem just below the apical meristem and in the proximal regions forming a cylinder of radial layers of cells. In young internodes, this cylinder of meristematic cells become initiating region for the secondary tissue develop during the subsequent years of growth. Although monocotyledons lack a vascular cambium of the type found in dicotyledons and conifers, lateral meristems still play an important role in the establishment of their growth habits. The presence near the shoot apex of a Primary Thickening Meristem (PTM), which is probably plesiomorphic in monocotyledons, predisposes evolution into the many pachycaul (trees with disproportionately thicker trunk for their height) forms. A PTM occurs in virtually all monocotyledons, whereas the Secondary Thickening Meristem (STM), which is morphologically similar, is limited to a few genera of Liliiflorae. these records are reviewed in a systematic context. To a greater or lesser extent in different taxa, the PTM is responsible for primary stem thickening, adventitious root production, and formation of linkages between stem, root and leaf vasculature. The STM largely contributes to the body of the stem. This primary thickening meristem is responsible for increase in girth in the perennial monocot species as a result of increase in layers of cells in the peripheral regions in stems and roots.

Primary Tissue Regions of Leaf

In the shoot system of plants, the leaves are the most important lateral appendages having determinate growth. There are two types of foliage leaves- microphyllous leaves and macrophyllous leaves. The microphyllous leaves have a single vein running from the base to the apex of leaf. Whereas, in macrophyllous leaves the vein is branched forming a venation network. The venation maybe open or closed. Schmidt in 1924 postulated that shoot apical meristem of gymnosperms and angiosperms consist of two distinct zones- **tunica** and **corpus**. Tunica is the surface layer and it encloses the corpus. Tunica may consist of a single layer or several layers of cells. The corpus always consists of many layers. These two regions- tunica and corpus are distinguished on the basis of orientation of cell division. In the tunica region, the cells divide in anticlinal plane. In anticlinal division the cell walls are laid down perpendicular to the surface of tunica. The anticlinal division results in growth of tunica as sheets. On the other hand, the cells in corpus region divides in anticlinal as well as periclinal plane. In periclinal division the cell wall is laid down parallel to the surface of tunica. Therefore, the cells of corpus can divide in any direction resulting in three-dimensional growth of corpus in contrast to only two-dimensional growth in tunica.

The initiation of leaf formation starts with the lateral protrusion on the apical meristem. This is the leaf buttress. Later, leaf primordium develops on the leaf buttress. The two growth zones- tunica and corpus participate in the development of leaf primordium. In case of single layered tunica- known as **monostratos,** the first division to form leaf occurs in corpus (example *Scrophularia nodosa*). In case of multilayer tunica, known as **multistratos tunica,** the initial divisions occur in the innermost layer of three-layered tunica (example *Vinca minor*). In a study, tunica and corpus both were found to be involved in the initial divisions of the development of *Acacia* phyllode. In most dicots, the first periclinal division generally occurs in the sub-surface layers, i.e., cells of one or more layers underneath. The surface layer in dicots does not form the inner tissues of the leaf. It divides by its characteristic anticlinal division along with the growth of leaf primordium which originates as a result of periclinal division of inner tissues. The protoderm of a young developing leaf differentiate from the surface layers. In grasses and many other monocots, the tunica is monostratos and some members have two layered tunica. Irrespective of the number of layers, the cells of tunica divide periclinally. As a result, the major portion of the leaf primordium develops from the cell situated at surface and sub surface layers of the shoot apex. Tradition is also noted in the initiation of leaf primordia in gymnosperms.

The periclinal divisions of superficial no tunica in monocots and periclinal divisions of the underlying layers of dicots form the leaf primordium. Also, divisions of the adjoining and underlining cells usually follow the initial periclinal division. As a result, the leaf primordium is raised about the surface of the apical meristem. Then several meristems originate in the leaf primordium and function either sequentially or simultaneously contributing to the tissues in the growth of a leaf primordium to form a leaf. The growth includes apical growth, intercalary growth, marginal growth, adaxial growth and lateral growth.

Apical growth occurs by the activity of apical meristem. In vascular cryptogams, apical meristem formed at the tip of leaf primordium shows prolonged activity. In ferns, the apical meristem can function for an extended period. In seed plants, the apical growth stops relatively early even though there is apical meristem. The development of young primordium and, subsequent elongation and extension of leaf occur by cell division throughout the young primordium. The growth of the leaf stops first at the tip and last at the base. Most of the leaves grow in length due to **intercalary growth**. The intercalary meristem occurs at the base of the leaf primordium of most monocots. In a study the intercalary meristem located in the developing leaf primordium of an aquatic plant was shown to cause the elongation of petiole, raising the lamina above the water surface (Cutter, 1978).

In the stem, the vascular tissues are organized as collateral vascular bundles, i.e., primary xylem lying at the interior region and the primary phloem at the peripheral or outer region of the vascular bundles. As the vascular strands diverge to enter the leaf, the primary xylem is positioned towards the adaxial (upper) surface of the leaf and the primary phloem towards the abaxial (lower) surface.

NOTES

The vascular strand that diverge from the stem to enter the leaf is known as 'leaf trace' (Refer Figure 5.3). In seed plants, the vascular tissue system of the leaf originates from the 1-5 or more leaf traces. The single vascular strand in small petiolate leaves of dicotyledons may be an extension of single leaf trace or fusion of 2 leaf traces. This vascular strand becomes mid vein of the lamina.

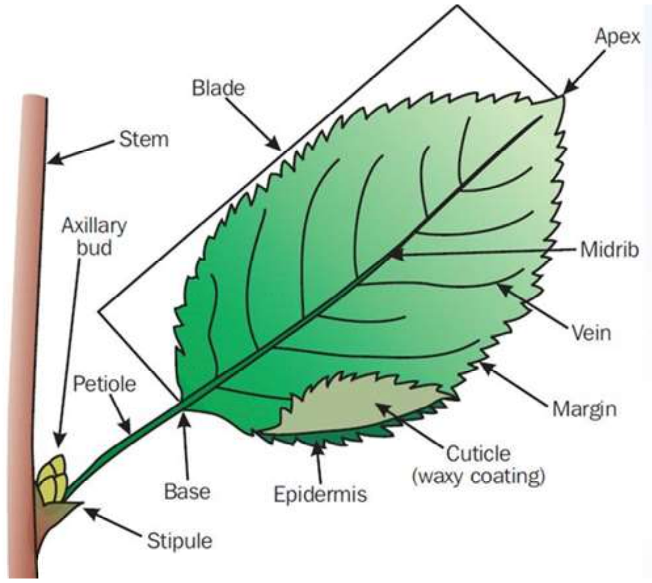

Fig. 5.3 *Divergence of Vascular Strand to Leaf Showing Leaf Trace and Leaf Gap*

However, in large leaves more than 2 leaf traces may give rise to the vascular strand of petiole which extends as midvein and branching lateral veins forming the network of veins in the leaf lamina. This network may further form anastomosing (fusing) system of veins giving rise to reticulate venation pattern in dicots and parallel venation pattern in monocots (Refer Figure 5.4).

(a)

(b)

Fig. 5.4 *Leaf Venation Patterns; A: Reticule Venation of Dicot Leaf; B: Parallel Venation of Monocot Leaf*

NOTES

The vascular bundles of the veins in leaf blades are enclosed by one or more layers of parenchytamous (or sometimes collenchytamous or sclerenchytamous) cells forming the bundle sheath. For example, prominent bundle sheath of parenchymatous photosynthetic cells is present in leaves of some grasses giving it distinctive anatomy (Kranz anatomy).

5.3 NODAL ANATOMY

A stem consists of nodes and internodes. At each node, part of the vascular system is deflected into the leaf attached at this node. A primary vascular connection between the stem vascular system and the leaf vascular supply at the base forms **leaf trace**. The leaf trace is a vascular bundle that connects the vascular system of the leaf with that of the stem. Leaf traces provide a means of access to water and essential minerals from the roots via stem, and transport of photosynthates to the developing meristems, flowers, fruits and, stem and roots for storage and/or consumption for their growth and development. The leaf traces may diverge from the stem vascular system near the nodes or some distance below the nodes (Refer Figure 5.5).

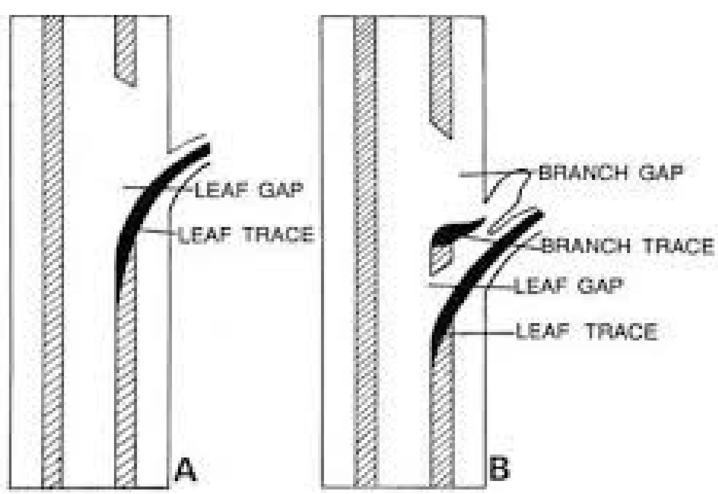

Fig. 5.5 *Leaf Trace Arising at Node*

The vascular strand of leaf traces consists of protoxylem, metaxylem, protophloem and mataphloem. The leaf traces are often larger than vascular bundles of their origin, containing more tracheary elements.

The parenchymatous regions in the vascular system of the stem, located above the diverging leaf traces, are called **leaf gaps** or **lacunae**. The gaps are quite conspicuous in the ferns and angiosperms where the vascular system in the inter-nodal parts of the stem forms a more or less continuous cylinder. In fact, these gaps are not discontinuity of the vascular system of the axis. Lateral connections occur between the tissues above and below the gap. In transverse sections of an axis at the level of a leaf gap, the gap resembles an inter-fascicular area. The transverse sections of such stems show a circle of vascular bundles with the parenchymatous leaf gaps. On the basis of number of gaps and leaf traces diverging from the stem vascular system, there are three common types of nodes in the dicotyledons- **Unilacunar** node with a single gap and a single trace to a leaf, **Trilacunar** node with three gaps and three traces to a leaf (one median and two lateral) and **Multi-lacunar** node with several to many gaps and traces to a leaf (Refer Figure 5.6 and 5.7).

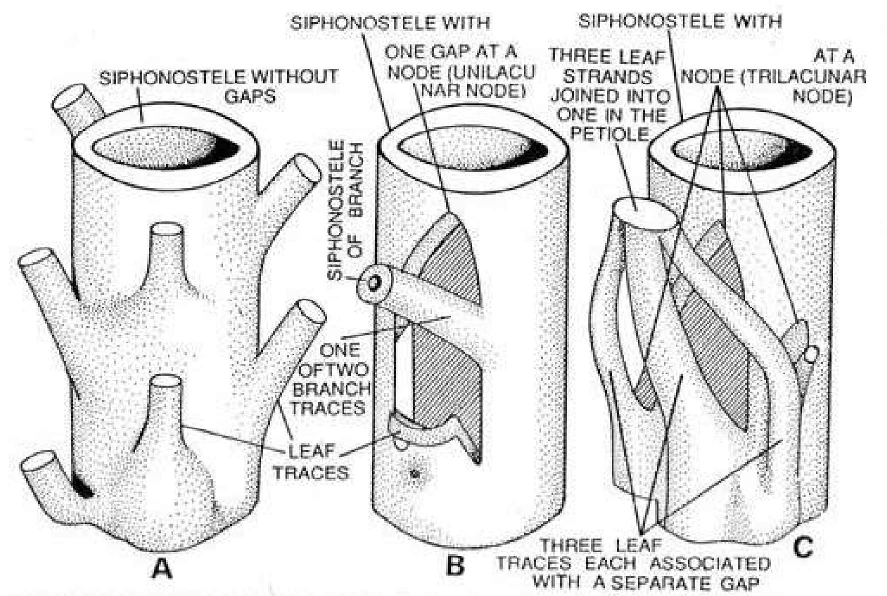

Fig. 5.6 *Primary Vascular System*

The above Figure 5.6 shows the primary vascular system; A). siphonostele type vascular system in *Selaginella*, without leaf-gaps; B). unilacunar node in nicotiana, siphonostelic with leaf gap; C). trilacunar node in salix, siphonostelic with leaf gaps

The trilacunar condition is considered as primitive condition in the dicots and the unilacunar and the multi-lacunar are thought to be derived from trilacunar condition. Several monocot plants possess leaves with sheathing bases and nodes with a large number of leaf traces separately inserted around the stem. In case of ferns, the number of traces to a leaf varies from one to many, but they are always associated with a single gap. In gymnosperms a unilacunar node is common. The leaf trace relationships at the nodes are thought to be of phylogenetic importance, and therefore, nodal anatomy is concerned with the study of systematics and phylogeny of angiosperms.

NOTES

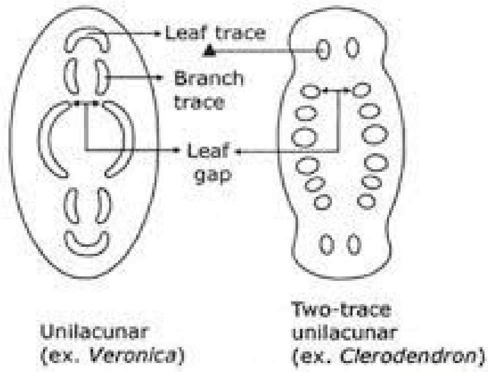

Fig. 5.7 Different Types of Nodal Structures as Seen in Cross-Section of Stems

At the nodal region three types of vascular bundles are observed: Leaf trace bundles, Cauline bundles and common bundles. **Leaf trace bundles** is a single vascular bundle that connects the leaf base with the main vascular cylinder of stem. **Cauline bundles** forms the vascular system of stems in totality. Sometimes these bundles anstomose (fuse) with each other and form continuous vascular system from stem to leaf as leaf traces. **Common bundles** run unbranched through a few successive nodes and internodes. Ultimately the vascular bundles terminate as leaf traces. The arrangement of vascular bundles at the nodes is more complex than the internodes due to emergence of vascular traces to the leaves, buds, stipules, etc., present at the node. These arrangements are as follows:

Leaf Trace and Leaf Gap

A leaf trace is demarcated as the cauline part of vascular tissue that deviates from the vascular tissue of stem towards leaf base. Leaf trace may be a portion of cauline bundle as it occurs within the caulis, that is, stem. Cauline bundles entirely form the vascular system of stems. Sometimes cauline bundle departs from the stele towards leaf base thus forming leaf trace. Leaf trace is seen in the nodal region of stem. Leaf trace is an independent bundle that may occur through one or more nodes and internodes before bending away from the stem toward the leaf. (Refer Figure 5.8 and 5.9).

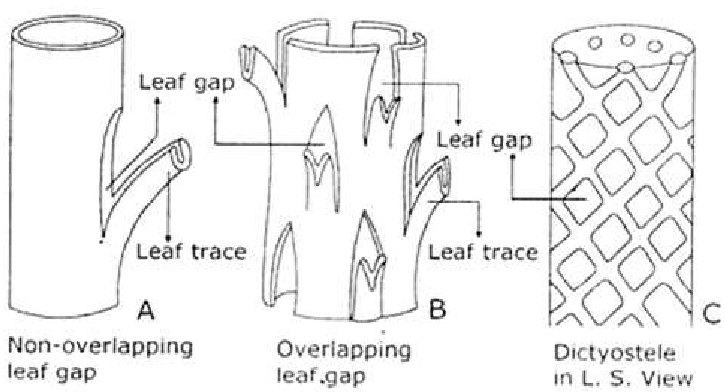

Fig. 5.8 Diagrammatic Illustration of Vascular Cylinder at Node with Leaf Gap in Three-Dimensional View

A leaf trace originates from the apical meristem of leaf primordium. After complete differentiation it joins with the vascular tissue of stem. Apart from leaf trace other vascular strands entirely occur in the stem. They constitute the cauline (stem) bundle and originate from apical meristem of shoot apex. Some cauline bundles may bend towards leaf thus forming leaf trace and these bundles are referred to as common bundles.

In the nodal region, a leaf trace bends away from the vascular cylinder of stem toward the petiole of leaf. From the base of petiole leaf trace extends into leaf blade where the trace forms vascular bundle of leaf. In the stem phloem occurs on the peripheral side of vascular cylinder.

As the leaf trace is bent away from the vascular cylinder toward petiole phloem in the vascular bundle of leaf occurs on the abaxial side of leaf. As a result, the vascular bundle of leaf has an inverted orientation of xylem and phloem in relation to vascular bundle of stem.

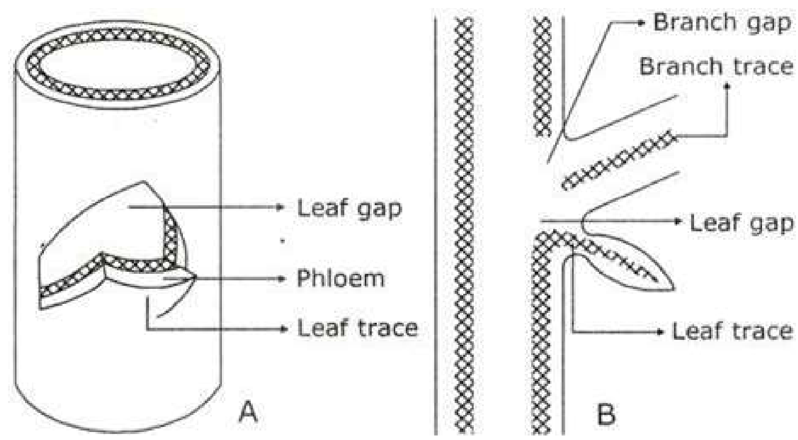

Fig. 5.9 *Illustration of Position of Phloem at the Time of Leaf Trace Entrance to Leaf Base*

The above Figure 5.9 shows Positions of Leaf Gap and Branch Gap in Longitudinal View of Stem at Node

A cross-section through node discloses that, there is a break in the vascular cylinder of stem, that is, the vascular cylinder is not in the form of a continuous ring. In this region the vascular tissue is interrupted, and parenchyma cells fill the gap. Pith and cortex are continuous through this gap. Such region is referred to as leaf gap and occurs opposite to leaf trace. A leaf gap is defined as the wide interfascicular region that is located opposite the upper part of leaf trace and is filled up with parenchyma cells through which pith and cortex become continuous. There exist many variations in the number of leaf gaps and the number of leaf traces in different plants. The variation may be different in the same plant at different levels, for example *Hypecoum procumbens*—the lower node of which has three traces per leaf whereas the upper nodes have single trace per leaf. The variations are subjects of comparative studies and therefore have taxonomic and phylogenetic significance. Atactostele is the characteristic of monocot stem and the arrangement of vascular strands at the node is highly complex. Comparatively the anatomy at the node of dicotyledonous stem is less complex. To describe the nodal anatomy of stem different terms are used.

Branch Trace and Branch Gap

Branch trace can be defined as the vascular trace that originates from the vascular cylinder of stem and enters to a branch. The position of the origin of a branch is from the axil of a leaf. In this position the vascular cylinder of stem is discontinuous. Parenchyma occupies this region as observed in a cross-section of stem at node. This interrupted region of vascular cylinder due to the presence of branch trace is designated as branch gap. Two branch traces are associated to a single leaf gap. Branch trace directly diverges to a branch from the main vascular cylinder of stem without running obliquely through the internode.

The branch traces depart from the main vascular cylinder of stem toward right and left of the median leaf trace. After a short distance the traces coalesce and form a complete stele similar to main vascular cylinder. Therefore, the vascular bundle of branch has the same orientation of xylem and phloem in relation to the vascular bundle of stem. It is previously mentioned that branch develops from axillary bud that originates on the stem at the axil of leaves. From the time of initiation, the buds are connected by vascular traces to the vascular strands on the main axis. These vascular traces are referred to as **bud trace** or **branch trace** or **ramular trace**. Axillary buds form axillary shoots whose first foliar structures are the prophylls. In dicotyledons, usually two branch traces emerge out from the vascular cylinder of stem. In exceptional cases the branch trace may be one (for example, *Peperomia*, *Cayratia,* etc.) or more than two. Sometimes medullary bundles may enter into the bud (for example, *Dahlia*). In case of single branch supply the vascular cylinder appears as crescent or horseshoe shaped in cross sectional view with the opening downward. After a short distance the opening closes and the cylindrical stele of the branch is formed. When the branch traces are more than one, they coalesce after a short distance, forming a complete stele like that of the main axis.

Two prophylls occur in dicotyledons oriented in such a way that their plane of bisection is parallel with the plane of the axillant leaf. Initially, two branch traces supply the prophylls. The branch traces are composed of one or more bundles that later increase in size due to the formation of vascular traces to the other leaves of the branch, situated above. Thus, the branch traces, are *in facto* the leaf traces of the axillary shoot. The continuity of the vascular cylinder of stem is interrupted at the nodal region due to the emergence of branch traces. At this region and above the point of departure parenchyma differentiates instead of vascular tissues. The parenchymatous area in the vascular cylinder of stem at the node immediately above the branch trace is the branch gap through which pith and cortex become continuous. Branch gap occurs in vascular plants having pith. In pteridophytes, where the vascular cylinder is protostele and devoid of pith, branch gap is absent. Therefore, the branch gap in association with leaf gap results in the formation of dissected siphonostele. There is a definite correlation between leaf and branch trace. As seen in cross-section of a stem at node a leaf trace occurs on the peripheral side. It is followed by branch trace towards the inner side. A node that bears a single leaf exhibits the following sequences from periphery towards center —leaf trace, branch trace and leaf gap on the side where the leaf is inserted.

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Nodal Anatomy in Wheat (Monocot) Stem

In the wheat stem the course of the vascular bundles through the internode and the leaf sheath is almost parallel. Near the node the leaf sheath is considerably thick and attains its maximum thickness just above its union with the stem. On the other hand, the stem has the smallest diameter above the junction with the leaf sheath. The stem is hollow in the internode and solid at the node. The sheath remains open on one side at higher levels, just near the node. Enormous collenchymatous bundle caps are present in the bundles of leaf sheath. Just beneath the intersection of the leaf sheath and stem the smaller of the leaf traces are continued in the peripheral part of the axis, and the larger leaf traces become part of the inner cylinder of strands.

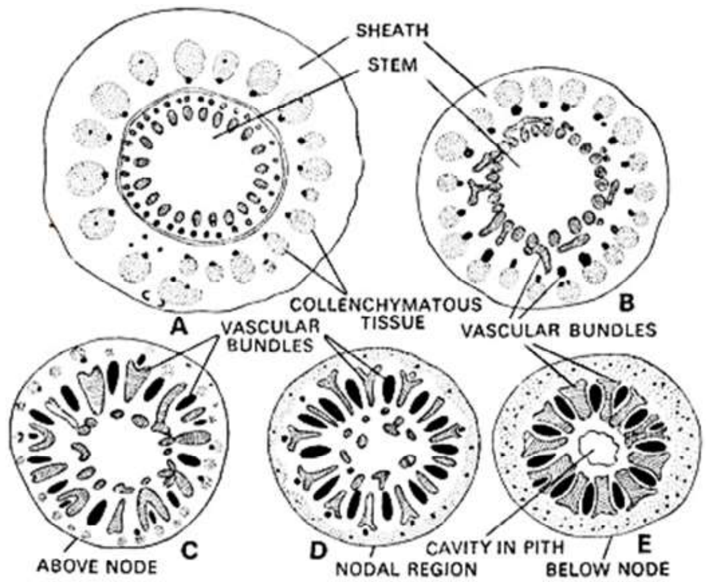

Fig. 5.10 *Nodal Anatomy of Wheat Stem*

The above Figure 5.10 shows the nodal anatomy of wheat stem. Bundles of sheath and their traces are depicted in black; vascular tissue of internode and its continuation through node is hatched. A-E Transections of stem at various levels. Towards node, sheath increases, and stem decreases in thickness.

The inter-nodal bundles located above the leaf insertion assume, just above the node a horizontal and oblique course, and are reoriented toward a more peripheral position in the node and below it. These horizontal and oblique bundles variously branch and coalesce, and their number reduces. The large leaf traces and the bundles from the internode above the insertion of the leaf make the inner cylinder of the bundles of the next lower internode. In this cylinder approximately half of the bundles are leaf traces from the nearest leaf above and the other half of the bundles are from the internode above the insertion of the leaf. The peripheral bundles are mostly leaf traces. The most conspicuous character of grass stems is the presence of transverse bundles in the nodal regions.

The anatomy of the node is regarded an important aspect in the study of phylogeny in dicotyledons, since a definite nodal type characterizes a taxon. During the evolution of nodal region, fusion, deletion and additions of leaf traces have occurred in the remote past. Apart from the phylogenetic significance, the nodal anatomy is a good taxonomic character used in the systematics of higher plants.

Check Your Progress

1. How many types of vascular tissues consists of?
2. What does xylem tissue consists of?
3. What does Phloem tissue consist of?
4. Where does primary vascular tissues arise from?
5. What is residual meristem?
6. What is epidermis?
7. How does apical growth occur?

5.4 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Vascular tissues consist of two basic types-xylem and phloem.
2. The xylem tissue, consisting of the tracheary elements (tracheids and vessels), xylem fibers and xylem parenchyma, transports water, minerals, phytohormones, and provides mechanical support.
3. Phloem tissue, on the other hand, transports photosynthesis products (sugars), proteins and other solutes required for plant growth and development. Phloem consist of sieve elements, companion cells, phloem fibers and phloem parenchyma cells.
4. The primary vascular tissues arise from the provascular cells present as lateral meristems in the growing apical regions during the development of primary plant body.
5. In many taxa, the provascular strand differentiates in a cylindrical zone immediately below the apical meristem called residual meristem.
6. The epidermis is the outermost layer forming the ‘skin’. It is usually single-layered due to anticlinal (at right angles to the axis) division of the mother cells and provides protective covering to the plant body.
7. Apical growth occurs by the activity of apical meristem. In vascular cryptogams, apical meristem formed at the tip of leaf primordium shows prolonged activity. In ferns, the apical meristem can function for an extended period.

5.5 SUMMARY

NOTES

- Plant vascular tissues evolved about 430 million years ago. This enabled long distance transport of water and food, and therefore, paved a way to land colonization by plants.
- In lower vascular plants, vascular tissues are organized in a simple manner as xylem at the center surrounded by phloem.
- The most common vascular organization within a vascular bundle is parallel placement of xylem and phloem tissue.
- Vascular tissues consist of two basic types-xylem and phloem. The xylem tissue, consisting of the tracheary elements (tracheids and vessels), xylem fibers and xylem parenchyma, transports water, minerals, phytohormones, and provides mechanical support.
- Phloem tissue, on the other hand, transports photosynthesis products (sugars), proteins and other solutes required for plant growth and development.
- Phloem consist of sieve elements, companion cells, phloem fibers and phloem parenchyma cells.
- Tracheary elements of xylem and sieve elements of phloem forms continuous columns- a vascular system throughout the plant body.
- The conducting elements of xylem and phloem maintain a continuous supply of water, nutrients phytohormones and food throughout the plant body.
- The primary plant body is developed by division and differentiation of cells arising from the apical meristems at the root and shoot apices.
- At the meristematic regions, the meristematic cells give rise to the progenitor cells, which further differentiate to form the primordial epidermal, ground and stellar tissues. These primordial tissues further give rise to permanent epidermal tissue systems, ground tissue system and vascular tissue system as a result of morphogenesis.
- Ultimately, protoderm will develop into epidermis, ground meristem will give rise to cortex and pith, and the provascular tissue will form primary vascular system of the mature stem.
- The cells closest to the apical regions are produced recently and therefore are younger as compare to the cells at a distance from apices.
- The primary vascular tissues arise from the provascular cells present as lateral meristems in the growing apical regions during the development of primary plant body.
- The tissue organization of these fundamental organs is more or less similar consisting of all the basic tissue systems. Starting from the periphery, the plant axis has three zones or regions – the epidermis, cortex and stele.

- The epidermis is the outermost layer forming the 'skin'. It is usually single-layered due to anticlinal (at right angles to the axis) division of the mother cells and provides protective covering to the plant body. The next internal zone to epidermis is the cortex.
- The vascular bundles perform the function of translocation of water and solutes as well as give mechanical support to the plant.
- A lateral meristem, cambium, may be present in between the xylem and phloem, as in the stems of dicotyledons and gymnosperms.
- Xylem and phloem tissues are arranged radially in the roots while occur on the same radius in other organs. Sometimes vascular stele encloses a central, soft parenchymatous pith or medulla, which is continuous in-between the vascular bundles looking like rays radiating from the pith — called pith rays or medullary rays.
- In between the vascular bundles and endodermis there occurs one or more layers of non-conducting cells known as pericycle.
- The meristematic regions between the mature tissues are known as intercalary meristem. These tissues have been extensively studied in the stems of grasses. The initial internodes in the developing shoot in grasses are very short and entirely meristematic.
- The basal meristems of many developing leaves, especially those with prominent petioles or that are needle-like, for example leaves of pine, are also considered to be intercalary meristems by many workers.
- All the tissues forming the plant body are derived from the apical meristem present at the tips or apices of the axis.
- The presence near the shoot apex of a Primary Thickening Meristem (PTM), which is probably plesiomorphic in monocotyledons, predisposes evolution into the many pachycaul (trees with disproportionately thicker trunk for their height) forms.
- A PTM occurs in virtually all monocotyledons, whereas the Secondary Thickening Meristem (STM), which is morphologically similar, is limited to a few genera of Liliiflorae.
- To a greater or lesser extent in different taxa, the PTM is responsible for primary stem thickening, adventitious root production, and formation of linkages between stem, root and leaf vasculature. The STM largely contributes to the body of the stem.
- The microphyllous leaves have a single vein running from the base to the apex of leaf. Whereas, in macrophyllous leaves the vein is branched forming a venation network. The venation maybe open or closed.
- In ferns, the apical meristem can function for an extended period. In seed plants, the apical growth stops relatively early even though there is apical meristem.

NOTES

- The development of young primordium and, subsequent elongation and extension of leaf occur by cell division throughout the young primordium.
- The growth of the leaf stops first at the tip and last at the base. Most of the leaves grow in length due to intercalary growth.
- The vascular bundles of the veins in leaf blades are enclosed by one or more layers of parenchytamous (or sometimes collenchytamous or sclerenchytamous) cells forming the bundle sheath.
- A primary vascular connection between the stem vascular system and the leaf vascular supply at the base forms leaf trace.
- The parenchymatous regions in the vascular system of the stem, located above the diverging leaf traces, are called leaf gaps or lacunae.
- A cross-section through node discloses that, there is a break in the vascular cylinder of stem, that is, the vascular cylinder is not in the form of a continuous ring. In this region the vascular tissue is interrupted, and parenchyma cells fill the gap.
- Pith and cortex are continuous through this gap. Such region is referred to as leaf gap and occurs opposite to leaf trace.
- A leaf gap is defined as the wide interfascicular region that is located opposite the upper part of leaf trace and is filled up with parenchyma cells through which pith and cortex become continuous.
- Atactostele is the characteristic of monocot stem and the arrangement of vascular strands at the node is highly complex.
- Branch trace can be defined as the vascular trace that originates from the vascular cylinder of stem and enters to a branch. The position of the origin of a branch is from the axil of a leaf. In this position the vascular cylinder of stem is discontinuous.
- The parenchymatous area in the vascular cylinder of stem at the node immediately above the branch trace is the branch gap through which pith and cortex become continuous. Branch gap occurs in vascular plants having pith.
- In pteridophytes, where the vascular cylinder is protostele and devoid of pith, branch gap is absent. Therefore, the branch gap in association with leaf gap results in the formation of dissected siphonostele.
- A node that bears a single leaf exhibits the following sequences from periphery towards center —leaf trace, branch trace and leaf gap on the side where the leaf is inserted.

5.6 KEY WORDS

- **Protostele**: In lower vascular plants, vascular tissues are organized in a simple manner as xylem at the center surrounded by phloem known as protostele**.**
- **Amphivasal vascular bundles:** In monocots, like *Dracaena* and *Acorus*, phloem is surrounded by a continuous ring of xylem, such pattern is called amphivasal vascular bundles.
- **Residual meristem**: In many taxa, the provascular strand differentiates in a cylindrical zone immediately below the apical meristem called residual meristem**.**
- **Annuals**: some plants grow only for one season forming only the primary tissues, and at the commencement of unfavorable conditions, complete their life cycle and die off known as annuals.
- **Epidermis**: The epidermis is the outermost layer forming the 'skin'.
- **Pericycle**: In between the vascular bundles and endodermis there occurs one or more layers of non-conducting cells known as pericycle.
- **Intercalary meristem**: The meristematic regions between the mature tissues are known as intercalary meristem.

5.7 SELF ASSESSEMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. What does xylem and phloem consists of?
2. How are transitional tissue regions formed?
3. Define pericycle.
4. Write a short note on intercalary meristem.
5. What is secondary growth?
6. What is bud trace?

Long Answer Questions

1. Write a note on vascular differentiation at meristems.
2. Discuss about the primary tissue regions of stem and root.
3. Briefly discuss about the primary thickening of meristem giving examples.
4. Explain the primary tissue regions of leaf
5. Explain the about nodal anatomy in detail.

5.8 FURTHER READINGS

NOTES

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UNIT 6 ROOT STEM TRANSITION

NOTES

Structure

6.0 INTRODUCTION

The change in orientation of vascular tissues from exarch radial type in root to endarch and conjoint collateral type in stem is designated as root-stem transition. The continuity between the vascular strands of roots and stems is maintained but the orientational change takes place through splitting, twist-ing and inversion of xylem strands at the very short transition zone which is neither a root nor a stem. Transition occurs at the hypocotyl region either gradually or abruptly. There exist two main concepts on the nature of root-stem transition.

According to Eames and MacDaniels (1947) there are three types of root-stem transitions in dicot and single type in monocot. In the diagram the row of circles at the base repre-sents the transverse sections of roots while the uppermost row is the transverse sections of stems. The three intermediate rows are the suc-cessive transverse sections through transition zone.

In type I there are four strands of xylem and phloem in the root and stem. The phloem remains in same position in both root and stem. In this second type the number of bundles in stem is twice than in root. In root there are two alternate xylem and two phloem strands. In type III, like type I, the number of vascular bundles in the stem remain same as that of phloem strands in the root after transition, but the xylem and phloem become conjointly oriented instead of radial. This is a reductional transition in which the number of vascular bun-dles in stem becomes half of the number of phloem strands present in root.

In this unit, you will study about root stem transition, molecular aspects of developing vegetative organs in detail.

6.1 OBJECTIVES

After going through this unit, you will be able to:

- Discuss the concepts regarding stem-root transition

- Explain the significance of root-stem transition
- Discuss molecular aspects of developing vegetative organs

NOTES

6.2 ROOT STEM TRANSITION

The root and shoot form a continuous axial structure in higher plants. The simplest organization of this axial structure is exhibited by Psilophytales. The differentiated complex organization of this system into root, stem and leaf is considered as an evolutionary specialization in the higher plants. The differentiation of root and stem is initiated at the time of embryogenesis in the embryo axis. In Angiosperms, an embryo is made up of one or two cotyledons. The primordium of shoot-plumule occurs towards the upper end just above the insertion of cotyledons and the region between the insertion of cotyledon and plumule is the epicotyl. The plant developing from the embryo axis shows a continuity of root and stem externally. The tissues of axis- epidermis, cortex, endodermis, pericycle and secondary vascular tissues are directly continuous from root to stem internally also. Similar continuity is present in primary vascular tissues; however, they do not unite directly because the orientation of primary vascular tissues is markedly different in root and stem.

In root, the primary vascular tissue is of radial type, having independent strands of phloem and xylem that show alternate arrangement, the xylem being exarch. In contrast, the stem shows collateral arrangement of primary vascular tissues with endarch protoxylem. Therefore, the primary vascular tissues of root and stem though apparently continuous merge with each other by changing one type of arrangement and structure to the other type. This change of arrangement of primary vascular tissues is usually referred to as vascular transition. The change occurs at successive levels of radicle-plumule axis. The place where the change of orientation of vascular tissues occurs, is designated as transition region. The exact region of vascular transition varies, it may be at the top, center or base of hypocotyl, or at the top of radicle. Similarly, the length of transition region is also variable. It may be short and the length ranges from one to three millimeter where the vascular transition occurs abruptly. On the other hand, in long transition region it may be several centimeters in length and the vascular transition may occurs gradually. The transition region may be visible externally as a zone of depression or change in diameter. However, in many plants the external morphology and transition region do not correspond precisely.

Root-Stem Transition

The transformation in arrangement of vascular tissues of roots having discrete radial strands of phloem and xylem with exarch protoxylem into collaterally placed phloem and xylem with endarch protoxylem of stem is generally stated to as **root-stem transition**. The continuity between the vascular strands of roots and stems is maintained, but the orientational change takes place through splitting, twisting and inversion of xylem strands at the very short **transition zone** which is neither a root nor a stem. Generally, transition occurs at the hypocotyl region either gradually or abruptly.

Concepts Regarding Stem-Root Transition

Two main concepts exist regarding the nature of root-stem transition, i.e., as follows:

Classical Concept

According to Eames and MacDaniels (1947), there are three types of root-stem transitions in dicot and solo type in monocot (Refer Figure 6.1). The row of circular structures at the base represents the transverse sections of roots while the uppermost row is the transverse sections of stems, and the three intermediate rows are the successive transverse sections through transition zone.

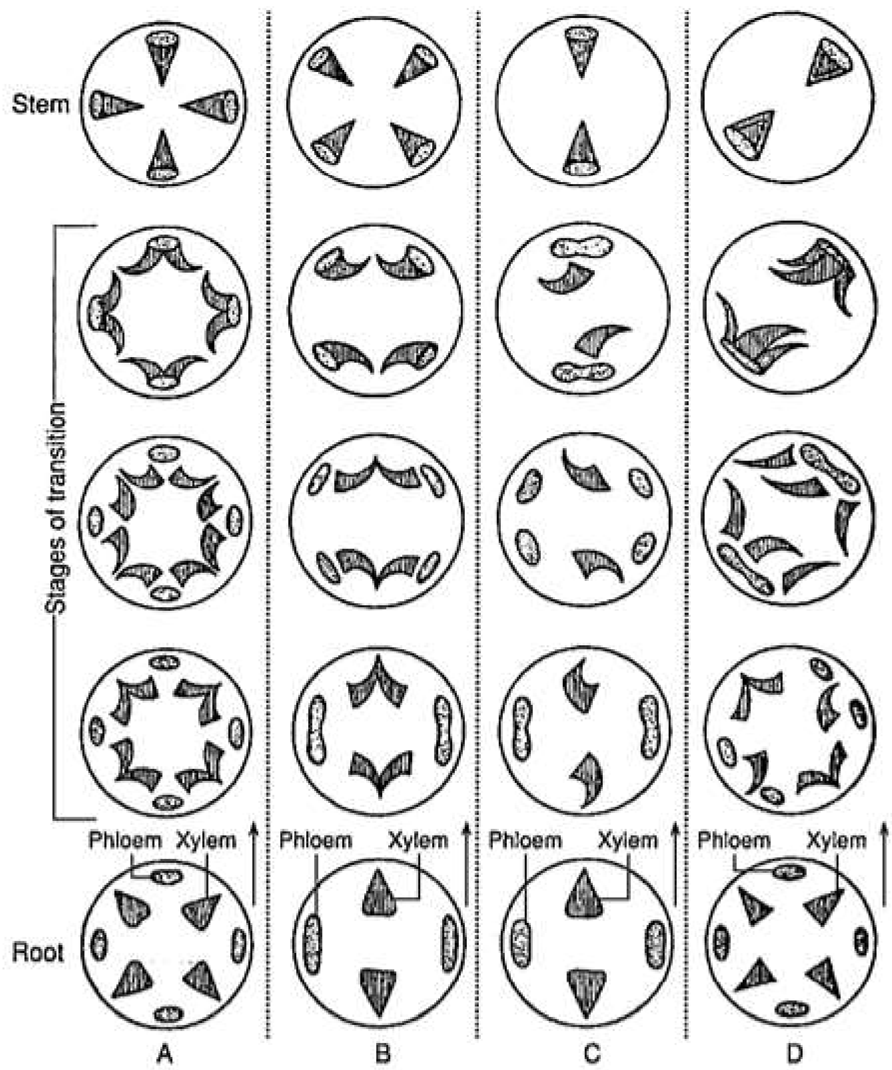

Fig. 6.1 Root Stem Transition

NOTES

Type A: There are four strands of xylem and phloem in the root and stem in this type. The position of phloem remains same in both root and stem. Each xylem strand of root splits by radial division into two branches. The two branches, gradually, swings laterally at the upper region to opposite directions by 180° and join the phloem strand in between. Therefore, the two xylem halves of root are inverted and become conjoint and endarch in stem. In this manner, the radial bundles and exarch xylem become conjoint collateral with endarch xylem orientation. Examples- *Dipsacus*, *Fumaria* and *Mirabilis*.

Type B: In this type, the number of bundles in stem is twice that in root. Also, in root there are two alternate xylem and two phloem strands. Phloem becomes elongated and dumb-bell shaped due to constriction at the middle in its upstream regions. While in the upper region, the constriction becomes deep and ultimately the phloem strand is divided into two. Consequently, the number is doubled to four in the stem. The two xylem strands also split and become inverted like type A. The four xylem halves thus produced, join with the phloem inside to become conjoint. Examples- *Acer, Cucurbita*, *Phaseolus* and *Tropaeolum.*

Type C: In this type, the number of vascular bundles in the stem remain same as that of phloem strands in the root after transition, like type A, but the orientation of xylem and phloem become conjoint instead of radial. The xylem strands in the upstream do not split but get inverted through 180 degree. The two phloem strands divide into four strands during transition, swing laterally and unite to form two strands that join the xylem on outside. Consequently, the same number of xylem and phloem is maintained in root as well as in stem. Examples- *Lathyrus*, *Medicago* and *Phoenix*.

Type D: This type represents a reductional transition, where the number of vascular bundles in stem becomes half of the number of phloem strands present in root. There are four strands of phloem in root which unite to form two strands during root-stem transition. One of the two diagonal pairs of xylem tissue do not split but gets inverted through 180° rotation and joins with the phloem inside. The other diagonal pair of xylem splits radially into two halves and during upstream transition, one of the two halves swings laterally to right and the other to the left. Ultimately all the three xylem strands (one full and two half strands) join with the phloem inside. Thus, a single conjoint vascular bundle of stem consisting of the five vascular elements of root is formed. Example *Anemarrhena* in the family Liliaceae of monocots.

The above root-stem transition types are based on the study of continuous serial sections of the fully differentiated transitional zone. However, a entirely different image is offered by the developing transitional zone.

Recent Concept

According to Esau (1965), initially vascular continuity is established between root and cotyledon through hypocotyls during ontogeny. After differentiation, the epicotyl traces are superimposed over the root-hypocotyl-cotyledon traces. Further, the tissues present between them are mutually accommodated. This interpretation is now regarded as recent concept of root-stem transition. The vascular transition of *Beta vulgaris* and *Daucus carota* has been cited based on ontogeny in agreement with this recent concept. There is an epicotyl shoot in between the two cotyledons of the *Beta vulgaris* seedling and the hypocotyl and root on the lower side. Anatomically, the root shows two exarch xylems and two phloem strands arranged consecutively in radial manner. The cotyledon traces consist of two vascular bundles that are partially fused along the protoxylem. The exarch condition of protoxylem in the root is maintained up to hypocotyl. Later, at the more upstream level, two metaxylem gradually differentiate towards the periphery on the lateral side of protoxylem leading to the endarch arrangement of xylem. The diarch root xylems thus gradually become four-stranded cotyledonary traces. The two phloem strands in the root at the hypocotyl region branch into four phloem strands. Each phloem strand associates with one metaxylem plate outside. Accordingly, conjoint collateral vascular bundles are produced which continues in the cotyledons.

The collateral, endarch epicotyl traces develop after the root-hypocotyl-cotyledon vascular strands are partially differentiated. The epicotyl traces remain connected with similarly oriented tissues in the root. They appear as superimposed over the root-hypocotyl-cotyledon vascular traces. Therefore, in *Beta vulgaris* there is no vascular transition between root and stem. But a mutual accommodation of vascular tissues is markedly visible.

In *Daucus carota* also the vascular continuity exists between radicle and cotyledon and the epicotyl traces join with root-cotyledon traces. Each cotyledon consists of three vascular bundles. Out of these, the median one consisting of exarch protoxylem continuous with that of the root. While the two phloem strands remain lateral to the median xylem strand in root. The other two lateral vascular bundles are collateral with endarch xylem and originate from the diarch xylem of root. Therefore, the primary vascular tissues of cotyledon and root remain same. The conjoint and collateral epicotyl traces develop later, and they ultimately join with radicle- hypocotyl-cotyledon traces. It may be concluded that the ontogenetic studies of vascular transition of *Beta* and *Daucus* reveals no root-stem transition as illustrated by Eames and MacDaniels (1947) in the earlier common concept.

The modern concept, which is based on developmental studies, discloses that during ontogeny vascular associations are established between radicle and cotyledon via hypocotyl. The epicotyl traces are developed later from procambial strand, which ultimately join with the fully differentiated radicle-hypocotyl-cotyledon unit and the tissues between the traces are accommodated mutually.

Significance of Root-Stem Transition

The internal tissue arrangement is entirely different from that of root and stem in the transition zone. Therefore, this region does not belong to any of these categories. Several interpretations are available to describe the structure and evolutionary significance of the transition zone. The oldest and most common concept is that the seedling has a unit vascular system which is morphologically equivalent to root and stem. The anatomical differences in this zone are due to splitting, twisting, rotation, inversion, etc. According to this concept- the protoxylem, metaxylem and phloem differentiate in the same positions as they occur in the mature state. At the transition zone, these vascular elements are differentiated in such a manner that they can maintain the continuity of unit vascular system.

According to the other concept (Esau, 1965), there is binary origin of the vascular system. There are two discontinuous regions of the vascular system in the seedling. One is the radicle-hypocotyl region and the other is the cotyledon region. These two regions of the vascular system are joined at the upper region of hypocotyl. The root and shoot apices of the seedling have their own meristem which forms the root and stem, respectively. During development, vascular connections are established between radicle and cotyledon through hypocotyl. The epicotyl traces are joined with the radicle-hypocotyl-cotyledon unit and tissues between the traces are mutually accommodated. The radial arrangement of xylem and phloem is usually considered as primitive while the collateral arrangement is regarded as advanced. Therefore, the xylem and phloem arrangements at the upstream transition zone represent the different evolutionary stages which terminate into collateral arrangements in the stem.

Molecular Aspects of Developing Vegetative Organs

The variability of shoot architecture in plants is prominent and is one of the most extreme examples of adaptive growth in higher organisms. Flexibility in stem growth basically contributes to this variability, mediated by the differential activity of apical and lateral meristems. Despite the importance of role of different molecular events taking place at the meristematic regions, the regulation of major events in stem development is largely unexplored. Recently, however, new methods using knowledge from root and leaf development are starting to give insights on molecular mechanisms that regulate this essential plant organ.

Stems as Central Organs of Plant

Plant growth is flexible, especially for shoots, showing great variation in size, architecture and function. Generally, shoots of higher plants have been divided into repetitive units called **phytomers**, each of which consists of a leaf, a leaf attachment site including an axillary bud (**nodium**) and an associated piece of stem (**internodium**). In phylogenetic and ontogenetic terms, the alteration of this unit is fundamental for establishment of the large diversity of plant growth forms and the adaptability of plants to various environmental conditions. Further, modification of stem development is essential for this flexibility, as stems are the central part of the plant, connecting various body parts and providing or transporting substances important for long-distance cell-to-cell communication. Interestingly, regardless of its fundamental role in plant growth, our knowledge of how stem development is regulated is limited and unexplored. Moreover, in a large range of species, stems have the capacity to grow laterally. Mediated by stem cell-like (meristematic) tissues (predominantly the cambium in case of higher plants), lateral growth of stems and roots is essential for generating large plant bodies. Thereby, it substantially contributes to the dominance of seed plants in terrestrial ecosystems, to wood formation and thus to carbon immobilization. The initiation of lateral meristems has not been studied in detail at the cellular level; this is another underexplored part in our knowledge of the regulation of stem anatomy and growth dynamics.

Plant Organs Diversified During Evolution

Apical growth mediated by one or several stem cells leading to the formation of organs from cylindrical tip is a characteristic feature of land plants. Based on fossil records, it is presumed that instead of forming distinct shoot and root systems, early land plants consisted of simple leafless growth axes (**telomes**), growing predominantly horizontally and containing pro-vascular tissue organized as a protostele. According to this opinion, an important adaptation to a land-based lifestyle was the diversification of telomic structures into organs specialized for aboveground and underground growth. Prehistoric organ diversification is supported by anatomical similarities in stems and roots. For instance, the observation that in extant species similar molecular mechanisms regulate the dynamics of both shoot and root apical meristems. In addition, shoot poles can be transformed into root poles and vice versa by ectopic expression of PLETHORA and CLASS III HOMEODOMAIN-LEUCINE ZIPPER (HD-ZIPIII) genes, respectively, indicating that polar growth does not depend on the establishment of two different organ identities and that growth axis identities are transformable by the activity of selected key regulators.

A strong phylogenetic relationship also seems to exist between stems and leaves. According to Zimmermann's **telome theory**, leaves are derived from shoot-like precursors in euphyllophytes (ferns and seed plants). Starting with overtopping by the main shoot, lateral stem clusters are thought to have undergone planation and subsequent fusion by photosynthetically active tissue (**webbing**). In fact, the presence of the same signaling modules regulating, for instance, lateral organ formation at the flanks of the SAM and the formation of leaflets in growing leaves supports a strong evolutionary link between both organs and provides scenarios for the molecular bases for the distinct transformation steps during the evolution of leaves. Thus, postulating a tight phylogenetic relationship between stems and other organs, the analysis of stem development can be expected to be rewarding for an understanding of the development and origin of various plant body structures.

Initiation of Lateral Growth

Stems of gymnosperms and most angiosperms grow in diameter by the cambium-based production of secondary vascular tissue. Fossil records advocate that the

bifacial vascular cambium, as known from extant (living) species, evolved approximately 400 million years ago in early seed plants, which thereby overcame hydraulic constraints and subsequently achieved a dramatic increase in growth-form plasticity and increased adaptability to different environments.

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Auxin is Essential for Lateral Growth

In ontogenetic terms, cambium-based lateral growth is closely connected to the establishment of primary vascular bundles in an 'open' conformation, meaning that procambium attributes are maintained in the bundle center. The established view is that after determination of procambial strands, xylem and phloem differentiation starts from adaxial and abaxial bundle poles, respectively, progressing towards the bundle center. Information regarding the factors important for the maintenance of pro-cambium characteristics in the bundle center, that is, for the distinction between open and closed bundles, is not clear. Although, other hormones partly have a strong influence on cambium activity, one strong candidate for the maintenance of procambium characteristics is the differential regulation of auxin transport, perception and/or production during bundle differentiation. Auxin has been shown in numerous studies to be essential for inducing and maintaining fascicular and interfascicular cambium activity. Snow demonstrated 75 years ago that decapitated sunflower seedlings activated vascular cambium in the stem only when treated apically with auxin. The same type of experiment has confirmed the necessity of apex-derived auxin for secondary growth in other species such as *Arabidopsis* and *Populus*. Certainly, measurements in the stem of *Pinus sylvestris* and *Populus* along the radial sequence of tissues show that auxin concentration peaks in the vascular cambium.

In *Arabidopsis*, the size of the domain in the bundle center displaying high levels of auxin signaling and cambium activity itself is defined by the interplay between KAN and HD-ZIPIII genes. Removal of genes from either group increases the pro-cambium domain, indicating that cambium characteristics are suppressed in adaxial and abaxial bundle domains to allow cell differentiation. Consistently, REV-deficient stems display enhanced cambium activity and ectopic expression of KAN1 inhibits pro-cambium formation. On the other hand, overexpression of a REV ortholog from *Populus* (PRE) leads to pleiotropic defects, one of them being ectopic cambium formation in the cortex, also suggesting a positive effect of the gene on cambium activity. However, considering the complex interaction among the HD-ZIPIII family members, this effect could be due to the repression of other family members, for example the *Populus* CNA ortholog, which is believed to promote cell differentiation. Lack of maintenance of an active cambium in leaves even though initial events of bundle formation are very similar to those in stems may be attributed to the fact that production of secondary vascular tissue in leaves is only rudimentary in most species, including *Arabidopsis*. However, the two cambium markers PHLOEM INTERCALATED WITH XYLEM (PXY) and WUSCHEL-RELATED HOMEOBOX4 (WOX4) are expressed in leaf bundles, suggesting that the cambium-specific stem cell niche is established during leaf development and that leaf bundles keep their open character. One possible explanation for the missing cambium activity is the attenuation of auxin production in older leaves. Auxin treatments of leaf explants in tissue culture lead to plant regeneration, often starting with proliferation of cells from the vasculature, suggesting that, even when they are not actively dividing, cells within the vasculature harbor a particular meristematic potential, which can be activated by elevated auxin levels. Thus, establishment and maintenance of the cambium-specific stem cell niche throughout different plant organs might be one important prerequisite for the high degree of plant growth plasticity.

Check Your Progress

1. When is differentiation of root and stem initiated?
2. What type of roots are there in primary vascular tissue?
3. What is root-stem transition?
4. What is phytomers, nodium and internodium?
5. Write briefly about initiation of lateral growth.

6.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. The differentiation of root and stem is initiated at the time of embryogenesis in the embryo axis.
2. In root, the primary vascular tissue is of radial type, having independent strands of phloem and xylem that show alternate arrangement, the xylem being exarch.
3. The transformation in arrangement of vascular tissues of roots having discrete radial strands of phloem and xylem with exarch protoxylem into collaterally placed phloem and xylem with endarch protoxylem of stem is generally stated to as root-stem transition.
4. Plant growth is flexible, especially for shoots, showing great variation in size, architecture and function. Generally, shoots of higher plants have been divided into repetitive units called phytomers, each of which consists of a leaf, a leaf attachment site including an axillary bud (nodium) and an associated piece of stem (internodium).
5. Stems of gymnosperms and most angiosperms grow in diameter by the cambium-based production of secondary vascular tissue. Fossil records advocate that the bifacial vascular cambium, as known from extant (living) species, evolved approximately 400 million years ago in early seed plants, which thereby overcame hydraulic constraints and subsequently achieved a dramatic increase in growth-form plasticity and increased adaptability to different environments.

6.4 SUMMARY

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- The root and shoot form a continuous axial structure in higher plants. The simplest organization of this axial structure is exhibited by Psilophytales.
- The differentiated complex organization of this system into root, stem and leaf is considered as an evolutionary specialization in the higher plants.
- The differentiation of root and stem is initiated at the time of embryogenesis in the embryo axis.
- In Angiosperms, an embryo is made up of one or two cotyledons.
- The primordium of shoot-plumule occurs towards the upper end just above the insertion of cotyledons and the region between the insertion of cotyledon and plumule is the epicotyl.
- The plant developing from the embryo axis shows a continuity of root and stem externally.
- The tissues of axis- epidermis, cortex, endodermis, pericycle and secondary vascular tissues are directly continuous from root to stem internally also.
- The row of circular structures at the base represents the transverse sections of roots while the uppermost row is the transverse sections of stems, and the three intermediate rows are the successive transverse sections through transition zone.
- Type A: There are four strands of xylem and phloem in the root and stem in this type. The position of phloem remains same in both root and stem. Each xylem strand of root splits by radial division into two branches.
- The two branches, gradually, swings laterally at the upper region to opposite directions by 180° and join the phloem strand in between.
- Type B: In this type, the number of bundles in stem is twice that in root. Also, in root there are two alternate xylem and two phloem strands. Phloem becomes elongated and dumb-bell shaped due to constriction at the middle in its upstream regions.
- Type C: In this type, the number of vascular bundles in the stem remain same as that of phloem strands in the root after transition, like type A, but the orientation of xylem and phloem become conjoint instead of radial.
- Type D: This type represents a reductional transition, where the number of vascular bundles in stem becomes half of the number of phloem strands present in root. There are four strands of phloem in root which unite to form two strands during root-stem transition.
- According to Esau (1965), initially vascular continuity is established between root and cotyledon through hypocotyls during ontogeny.
- After differentiation, the epicotyl traces are superimposed over the root-hypocotyl-cotyledon traces. Further, the tissues present between them are mutually accommodated. This interpretation is now regarded as recent concept of root-stem transition.

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- The vascular transition of *Beta vulgaris* and *Daucus carota* has been cited based on ontogeny in agreement with this recent concept.
- Anatomically, the root shows two exarch xylems and two phloem strands arranged consecutively in radial manner.
- The cotyledon traces consist of two vascular bundles that are partially fused along the protoxylem.
- In *Daucus carota* also the vascular continuity exists between radicle and cotyledon and the epicotyl traces join with root-cotyledon traces.
- The internal tissue arrangement is entirely different from that of root and stem in the transition zone.
- At the transition zone, these vascular elements are differentiated in such a manner that they can maintain the continuity of unit vascular system.
- The root and shoot apices of the seedling have their own meristem which forms the root and stem, respectively.
- The epicotyl traces are joined with the radicle-hypocotyl-cotyledon unit and tissues between the traces are mutually accommodated.
- In phylogenetic and ontogenetic terms, the alteration of this unit is fundamental for establishment of the large diversity of plant growth forms and the adaptability of plants to various environmental conditions.
- Mediated by stem cell-like (meristematic) tissues (predominantly the cambium in case of higher plants), lateral growth of stems and roots is essential for generating large plant bodies.
- The initiation of lateral meristems has not been studied in detail at the cellular level; this is another underexplored part in our knowledge of the regulation of stem anatomy and growth dynamics.
- Apical growth mediated by one or several stem cells leading to the formation of organs from cylindrical tip is a characteristic feature of land plants.
- Prehistoric organ diversification is supported by anatomical similarities in stems and roots.
- A strong phylogenetic relationship also seems to exist between stems and leaves. According to Zimmermann's telome theory, leaves are derived from shoot-like precursors in euphyllophytes (ferns and seed plants).
- Starting with overtopping by the main shoot, lateral stem clusters are thought to have undergone planation and subsequent fusion by photosynthetically active tissue (webbing).
- Auxin has been shown in numerous studies to be essential for inducing and maintaining fascicular and interfascicular cambium activity.

6.5 KEY WORDS

- **Phytomers**: Shoots of higher plants have been divided into repetitive units called phytomers.
- **Nodium**: A leaf attachment site including an axillary bud I stermed as nodium.
- **Internodium**: An associated piece of stem is called as internodium.

6.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

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Short Answer Questions

1. What is root-stem transition?
2. Give significance of root-stem transition.
3. What is initiation?
4. What is auxin?

Long Answer Questions

1. Discuss the concepts regarding stem-root transition.
2. Explain the significance of root-stem transition.
3. Discuss molecular aspects of developing vegetative organs.
4. Write a note on 'stems as central organs of plant'.
5. 'Plant organs are diversified during evolution'. Elaborate.
6. Discuss about initiation of lateral growth.
7. How is auxin essential for lateral growth? Explain giving examples.

6.7 FURTHER READINGS

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UNIT 7 CAMBIAL VARIANTS AND FLORAL VASCULATURE

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Structure

7.0 INTRODUCTION

Cambial variants is a deviation from normal secondary growth and production of secondary vascular and non- vascular tissues. A normal cambium with abnormal activity, accessory cambia or abnormally situated cambia with normal activity can produce anomalous secondary growth. Secondary growth from vascular cambia results in radial, woody growth of stems. The innovation of secondary vascular development during plant evolution allowed the production of novel plant forms ranging from massive forest trees to flexible, woody lianas. We present examples of the extensive phylogenetic variation in secondary vascular growth and discuss current knowledge of genes that regulate the development of vascular cambia and woody tissues. From these foundations, we propose strategies for genomics based research in the evolution of development, which is a next logical step in the study of secondary growth.

A flower is regarded as a modified determinate shoot. Its parts are regarded as different forms of modified leaves. A majority of botanists agree that a flower is equivalent to crowded appendages bearing compressed shoot. The entire plant body is formed from two meristematic apical regions- Shoot Apical Meristem (SAM) and Root Apical Meristem (RAM). These apices are recognized at 2-celled stage of developing embryo. These apical regions later, becomes plumule and radicle, respectively, and remain dormant for some time inside a seed. On germination of seed, the plumule gives rise to the shoot system and the radicle gives rise to the root system of the plant. The seedling formed after germination establishes itself and grows to enter juvenile stage. After a period of time the growing plant enters the vegetative phase of its life cycle. Duration of this phase varies greatly in different plant species, ranging from few days to decades. At appropriate time and in presence of specific external and internal signals, the plant enters its reproductive phase and some of the lateral and/or terminal apices gives

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rise to flowers or inflorescences. At the time of flowering. Different floral organs or appendages are formed as a result of 'switching' of vegetative phase to reproductive phase.

In this unit, you will study about cambial variants and floral vasculature in detail.

7.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand about cambial variants
- Discuss floral vasculature

7.2 CAMBIAL VARIANTS

Growth is by far the most intricate of all physiological processes. Several authors confine the term 'growth' as irreversible change in size and weight i.e. cell division and cell growth process which eventually results in increase in height and size. In plants, growth is broadly divided into two classes; vegetative growth and reproductive growth. **Vegetative growth** is responsible for the development of vegetative organs, whereas **reproductive growth** gives rise to reproductive organs of plant like gynoecium, androecium and embryo. Based on its pattern, growth is further classified as primary and secondary growth. **Primary growth** is initiated in apical region of shoot and root meristem. It results in the building of primary tissues of a plant which accounts for overall increase in the length of the plant axis at both stem and root tips, and in the development of the branching system of the stems and roots (Refer Figure 7.1). Primary growth is the only type of growth in plants growing annually, i.e., only for one season. However, in gymnosperms and most dicotyledons, growth continues for many years (perennials). This extended growth pattern is known as **secondary growth**. The stems and roots of such angiosperms and gymnosperms not only grow continuously by proliferation of the fundamental tissues of these organs but also increase in diameter as a result of the activity of the lateral meristem called as the '**vascular cambium**'. In most of the dicotyledons and gymnosperms, vascular cambium remains functional throughout the life span.

In any plant, secondary growth is affected by the cell division activity of the vascular cambium. These growing layers in the cambium due to cell division activity continuously provide additional and renewed conducting and supporting elements of secondary xylem and phloem. Owing to its dynamic nature and growth patterns, it forms one of the important plant tissues responsible for secondary growth and for the scientific studies also. Primary growth chiefly increases the length of the axis and adds the appendages, whereas, secondary growth increases the diameter of the axis (after initial increase) of the large body of woody plants. Only in tree ferns and a few of the monocotyledons a large body (thick stem) is present which is wholly primary in nature. Majority of the larger monocotyledons, including some species of palms, woody *Yuccas* and lilies, possess secondary growth of special type.

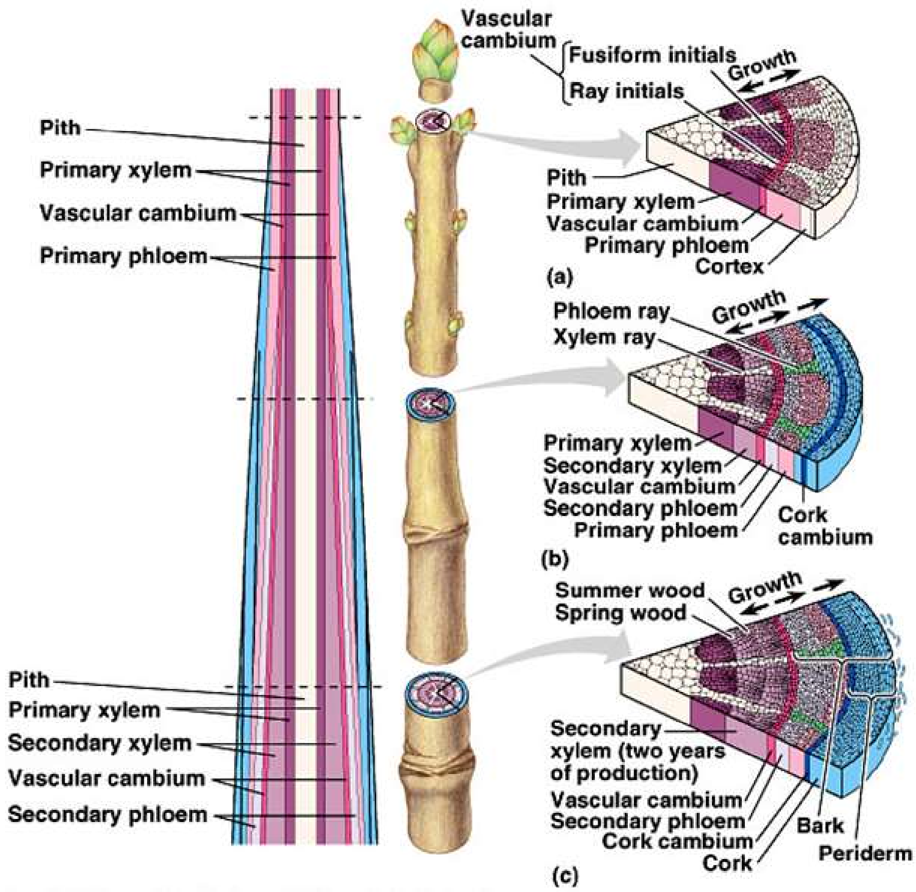

Fig. 7.1 *Plant Showing Primary and Secondary Growth in Stem*

Various patterns of secondary growth that can be observed in herbaceous species are:

- Very little or almost no cambial activity in some herbaceous dicots (annuals) consequently resulting into only primary growth, i.e., no prominent secondary growth,
- Limited amount of secondary growth due to the cell division and differentiation activity of cambium within each vascular bundle in some dicots.
- Parenchyma cells between the vascular bundles acquire meristematic character and form an interfascicular cambium that joins with the fascicular cambium to form a continuous ring leading to secondary vascular cylinders in some dicots (perennials).

The vascular cambium is primarily derived from **procambial** cells. The procambial cells differentiated acropetally from pre-existing **promeristem** strands into the apex of elongating primary shoot. The vascular cambium further generates the

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primary xylem and primary phloem tissues. Following the maturation of primary xylem and phloem, the cells located between primary xylem and phloem remains meristematic in nature called **fascicular cambium**. At the time of initiation of secondary growth, the cells located between the adjacent vascular bundles acquire meristematic nature and form **interfascicular cambium**. These fascicular and interfascicular segments of cambium join to form a complete cylinder of vascular cambium.

In the young apical shoots, vascular bundles arranged in the form of ring became joined by interfascicular and form continuous cylinder of vascular cambium. This ring of vascular cambium remains functional throughout the life of plant with small periods of dormancy alternating with the active period of cell division. During the cell division activity, a single ring of cambium forms **secondary xylem** occurring centripetally (towards the center) and **secondary phloem** centrifugally (towards periphery). Such pattern of cell division is called as normal activity of cambium. However, in certain dicotyledons and few gymnosperms, activity of the cambium deviates from its normal activity and results in formation of anomalies. This deviation in the pattern of cell division and differentiation of its derivatives by the cambium is known as **anomalous secondary growth**.

Anomalous secondary growth is the term under which cambial confirmations, cambial products and cambial numbers have been grouped, which differ from the most common normal condition namely, a single cylindrical cambium that produce phloem externally and xylem internally. The term **cambial variant** is employed now days as a way of referring to the less common types as 'anomalous' may give the misleading impression of a disorderly action. Such growth includes, features like unequal activity of the cambium on different portions of the circumference of the axis, the alteration of the relative amount and position of the xylem and phloem, and the appearance of additional cambia that result into secondary growth differing from the normal secondary growth. Obaton (1960) reported cambial variant in 108 species of woody lianas in 21 families of plants in western Africa. According to him, the first reference to anomalous structure was given by De Mirbel (1828) who drew attention to the presence of four vascular bundles arising from the main vascular presence of various types that occur in mature or relatively mature stems but Westermaier and Ambronn (1881) made an early attempts to show how anomalous thickening began and develop ontogenetically.

Abnormal cambial activity can be attributed due to following reasons:

- Abnormal activity of normal cambium,
- Abnormally situated cambium forms normal secondary tissues,
- Formation of abnormal secondary tissues by accessory cambium, and
- Formation of anomalous inter-xylary and intra-xylary phloem.

Cambial Variants Due to Abnormal Activity

Vascular cambia of this category function mostly in two ways. At some regions, the segments of cambia cease producing secondary xylem. In its place these segments produce secondary phloem only towards exterior. The other segments of cambium produce secondary phloem and secondary xylem normally. As a result, a ridged and furrowed stele is formed (for example, *Bignonia*). In other cases, the interfascicular cambium forms non-vascular tissues, while vascular tissue formation is restricted to fascicular cambium only (for example, *Aristolochia*, *Tinospora*, *Clematis*, etc.).

Bignonia

Stem and mature branches of the different species of *Bignonia* (Refer Figure 7.2) exhibit wedges of bast (phloem) in xylem and separate xylem-masses owing to fission in the transverse sections. These anomalies are not visible in the very young branches that show a ring of secondary xylem with narrow vessels.

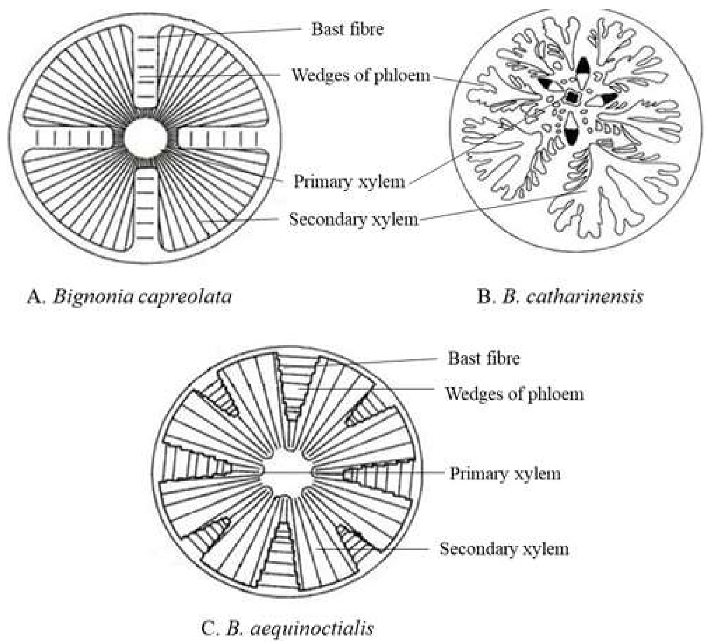

Fig. 7.2 *Diagrammatic Representation of Secondary Xylem and Secondary Phloem Stem of Different Species of Bignonia*

The cross section through mature branches of *Bignonia* show four wedges of phloem that form a definite pattern. The wedges of bast would form an orthogonal cross if it is imagined continuing as far as pith and intersect with one another at right angles at the pith. The primary vascular bundles of *Bignonia capreolata* are conjoint, collateral and open. The stems have normal ring of primary vascular bundles of different sizes. The primary vascular bundles are open type, having fascicular cambium. During secondary growth the parenchyma between the vascular bundles dedifferentiates and forms **interfascicular** cambium. The fascicular

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cambium and interfascicular cambium together form a normal continuous cambium ring. Initially, the stem shows normal cambial ring and normal ring of vascular tissues, generating secondary xylem towards interior and secondary phloem towards exterior the cambial ring. The amount of secondary xylem laid is more than that of secondary phloem.

The primary xylem has narrow vessels with small lumen. However, as soon as the cambial ring starts producing vessels with large lumen, the formation of wedges of phloem begins. Four small segments of cambial ring, situated in opposite regions, cease to form secondary xylem. Instead, these segments produce secondary phloem towards outside only. The rest of the alternate segments of cambial ring continue to produce normal secondary xylem and phloem. As a result, four **wedges** of phloem are formed in the cylinder of secondary xylem. The wedges of phloem are symmetrically arranged and corresponding in position to the larger primary vascular bundles. As the stem grows in thickness, the wedges of secondary phloem become deeper in xylem. At this stage, the vascular cambium is no longer in the form of a complete ring, however, it splits into eight strips. Four of these occur at the bottom of the wedges of phloem. The rest are present at the peripheral margin of the projected woods (secondary xylem) that lie alternate to wedges of bast (Refer Figure 7.3).

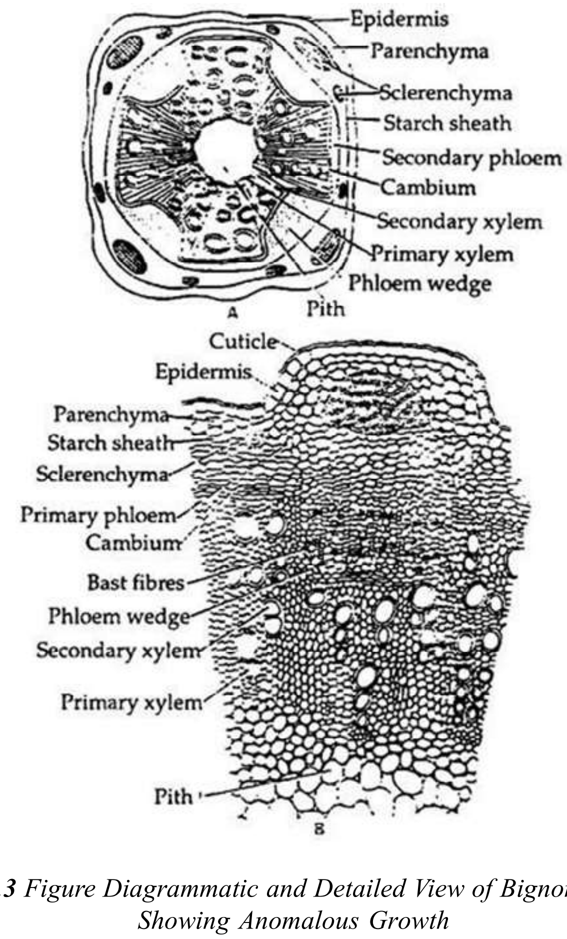
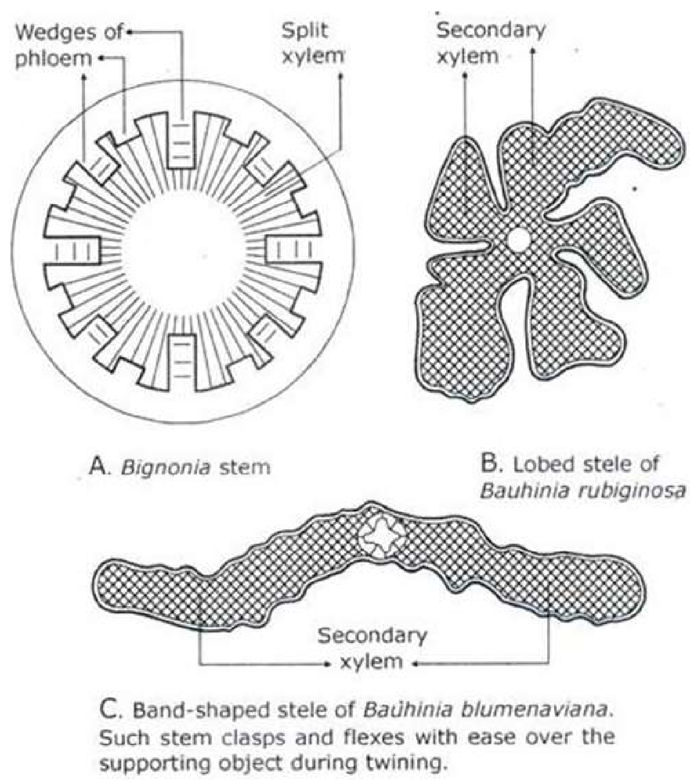


Fig. 7.3 *Figure Diagrammatic and Detailed View of Bignonia Stem Showing Anomalous Growth*

Majority of the species of *Bignonia* have four wedges of phloem. In some species, more than four wedges of secondary phloem may appear between the original four, for example, *Bignonia aequinoctialis*. For some time, the projecting regions of secondary xylem grow in thickness by the entire cambial strips occurring external to secondary xylem. Later, small cambial segments from the cambial strips that occur at the margins of projected wood suddenly begin to produce increased amount of bast and reduced amount of wood leading to development of additional four wedges of phloem. The newly formed wedges of phloem do not penetrate so deeply into the secondary xylem as the original wedges. More number of wedges of bast may be observed in the transverse section of stem at successive stages if the same phenomenon is repeated at frequent intervals.



7.4 Variation of Phloem Ridges Formations in Different Species of Bignonia

The mature stems of *Bignonia*, *Doxantha,* etc. exhibit split or fissured xylem in addition to original wedges of bast. The cells of pith and xylem parenchyma divide and enlarge to split the xylem mass. In case of *Bignonia*, the wood is split dichotomously.

In some other members of Bignoniaceae, like *Paragonia* (Refer Figure 7.5)*, Pyrostegia, Petastoma, Clytostoma, Amphilophium,* etc. a normal cambium ring is formed. It functions normally until a thin ring of secondary phloem and secondary xylem is formed at the peripheral and center side respectively.

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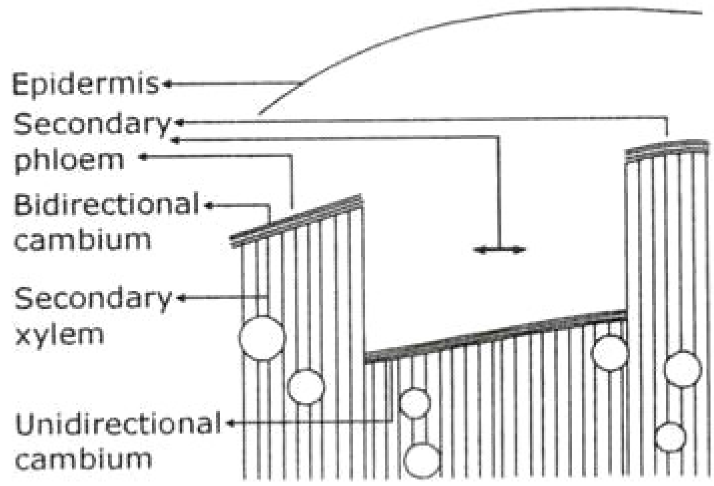

Fig. 7.5 *Diagrammatic Representation of a Portion of Paragonia Stem Showing Unidirectional and Bidirectional Cambium*

The four small segments of cambium located opposite to each other, become unidirectional after a brief period of activity, i.e., produce secondary phloem on the peripheral side only. These segments of cambia do not produce secondary xylem at all and as a result remain stationary within the stem and push out narrow wedges of secondary phloem on the peripheral side. The other four cambium segments, those situated alternate to unidirectional cambia, continue as bi-directional meristem, i.e., produce secondary xylem and phloem normally.

These four bi-directional cambia gradually move outward as more and more secondary xylem are produced. After a period of activity, it is noticed that the four unidirectional cambia are deep within the secondary xylem masses, which are produced by the bi-directional cambia. The narrow wedges of secondary phloem, formed by the unidirectional cambia, slide past the secondary xylem on their sides. In this way, the shoot grows, and secondary growth continues. After the shoot grows for a period, small segments within the bi-directional cambia are converted to unidirectional one, which also produces narrow wings of secondary phloem only on the peripheral side.

This process is repeated several times. In mature and large stems, where this process has occurred many times, it is noticed that there are several strips of unidirectional cambia situated at different sites of varying depths in the secondary xylem. These cambia have produced and pushed out narrow wings of secondary phloem. Usually, in *Bignonia* and *Doxantha*, the numbers of wedges of phloem correspond to the numbers of **orthostichies** (vertical rows) present in the stem and the furrows alternate with the orthostichies (Refer Figure 7.6).

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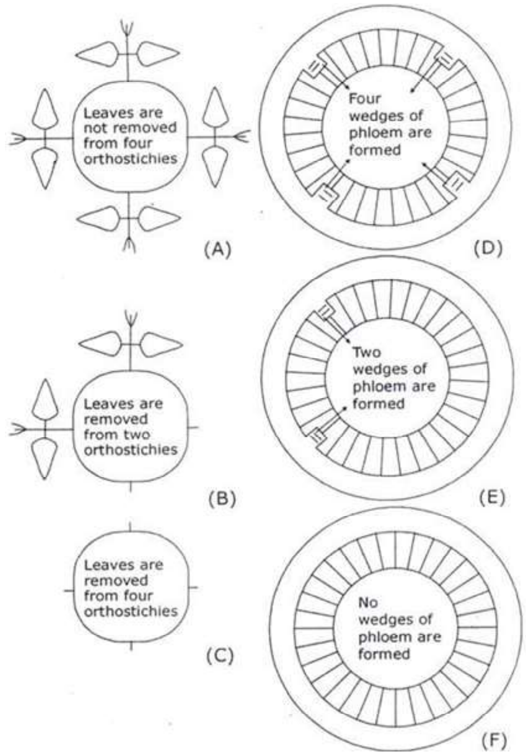

Fig. 7.6 *Experiment with Doxantha*

Aristolochia

The production of secondary ray parenchyma at the interfascicular region by interfascicular cambium leads to the anomalous growth in the stele of *Aristolochia* stem. Young stem of *Aristolochia* possess siphonostele. The endodermis present at the outer side of the stele delimits stele on the marginal side from the rest of the outer region. A cylinder of sclerenchymatous fibres is present just below the endodermis. These fibres are called **perivascular** fibre as they are located on the periphery of the vascular cylinder. Parenchyma occurs in between perivascular fibre and vascular strands (Refer Figure 7.7). The perivascular fibre and the subjacent parenchyma are referred to as **pericycle**.

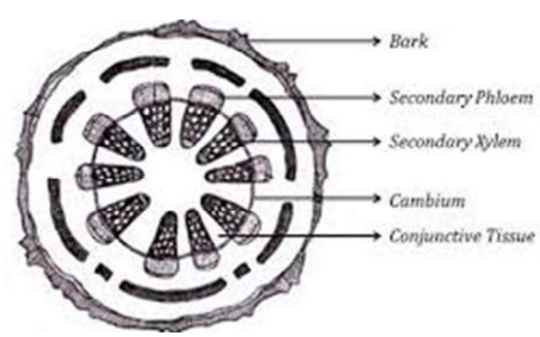

Fig. 7.7 *Diagramatic Representation of Anomalous Secondary Thickening Aristolochia Stem*

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The primary vascular bundles of *Aristolochia* stem are conjoint, collateral and open. The vascular bundles are arranged in an oval ring surrounding parenchymatous pith as visible in transverse section. The individual bundles vary in sizes, wedge-shaped and remain separated by wide interfascicular regions. The smallest bundles are the trace bundles. (Refer figure 7.8).

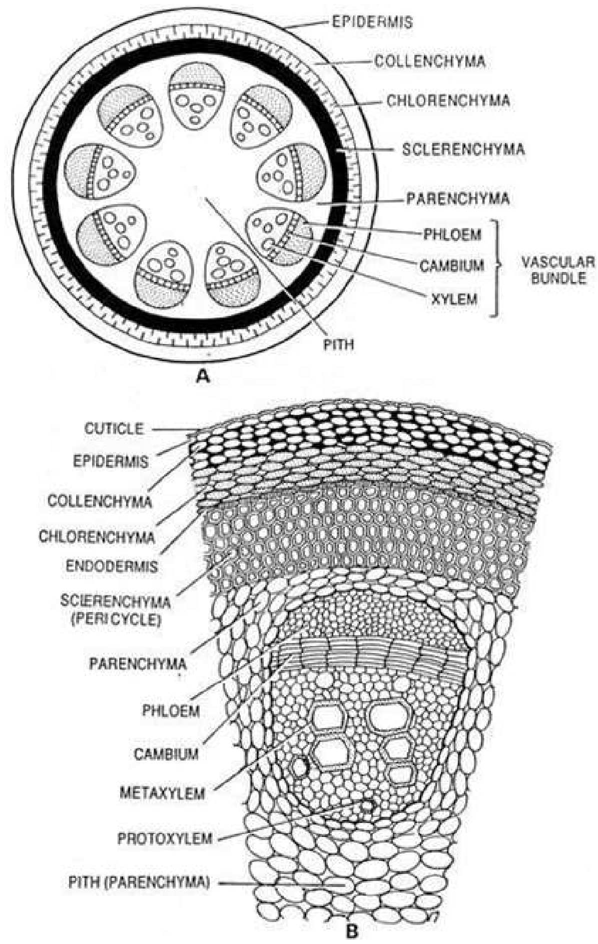

Fig. 7.8 *Detailed Diagrammatic Representation of T.S. Through Aristolochia Stem showing Anomalous Growth*

Each vascular bundle has fascicular cambium with primary phloem at the periphery. Primary xylem is situated inner to the fascicular cambium. At the onset of secondary growth, the parenchyma cells present at the primary medullary ray become meristematic. This secondary meristem is the **interfascicular** cambium. Fascicular- and interfascicular cambium join with each other forming a continuous cambium ring. However, production of secondary vascular tissue is restricted to fascicular cambium only. The fascicular cambium divides tangentially, and the inner derivative cells form the secondary xylem mother cell. The peripheral derivative cells are the secondary phloem mother cell. Secondary xylem mother cell, secondary phloem mother cell and fascicular cambium form a cambial zone. The secondary xylem mother cell and secondary phloem mother cell later differentiate into secondary xylem and secondary phloem respectively. As a result of formation of secondary vascular tissues, the primary phloem is pushed towards the peripheral side and the primary xylem is pushed inside.

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The primary phloem and secondary phloem consist of sieve tubes, companion cells and phloem parenchyma. The most conspicuous feature is that phloem lacks fibres. Also, sieve tubes and phloem parenchyma occur as bands in secondary phloem. These bands alternate with tangential bands of parenchyma. At later stages during growth, sieve tubes cease to function and get crushed by the formation of more secondary phloem. Consequently, a conspicuous banding appears in the phloem where uncompressed parenchyma alternates with compressed cells. All four elements are present in the xylem, where vessel, tracheids and xylem fibres are arranged in axial system. Abundant xylem parenchyma forms the radial system. Protoxylem and conspicuous metaxylem consist of vessels. The interfascicular regions of cambium produces parenchymatous rays, both inside and outside. As a result, the vascular strands remain separate.

The marks of increase in growth are noticeable in secondary xylem. As, the elements of xylem formed in the early and late part of growth season exhibit size difference (Refer Figure 7.9) as is visible in the rays associated with xylem. The tissues formed during the end of growth season are relatively smaller than those formed in the early part of growth season.

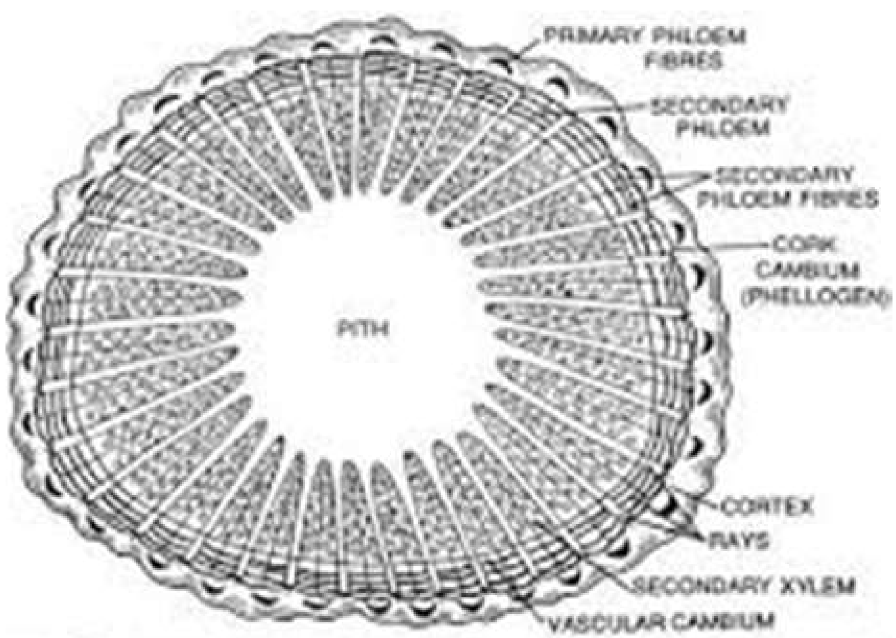

Fig. 7.9 *T.S. Through Old Aristilochia Stem Showing Anomalous Growth*

Due to secondary growth, the stem increases in girth (circumference). The individual vascular strand towards the periphery are larger. It is observed that new rays are intercalated into widening of vascular wedges. Continuous secondary growth causes shrinking of pith. Gradually, the pith cells and the associated ray

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cells are partially crushed. The continuous perivascular fibres of cylinder restricts the expanding vascular system, resulting the pith cells and associated ray cells to be crushed. However, secondary vascular tissue formation continues and the cylinder of perivascular fibre is unable to resist the expanding vascular strands. In due course, the cylinder ruptures (Refer Figure 7.10), mostly in front of rays and the adjacent parenchyma cells fill up the breaks. In some species, these parenchyma cells differentiate into sclereids that function like perivascular sclerenchyma.

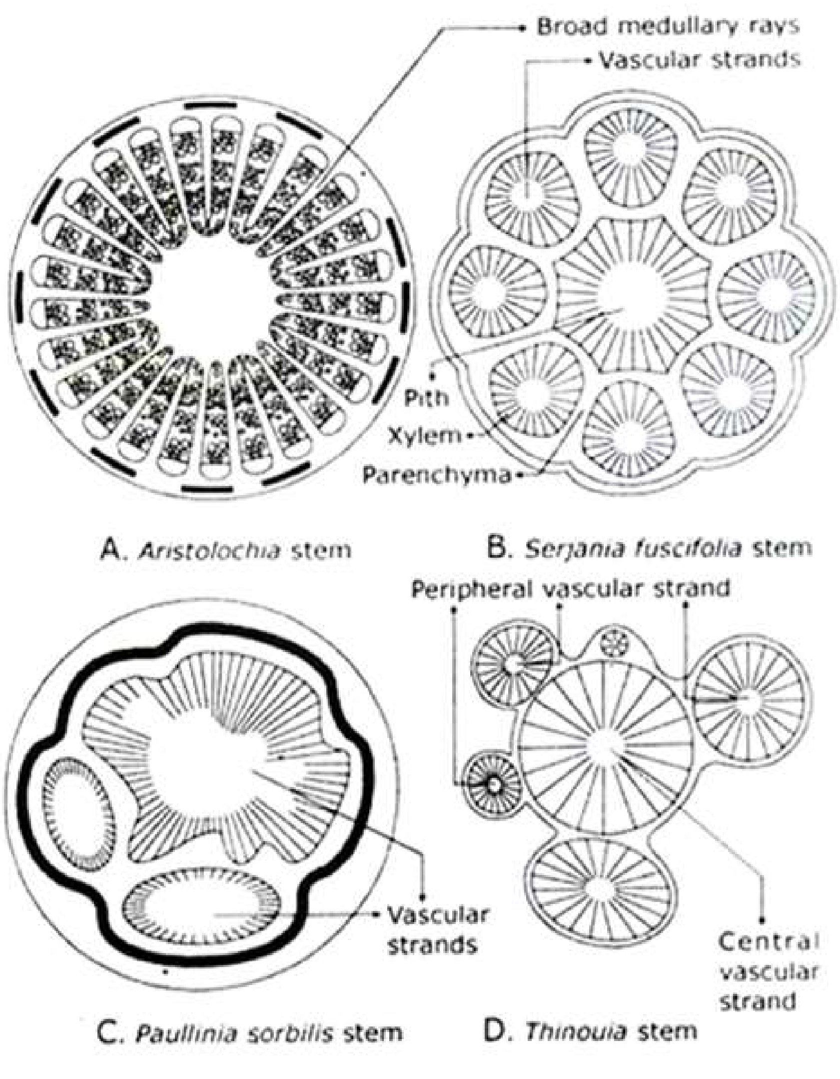

Fig. 7.10 *Different Stems of Plants*

In old stems of some species of *Aristolochia*, xylem patches become fissured owing to the development of medullary rays. The most noticeable feature of cambium ring is that certain cambial segments form ray-like parenchyma only. As the stem increases in width due to production of secondary vascular and non-vascular tissues, new cambial segments develop, and these cambial segments also donate rays of parenchyma. Therefore, a fluted vascular cylinder originates. In *Aristolochia triangularis* (Refer Figure 7.11) the vascular bundles have forked structure towards periphery due to development of rays of parenchyma by certain cambial segments, imparting fan-shaped appearance to the vascular cylinder.

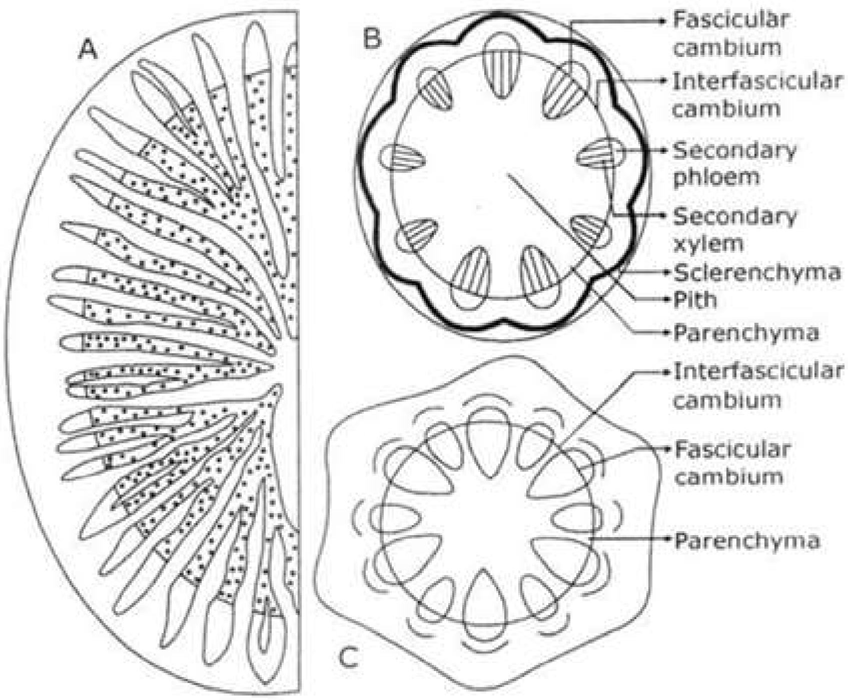

Fig. 7.11 *Cross Section of Aristilochia triangularis Showing Forked Vascular Bundels*

Tinospora

The siphonostele of *Tinospora* stem is surrounded by endodermis on the peripheral side followed by a cylinder of sclerenchyma (pericycle) just below it. The pericycle is composed of many layers of cells arching the vascular bundles in some regions. The primary vascular bundles are arranged in a ring and surround central parenchymatous pith. Each vascular bundle is conjoint, collateral and open. The vascular bundles remain separated by wide parenchymatous interfascicular region. The intra-fascicular cambium produces primary phloem on the outside and primary xylem inside. During secondary growth, some cells of the interfascicular region at the level of intra-fascicular cambium become meristematic by dedifferentiation forming the interfascicular cambium. The interfascicular cambia join with intra-fascicular cambia forming a continuous cambium ring. Some of the segments of the cambium ring function abnormally. The intra-fascicular part of cambium divides tangentially. The secondary vascular tissues gradually push the the primary xylem towards the centre and the primary phloem towards the periphery. The interfascicular part of cambium ring forms rays of parenchyma only both inside and outside. Production of secondary vascular tissues is restricted to individual

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vascular bundles only. Each vascular bundle with primary and secondary vascular tissues remains separated from other vascular bundles by wide interfascicular regions composed of primary and secondary parenchyma rays, resulting information of fluted. Similar anomalous secondary growth is also observed in *Clematis* and *Vitis,* etc. It is to observe that in *Clematis*, *Vitis*, *Bignonia*, *Aristolochia* and *Tinospora* the anomalous secondary growth starts from a single normal cambial layer with abnormal activity.

Bauhinia

Some dicot stems appear as flat ribbon like at maturity, for example in *Prestonia macrocarpa*, *Bauhinia divaricata* and *B. sericella*. The stele is also flattened strap shaped (Refer Figure 7.12). During secondary growth, a normal cambium ring is formed, and it gives rise to secondary xylem and phloem towards inner and peripheral side, respectively, in usual manner. During early stage, when secondary tissues formation is just initiated, the vascular cylinder is somewhat round and so the shoot is also round. At this stage, the secondary xylem consists of small tracheary elements surrounding the pith uniformly. In due course of development, two opposite sides of cambium become more active, while the alternate sides of it becomes less active. The secondary xylem produced by the alternating segments of cambium is also different- the secondary xylem possessed small tracheary elements at the less active region of cambium, while wide lumened vessels were present in the xylem at the more active region of cambium. Along with the continued growth, the stele gradually becomes flattened strap or band shaped and the shoot becomes flat and ribbon like. This type of stem is usually observed in those species of *Bauhinia*, which are vines. By becoming flat, they maintain the ability to flex and increase conductivity by forming vessels with large lumen.

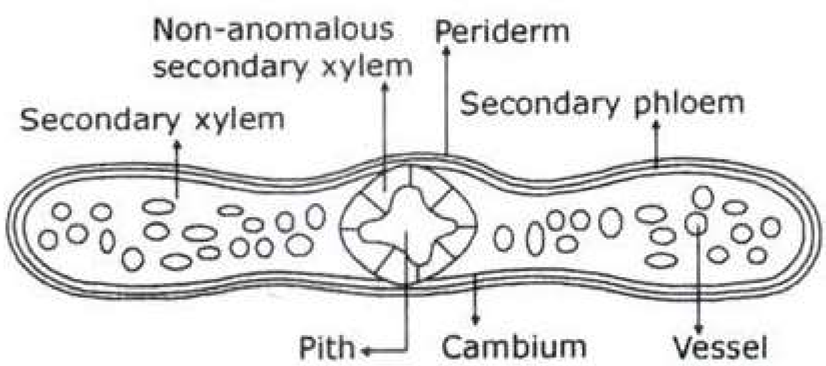

Fig. 7.12 *Transverse Section of Bauhinia Stem*

Cambial Variants due to Abnormal Positioning of Cambium

The cambial region of this category produces secondary vascular tissues in normal fashion, but their positions are anomalous. These cambia form discrete vascular cylinders and their arrangements differ according to species. The cross-section of most climbing species of *Serjania* stems exhibit a major vascular bundle surrounded by small peripheral vascular bundles, enveloped by the pericycle and further delimited by endodermis on the peripheral side.

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In *Serjania* stem several cambial layers are present and in the cross-section of stem these cambia are arranged in various ways. The stem of *Serjania caracasana* exhibit a central principal cambial cylinder surrounded by several minor cambial cylinders. While in *Serjania corrugata* central cambium is absent, and five to seven approximately equal peripheral cambial cylinders occur in a circle. In all species individual cambial layer behaves in normal fashion, i.e., donates secondary xylem on the inside and secondary phloem on the peripheral side. Consequently, numerous discrete cylinders of secondary vascular tissues enclosing parenchymatous pith are formed (Refer Figure 7.13).

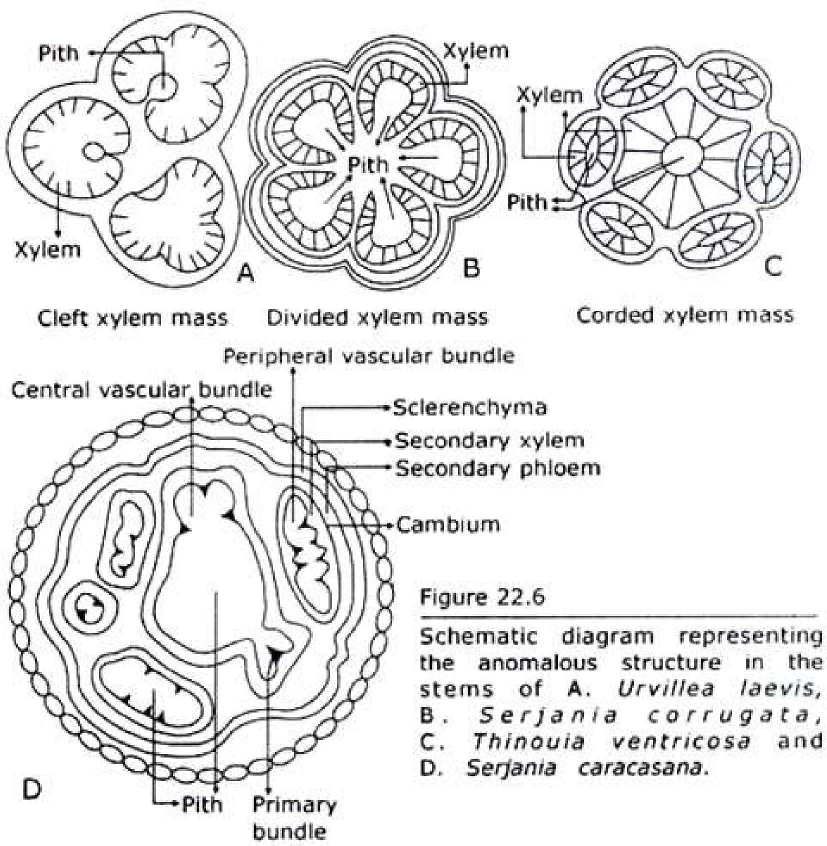

Fig. 7.13 *Anomalous Structure in Some Stems*

A continuous ring of sclerenchyma enclosing all vascular strands is also observed in all species of *Serjania*. The ring is composed of fibrous cells and is wavy in climbing species and occurs at the outer side of phloem. This wavy fibrous cylinder is regarded as pericycle. The procambial strand differentiates into primary vascular bundles. Normally primary bundles differentiate in a circle. In case of *Serjania* it is observed that primary leaf-trace bundles at certain points of circle are indented. These bundles tend to be abstracted from the circle of vascular bundles. Resulting in formation of individual groups of primary leaf-trace bundles. During early stages of secondary growth, a continuous cambial cylinder develops linking the abstracted groups of primary leaf-traces. Therefore, several separate cambial cylinders develop in the developing stele.

The formation of several cylinders of wood is predetermined as is visible in the apical meristem, which forms procambial strands that differentiate into primary vascular bundles where cambial cylinders develop. Therefore, the stele of *Serjania* consists separate woody cylinders from the beginning.

Four types of anomalous structure are exhibited by the lianas belonging to the family Sapindaceae, depending upon special arrangements of vascular bundles at their origin are:

The Cleft Xylem Mass: In the mature stems of *Urvillea laevis* and *Serjania piscatorial* shows either deeply lobed stele or separated vascular strands, each possesses a vascular cambium and discrete pith. The primary body of these stems shows normal structure but superficially grooved at certain regions due the presence of depressions in the cortex. The strips of cambia appear below the grooves at the onset of secondary growth, and the axis subsequently split into portions corresponding to the number of grooves. Each of the split portions possesses its own ring of cambium, which imparts the stem growth in thickness. Usually the stem is split into three or more portions. At maturity, the axis becomes ribbed due to unequal development of xylem at five or more points.

The Compound Xylem Mass: The stem or branch of *Serjania Juscifolia, Paullinia,* etc. exhibits a central ring of vascular bundles present at the middle. There are several peripheral rings of vascular bundles present around the central ring. Small amount of cortical parenchyma occurs between the central and peripheral ring of vascular bundles.

The number of peripheral bundle ring varies from three to ten and they are placed closely side-by-side. The central and peripheral bundle rings of vascular bundles possess pith and have their own cambium ring, through the activity of which the stem or branch grows permanently in thickness.

This cambium ring forms secondary xylem and phloem towards inner and peripheral side in normal way. The vascular bundles of central and peripheral rings join each other at the nodes. The leaf traces at first run through the central ring and subsequently pass into one of the peripheral rings.

At maturity, the stem or branch appears to be a cable like structure. This is an adaptive type of anomaly where the plant is benefited when exposed to stretching or torsion. In an estimate, it is recorded that this type of anomaly occurs in 91 out of 172 species of *Serjania* and 16 out of 122 species of *Paullinia*.

The Divided Xylem Mass: The young stem of Serjania *corrugate*, possesses 5-7 incomplete bundle rings lying side-by-side in a circle. Each bundle ring encloses pith at the centre and the peripheral pith is continuous with central pith in young stems. The bundle rings possess permanent growth in girth by a ring of cambium present in them. At maturity, the divided xylem mass encloses the pith lacking central ring vascular cylinder.

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The Corded Xylem Mass: The stem of *Thinouia*, exhibits a central ring of vascular bundles surrounded by several peripheral rings. Each vascular cylinder possesses ring of cambium with phloem and xylem enclosing pith. At young stage, the stems grow in thickness with only central vascular cylinder, like a normal cambium ring with normal activity. This normal growth in thickness continues till the fifth or sixth year. Later, new strands of accessory cambia originate at the cortex external to the original vascular ring, while the central vascular cylinder continues to grow. The new strands of accessory cambia, though abnormal in position, produce normal phloem and xylem towards exterior and interior, respectively, enclosing pith at the centre. The recently formed peripheral rings of vascular bundles are connected to one another but remains separated from the original vascular ring. This anomaly also occurs as a secondary complication in older stems of a few species of *Serjania* and *Paullinia*, which exhibit compound or divided xylem mass. The newly formed secondary vascular cylinder may be cylindrical or flat transversely. At maturity, the stems appear as cords.

Accessory Cambium

Some dicot species like *Baugainvillea*, *Amaranthus*, *Boerhaavia*, *Achyranthes*, *Celosia,* etc. exhibit accessory cambia that form vascular and non-vascular tissues. In stem of *Boerhaavia diffusa* (Refer Figure 17.14) endodermis delimits stele, however, all segments of endodermis are not always distinct. Just below the endodermis there occurs the narrow and one or two cells thick pericycle. A few scattered fibres are also present just below the endodermis in older stems. The position of fibres is of special interest as they locate the endodermis when it is indistinct. The other structures of stele include parenchymatous ground tissue, conjunctive tissues and primary vascular bundles.

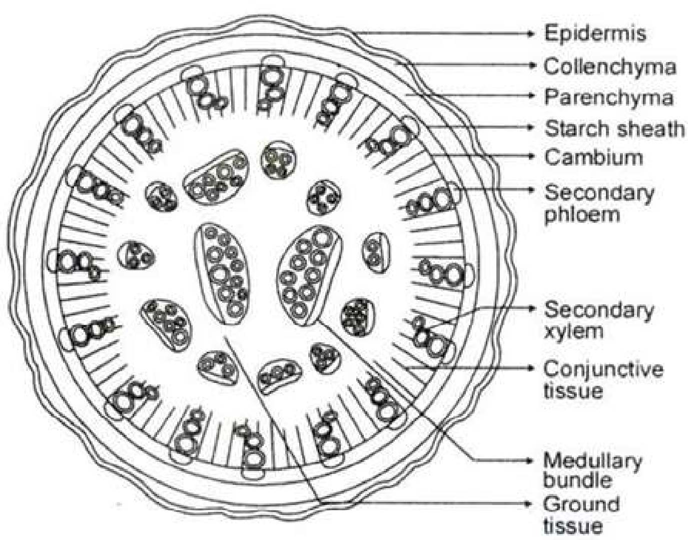

Fig. 7.14 *Transverse Section of Boerhaavia Stem*

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A cross-section of young stem shows the primary vascular bundles of different sizes, arranged in three rings. All vascular bundles are derived from procambial strands. The cross-section of a young stem of *Boerhaavia diffusa* exhibits two large central vascular bundles in the innermost ring. These are the largest bundles in the stem with a tangential diameter about twice as long as the radial. Each vascular bundle is conjoint, collateral and has intra-fascicular cambium that behaves in normal fashion. The cambium divides tangentially, and the inner derivative cells differentiate into secondary xylem while the peripheral derivative cells form secondary phloem. The secondary vascular elements are arranged in axial and radial rows. Production of secondary vascular tissues is restricted to individual vascular bundles only. Each vascular bundle has limited amount of secondary vascular tissue formation.

As secondary growth continues, the primary phloem cells are crushed. The dead remnants of crushed phloem appear as cap over the later formed secondary phloem. The interfascicular cambium does not develop in the inner ring of vascular bundles. The middle ring consists of s6-14 loosely arranged primary vascular bundles. The bundles are conjoint, collateral and open. Little amount of secondary vascular tissues is produced in these bundles by intra-fascicular cambium. However, interfascicular cambium is absent in the middle ring of vascular bundles. The outermost ring consists of 15-20 or more primary vascular bundles. The bundles are small, even minute and occur at the periphery of stele. Each bundle is conjoint, collateral and open. These bundles are also formed from procambial strands but are delayed in development in comparison to vascular bundles of other two rings. Each vascular bundle has intra-fascicular cambium which becomes continuous with intra-fascicular cambium on both of its lateral sides, resulting in the formation of a complete cambial cylinder. It is this cambial cylinder that is responsible for all subsequent anomalous secondary growth.

The cambial cylinder is very active, dividing tangentially. The intra-fascicular part of cambial cylinder forms secondary vascular tissues only. While the peripheral derivatives form secondary phloem, the inner derivatives of intra-fascicular cambium differentiate into secondary xylem. The peripheral derivatives form parenchyma cells, whereas the inner derivatives differentiate into internally situated conjunctive tissue and storage parenchyma. The conjunctive tissue consists of elongated living cells that are later transformed to sclerenchyma by lignin deposition on their walls. These sclerenchyma cells are like fibres and serve for food storage. With additional secondary growth, the cambial cylinder donates a wide zone of anomalous xylem towards interior. The anomalous wood consists of secondary xylem formed by intra-fascicular cambium, lignified conjunctive tissue and lignified adjacent cells of pith. In mature stele lignified conjunctive tissues and secondary xylem become embedded forming a zone of wood.

After some time, the activity of original vascular cambial cylinder declines and another cambial cylinder arises at the peripheral parenchyma cells formed by the original cambial cylinder. This new cambium donates conjunctive tissues inside and parenchyma outside. Some regions of new cambium form secondary xylem inside and secondary phloem outside. These secondary vascular tissues are always formed opposite to each other; as a result, collateral vascular bundles are formed.

After being active for some time, the function of new cambium stops. Then, another new additional cambium cylinder arises from the peripheral parenchyma cells produced by its predecessor.

The function of new additional cambium is same as that of the previous cambial cylinders. In this way, 4-5 additional cambial cylinders originate and accordingly growth rings are produced. All the supernumerary cambia have the same function, broadening the anomalous wood.

The important aspect to be noted is that in the stele of *Boerhaavia diffusa*, the original cambial cylinder does not develop *de novo* in the pericycle during secondary growth. Instead, the cambial cylinder is formed by the union between intra-fascicular cambium of peripheral small bundles and interfascicular cambium formed at interfascicular region of peripheral bundles. Later, additional (**accessory**) cambia originate from parenchyma produced by original cambial cylinder or from the parenchyma of their products.

In *Chenopodium*, isolated phloem patches termed **phloem islands** are found embedded in the conjunctive tissues, usually above the clusters of vessels. These phloem patches are formed centrifugally by the accessory cambium. Later, the arcs of new cambium are formed, that gives rise to conjunctive tissues to the inside and embeds the phloem.

Inter-Xylary Phloem

The secondary phloem that is surrounded by secondary xylem is referred to as **interxylary phloem**. It is also termed as **included phloem** or **interxylary soft bast** as it remains embedded in wood. Eames and MacDaniels illustrated the following two methods through which interxylary phloem becomes embedded in secondary xylem. In stems of *Combretum*, *Leptadenia* (Refer Figures 7.15 and 7.16) and *Entada*, a normal cambium ring is formed by the union of intra-fascicular and interfascicular cambium during secondary growth. The cambial ring functions normally, producing secondary xylem towards inside and secondary phloem towards outside. Subsequently, certain small segments of cambial ring donate secondary phloem toward the inside for a brief period. Normally, these segments produce secondary xylem. During the production of interxylary soft bast these segments form secondary phloem in place of secondary xylem.

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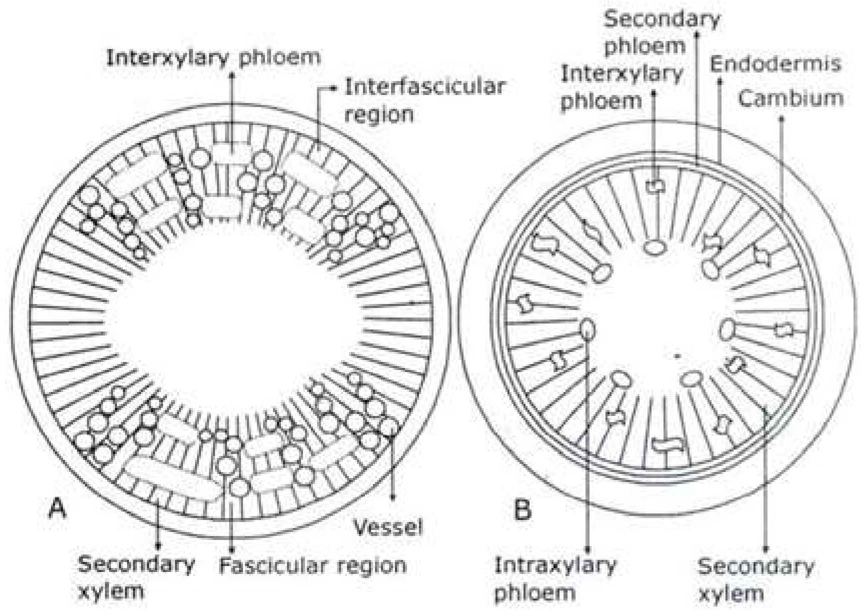

Fig. 7.15 *(a) Thunbergia coccinea Stem in T.S.*
(b) Leptadenia Stem in T.S. Showing Intraxylary and Interxylary Phloem

The production of secondary phloem continues and after a brief period of these abnormal segments of cambial region regain their normal activity by donating secondary xylem inside. As a result, the inner phloem gets buried in the secondary xylem. It is to note that the islands of soft bast are developed from the inner derivative cells of cambium. The other case, like *Strychnos* (family: Strychnaceae), the stem has siphonostele and the primary vascular bundles are conjoint, open and bicollateral. The inner phloem of the vascular bundle is referred to as **intra-xylary phloem** or **intra-xylary soft bast** or **internal phloem**.

Internal phloem is normally primary in origin and develops from procambial strands along with primary outer phloem and primary xylem. The internal phloem of *Strychnos* is in the form of isolated strands that form a ring surrounding the pith completely. In certain species, the isolated bast occurs opposite all or some of the vascular bundles of stem. During secondary growth, a normal cambial ring is formed by the union of intra-fascicular and interfascicular cambium. The cambial ring has normal function and forms secondary xylem toward inside. Secondary phloem is produced toward outside of stem. The formation of secondary tissues continues for some time. The interxylary phloem appears at a later stage of the growth of wood. During secondary growth certain small segments of cambial ring form the peripheral phloem strands toward the outside as a part of their normal function. Later the phloem strands become embedded in the secondary xylem.

These regions of cambium become inactive, while the rest of the cambial segments continue to produce secondary vascular tissues. The derivative cells of once active cambial segments differentiate into secondary vascular tissues. Consequently, the original cambial ring becomes interrupted. Later, it is restored by the production of new complementary strips of cambia on the outer side. Strips of cambia arise opposite the cambial segments that cease to function. The new cambial strips develop as secondary meristem. They originate either at the pericycle or in the phloem that is few rows away from the original cambium. Strips of cambia and the active segments of original cambia unite with their edges thus forming a complete cambial ring. This cambial ring has normal activity. The secondary xylem produced by this cambial ring encloses the secondary phloem formed by the once active original cambial segment. This process is repeated several times and as a result numerous scattered strands of interxylary phloem are formed embedded in secondary xylem.

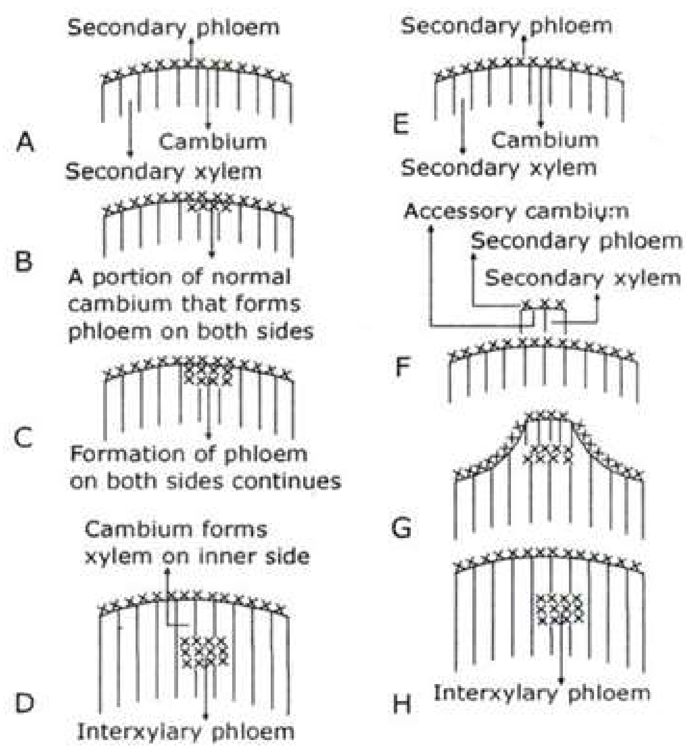

Fig. 7.16 *Schematic Representation of Interxylary Phloem Formation*

It is to be noted that in *Strychnos*, both internal and interxylary phloem are formed. The former is primary in origin and is regarded as primary anomalous structure. Interxylary phloem is formed as a result of anomalous secondary growth and the islands of soft bast in the wood are formed by the cambium on its outer side. So, the interxylary phloem is the normal secondary soft bast.

Interxylary phloem is also observed in several species of *Thunbergia* stem. The islands of soft bast occur in the form of bands in the wood. The characteristic of stem is that the bands of soft bast only arise in the interfascicular region. The bands remain surrounded by secondary xylem. The characteristic of wood is that vessels only occur at intra-fascicular region. The wood present at interfascicular region above and below of interxylary phloem consists of fibres and tracheids only. Interxylary phloem of *Thunbergia* is formed either from the inner derivative

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cells of cambium (like Combretum) or from the outer derivative cells of cambium (like *Strychnos*). In *Thunbergia coccinea*, *T. grandiflora*, *T. parva*, *T. sinuata*, *T. mysorensis,* etc. the islands of soft bast are developed from the inner side of the cambium. Whereas in *T. capensis*, *T. cyanea*, T. *hispida, T. hirta,* etc. wedges of bast are formed and from these some of the islands arise. Solereder stated- 'These wedges are partly formed by tissue produced from the inner side of the cambium and partly by tissue given off externally by the cambium'. It is to note that in the latter case the interxylary phloem is the normal secondary soft bast.

Intra-Xylary Phloem

Committee on Nomenclature (1957) suggests the term **internal phloem** in place of intra-xylary phloem to avoid confusion. Isolated phloem strands are observed in *Calotropis*, *Strychnos*, etc. while cylindrical phloem strand is present in *Asclepias curassavica*. Generally, internal phloem is primary in origin, developing from provascular strands. Exceptions are observed in *Campsis radicans* and *Campsis grandiflora* where internal phloem is secondary in origin. In these species internal phloem is developed as a result of anomalous secondary growth.

The stele of *Tecoma radicans* is siphonostele and the primary vascular bundles are arranged more or less in a ring, each vascular bundle being collateral, open with endarch protoxylem. During secondary growth, intra-fascicular cambium and interfascicular cambium unite to form complete cambium ring. The cambium ring has normal function, producing secondary phloem on the peripheral side and secondary xylem towards inner side, the secondary xylem being in excess of secondary phloem. Consequently, primary vascular bundles are pushed towards the centre. After a period of activity two strips of additional cambia originate below secondary xylem on two opposite sides of pith, each strip of cambium functioning abnormally. Each cambial strip donates secondary phloem towards the centre or pith side and secondary xylem towards the peripheral side.

As growth continues, two arcs of secondary vascular bundles are formed at the margin of pith. The bundles show inverse orientation of wood and bast. The bast that develops towards pith side is referred to as intra-xylary phloem/internal phloem. Subsequently the two patches of intra-xylary phloem crush the pith cells to a narrow band.

In young developing stems, the primary vascular bundles are conspicuous towards the inner margin of secondary xylem formed by the normal cambial ring. A few layers of parenchyma cells are observed between the wood formed by the normal cambial ring and additional cambium/accessory cambium. It is to note that anomaly in the stele of *Tecoma* is due the development of two arcs of medullary bundles with inverse orientation of wood and bast in contrast to normal vascular bundles. Anomaly in the stele is also owing to the formation of internal phloem/ intra-xylary phloem by additional/accessory cambium during anomalous secondary growth.

Anomalous Secondary Growth in *Dracaena* Stem

Dracaena is an arborescent plant belonging to the monocotyledonous family Agavaceae. The vascular bundles of monocotyledons are closed, without intra-fascicular cambium. So, monocotyledons lack normal secondary growth from a vascular cambium. In *Dracaena*, however, the stele is atactostele and the primary vascular bundles are distributed over the ground tissue without having any definite arrangement. They are not compactly arranged on the ground tissue and the interfascicular region is moderately wide. The ground tissue is composed of parenchyma cells without radial seriation of cells. Each primary vascular bundle is leptocentric/amphivasal, i.e., the xylem completely surrounding phloem and lacking intra-fascicular cambium. Each vascular bundle is circular or oval in transverse section. The xylem consists of tracheids only. Protoxylem with annular and spiral thickening is present.

The cross-section of mature stem of *Dracaena*, where certain amount of secondary growth has occurred, exhibits secondary vascular bundles and ground tissue commonly termed as conjunctive tissue. Conjunctive tissues are parenchymatous, the walls of which are thin and may sometimes become thickened or even lignified. The conjunctive tissue exhibits radial arrangement of cells and thus aids in differentiation from the primary interfascicular ground tissue. The secondary vascular bundles are to some extent arranged in radial rows. The vascular bundles are more or less compactly arranged and anastomose in some regions in contrast to primary vascular bundles. Each vascular bundle is oval in t. s. and leptocentirc/amphivasal like primary vascular bundles. The secondary phloem is small in amount in comparison to primary phloem. The secondary phloem elements are sieve tubes, companion cells and phloem parenchyma. The sieve tubes are short with transverse end walls and the sieve plate is simple.

The tracheary elements are composed of tracheids and xylem parenchyma. The tracheids are long and the associated xylem parenchyma may be lignified. The tracheids exhibit scalariform thickening and lack annular and spiral protoxylem. The secondary bundles appear to lie embedded in the conjunctive tissues. The secondary tissues (secondary vascular bundles and conjunctive tissues) surround the primary vascular bundles and ground tissue. Internally the stele of *Dracaena* stem before secondary growth remains surrounded by many layered parenchymatous cortex. The peripheral layer of stele is the pericycle that cannot be easily distinguished. The secondary growth of *Dracaena* is brought about by a special type of vascular cambium, also termed as secondary thickening meristem. This cambium originates in the older regions of stem that consists of parenchyma cells situated outside the vascular bundles.

Cambium originates either from cortical parenchyma or pericycle. The cambium is active in the part of axis that has ceased to elongate. The cambium does not function like the vascular cambium of dicotyledons. As seen in cross-sections, each cambial cell may be fusiform with both ends tapered or rectangular.

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Sometimes one end of a cambial cell may be truncated, and the other end is tapering. The cambial cells divide tangentially. Initially the cambial cells donate cell towards inside only and later a small amount of tissue is produced towards outside. Tangential divisions in individual cambial cell continue resulting in the formation of radial series of derivatives. The peripheral derivative cells may continue tangential divisions. Some of the derivatives may cease to divide. These cells then transform to secondary cortex. The inner derivate of cambial cells forms a radial series of cells.

Some of the derivative cells differentiate into thin walled parenchyma cells that form ground tissue. The ground tissue is termed as conjunctive tissue. Later, the thin walls of ground tissue may be thickened or lignified. The other derivatives of cambial cells differentiate into vascular strands. The cambial initials form longitudinal files of single cell where vascular bundles develop. Anticlinal, periclinal and irregular longitudinal divisions in the files of cells result in the formation of leptocentric vascular bundles. The vascular bundles interrupt the radial seriation of conjunctive tissues that are interfascicular secondary parenchyma. Each cell of parenchyma has moderately thick and pitted wall. So, each cell of secondary parenchyma may be regarded as conducting parenchyma.

It is to note that in *Dracaena* anomalous secondary thickening is brought about by a special cambium—termed secondary thickening meristem. Due to the activity of this meristem conjunctive tissue and secondary vascular bundles originate. The continuous activity of the meristem results in the formation of indefinite amount of secondary tissues. Sometimes weakly developed growth rings are observed. But the relation between rings to annual growth is yet to be established. Continuous formation of secondary tissues results in the increase of diameter in *Dracaena* stem. It is reported that in *Dracaena draco*, the stem attained a girth of 45 feet, height of 70 feet and the age was estimated to be of six thousand years old. Haberlandt grouped all the anomalous forms of secondary growth into two categories, namely **adaptive** and **non-adaptive**. The **adaptive** anomaly is an adaptation to definite external conditions. In contrast the **non-adaptive** anomaly is not an adaptation to definite external condition (ex. *Amaranthus, Mirabilis, Boerhaavia, Chenopodium etc*.). The adaptive anomalies are the characteristic of plants that are lianas (like *Aristolochia*, *Tinospora, Bignonia, Serjania and Bauhinia,* etc.), plants that have fleshy roots (like beet root) which principally serve for storage and plant with submerged stem where cambium devotes most of its derivatives to produce tissues that add buoyancy (like *Aeschynomene aspera*, *A. indica* and *Herminiera* etc.). Inextensibility, inflexibility and incompressibility are the essential mechanical requirements of a liana. A climbing plant is often thrown into several folds or frequently becomes extensively twisted over a living supporting organ. It swings freely and so is exposed to pulling strain. As a result, a twiner becomes inextensible. Sometimes the hanging stems are shaken by violent winds. So, a liana becomes inflexible. The twiners are often exposed to radial compression. This happens when supporting organ grows in thickness. All the above-mentioned mechanical requirements of liana stems are achieved by adaptive anomalous secondary growth.

The vascular organization of liana stems is constructed like a twisted rope or cable. This cable-like structure possesses high degree of strength combined with pliancy. In a liana, **pliancy** (flexibility) is often accomplished through splitting of the lignified xylem into isolated strands. Pliancy is also achieved by the interpolation of softer tissues like secondary phloem into lignified xylem. The anatomical features like splitting of xylem and interpolation of softer tissues into xylem is common to all liane-stems, but they are brought about in different ways.

In the stele of *Bignonia* four wedges of phloem split the xylem cylinder. The resulting lobe formation of secondary xylem increases the pliancy of stem. There are eight lateral sides where wedges of phloem and secondary xylem are in contact with each other. These sides are the planes of weakness of stele, but they are not detrimentally weak. Because parallel islands of bast fibres are differentiated in the wedges of phloem and these mechanical cells add strength to the planes of weakness. In *Aristolochia* stem a fluted vascular cylinder is formed. In the young stem pliancy is brought about by the development of broad medullary rays at interfascicular region. In mature stems the vascular strands are split by the development of rays of parenchyma.

In *Serjania* several vascular strands are formed from the beginning and they are held together by parenchymatous ground tissue. The presence of parenchyma between the vascular strands increases the pliancy of stem. In *Strychnos* and *Thunbergia*, pliancy is brought about by the formation of interxylary phloem. It is to be noted that the development of inter-xylary-leptome- strands is not confined to liane-stems only. They do occur in several woody plants that are not lianas. Schenck (Haberlandt) concluded that the formation of interxylary phloem is not an adaptive anomaly. It merely represents a variety of design.

Check Your Progress

1. What does vegetative growth and reproductive growth result in?
2. Where is primary growth initiated?
3. What is secondary growth?
4. Define vascular cambium.
5. What are the various patterns of secondary growth that can be observed in herbaceous species?

7.3 FLORAL VASCULATURE

A flower is regarded as a modified determinate shoot. Its parts are regarded as different forms of modified leaves. A majority of botanists agree that a flower is equivalent to crowded appendages bearing compressed shoot. The entire plant body is formed from two meristematic apical regions- Shoot Apical Meristem (SAM) and Root Apical Meristem (RAM). These apices are recognized at 2-celled stage of developing embryo. These apical regions later, becomes plumule and radicle, respectively, and remain dormant for some time inside a seed. On germination of seed, the plumule gives rise to the shoot system and the radicle gives rise to the root system of the plant. The **seedling** formed after germination establishes itself and grows to enter **juvenile** stage. After a period of time the growing plant enters the **vegetative** phase of its life cycle. Duration of this phase varies greatly in different plant species, ranging from few days to decades. At appropriate time and in presence of specific external and internal signals, the plant enters its **reproductive** phase and some of the lateral and/or terminal apices gives rise to flowers or inflorescences. At the time of flowering, different floral organs or **appendages** are formed as a result of '**switching'** of vegetative phase to reproductive phase.

Transition to Flowering

The shoot apex can grow for indefinite time period and hence shows **indeterminate** growth. On the other hand, when the vegetative apex transits to reproductive phase, it is characterized with short and **determinate** growth. According to the position of this 'transforming' shoot apex on the plant body, it may give rise to '**terminal**' flowers, '**axillary**' flowers or both types of flowers. Further, single axillary or terminal reproductive bud will produce **solitary** flowers, while multiple reproductive apices in group will form **inflorescence**. There is a great diversity and variation in form, size, colour and time of flower formation among the angiosperm families. However, certain morphological features are common to many taxa. For instance, flowers of dicots are generally pentamerous (having 5 sepals and petals) while monocot flowers are trimerous. Still, both monocot and dicot flowers may have superior or inferior ovary. Based on position of ovary flowers can be **hypogynous** (superior ovary), **perigynous** (other floral organs positioned at median position with respect to ovary) or **epigynous** (inferior ovary) the number of sepals, petals may not vary, but they may have difference in position.

Flowers are determinate structures in annual plants, vegetative growth of the plants terminates with flowering. However, in perennial plants, flowering occurs throughout the life of the plants. At the time of flower induction, the vegetative shoot apices undergo morphological changes. The internodes elongate and may give rise to numerous little buds below the apical meristems. The induced floral meristem becomes much broader then the it is vegetative form. Initially the rate of cell division increases in the rib meristem and central zone, and gradually over tunica. The reproductive apex shows a fluctuation in plastochron size during the development of floral parts or floral primordia. The apex may widen and become slightly flattened. Smith (1966) reported horizontal and vertical enlargement of the apex in *Carex*. Schwabe (1959) observed about 400 times increase in size of the apex of *Chrysanthemum* within a few hours during the formation of capitulum.

The changes in shape of the apex during transition to flowering is linked with the increase in mitotic activity of the shoot apex in the region no between the rib-meristem and central mother cell zone. Gradually, the mitotic division spread over the zone of central mother cell, adding cells to the tunica. Cutter (1971) observed that significant increase in cell division rate occur within 24 hours of inductive treatment in case of *Xanthium*. A clear variation can be observed in the growth pattern of vegetative and reproductive meristem. The vegetative meristems show the following characteristics:

- Produce foliage leaves continuously.
- Possess vacuolated cells.
- The tunica cells contain very less ribonucleic acid in the cytoplasm.
- The corpus cells have a small nucleolar volume.

In contrast, the characteristics in reproductive apices are:

- The tunica cells have increased nucleolar volume.
- The central cells have greater activity.
- The central axial cells have more ribonucleic acid.

Bouvet (1942) observed in a study with *Lupinus* that tunica cells become more meristematic at the onset of flowering. The cells in the corpus region also become more meristematic in appearance at this time. Various studies have established role of plant hormones, like gibberellins, and environmental conditions, to which the plant have been subjected previously, to determine the transition to flowering.

Induction of Flowering

Asaki (2001) reported role of about 80 genes in regulating the transition from vegetative to floral state. This dramatic phase change in plant development is indicated by several forms of signal transduction, external environment factors (such as photoperiod and temperature) and internal factors (plant hormones).

Development of floral organs is considered as a ‘continuous succession of events- a cascade in which successive events build on initial events’ (Tucker 1997). Many events occur during floral organ development and morphogenesis including:

- Determination of number of floral organs of different type
- Site of different floral organs
- Timing of initiation of floral organs
- Differentiation of form
- Size of floral organs
- Fusion within and/or between different floral organs
- Development of specialised features- nectaries, specially shaped petals, special inflorescence, etc.

Further investigation of control by regulatory genes of number and recognition of floral organs, floral patterning and development of floral structures may provide a clearer understanding of the underlying mechanism of floral development and morphogenesis.

Floral Organs

The vegetative shoot meristems show indeterminate (unlimited) growth, while flowering terminates this growth. The flower consists of an axis and lateral appendages arising from it. The axis is also known as **receptacle** and appendages as **floral parts** or **floral organs**. The floral organs consist of sterile organs and fertile productive organs. The floral parts are generally arranged in sequence beginning with **sepals** at the base and continuing through **petals**, **stamens** and **carpels**. During development of floral organs, referred to as **ontogeny,** initiation of various floral parts is **acropetal-** lowest organs (sepals) appearing first, then petals, stamens and carpels appearing last. However, this developmental sequence shows great variation. The variation in sequences characterise different species. In the flowers of more primitive angiosperm families, different floral organs remain separate or free, whereas in advance families, different organs often fuse. The most common events are- fusion of carpels forming **Pistil** and fusion of petals forming **Corolla**. (Refer Figure 7.17) Fusion of sepals forming **Calyx** and fusion of stamens forming various types is also seen in different families.

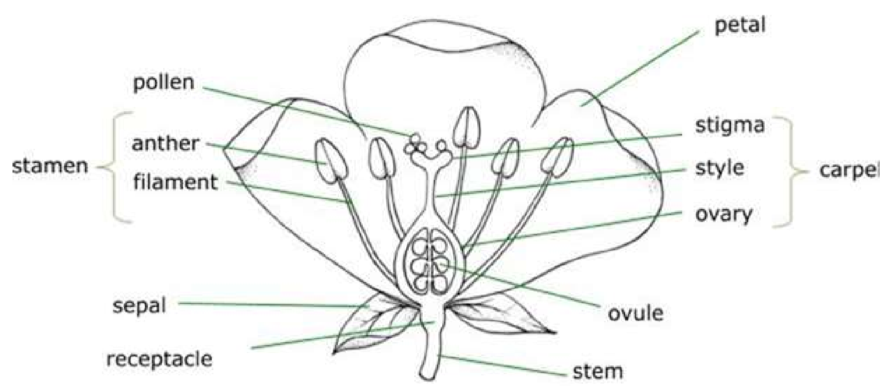

Fig. 7.17 *Different Organs of a Flower*

The floral organ **initial** appears as leaf primordia arising at nodes in apical meristems. However, the arrangement in somewhat circular in **whorls**. (Refer Figure 7.18) Hence each sequence of floral organ appears as whorl in a flower. Generally, a flower has following whorls of organs:

- **Sepals:** The sepals form the outermost whorl of a typical angiosperm flower. Together all the sepals form **calyx.** The sepals resemble leaves in their anatomy. However, number, form and colour very greatly in different species. Sepals are considered as sterile floral organs generally meant to protect the developing floral bud. Each sepal consists of epidermis, a branched vascular system and ground tissue comprising of parenchyma. The leaf traces are similar in origin and number. The anatomical evidences suggest that sepals are derived directly from leaves.

- **Petals:** The petals form the second whorl of the flower **-Corolla**. They also resemble leaves in their internal anatomy and, like sepals, consist of epidermis, branched vascular tissue and ground parenchyma. Petals also possess pigment containing chromoplast imparting colour to them. They may also possess glandular epidermal cells containing volatile essential oils which impart characteristic fragrance to the flowers. Sometimes, the epidermis of petals possesses trichomes and stomata. Petals also, like sepal, are sterile appendages. They act as organ of attraction for pollinators in case of insect pollinated plants.
- **Stamen**: The stamen are the male reproductive units of a flower. They are the site of synthesis of male gametes bearing gametophytes- **Pollens.** Generally, the stamen consists of two-lobed anther situated on a thin elongated **filament.** The filament possesses single vascular strand which supplies water, food and other nutrient to the developing anther and sporogenous cellular mass which later forms microspores. The two lobes are joint to the filament at a region known as **connective.** In certain primitive angiosperms the filament is flattened leaf like structure and possess three veins, whereas, in the advance families, they have single vein.
- **Carpel:** The carpels form the **Gynoecium** of a flower. A flower may have one carpel or several carpels. If two or more carpels are present, they may be unified or free from one another. Gynoecium having united carpels is known as **syncarpous,** whereas, the free carpels are known as **apocarpous**. An apocarpous single carpel is also referred to as a ***simple pistil***. On the other hand, syncarpous gynoecium is also known as ***compound pistil***. The carpel consists of a swollen basal region known as **ovary**, an elongated tubular structure extending in upward direction as **style** which terminates into a **stigma**. The size, shape, position of ovary, style and stigmas vary greatly in different families. The ovary generally consists of an **ovary wall** enclosing the hollow chamber known as **locule**, bearing one or many **ovules**. The ovules are attached to the ovary through **placenta**, a specialized tissue meant to provide nourishment to the developing ovule, egg, embryo sac and zygote. The position of placentae is believed to be related to the method of the union of carpels during formation of syncarpous gynoecium. The position of placenta lies near the margin of a carpel. When two carpels fuse, two margins are formed, doubling the placenta. The two carpels may unite, and the middle walls may dissolve giving rise to single locule or the walls may be retained creating partitions and generating separate locules. The number of locules represents the number of carpels united. Sometimes,

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a false septum may form during maturation giving rise to multiple locules. Example- members of Solanaceae consist of two united carpels forming syncarpous bilocular ovary, which later, may become multilocular due to formation of false septum.

Fig. 7.18 *Development of Different Floral Organs*

Vasculature of Floral Organs

The flower is considered as a determined shoot with appendages morphologically. The appendages are homologous with leaves. The anatomy of flower and floral appendages support this commonly accepted view. The vasculature of flower is more complex than that of leaves or stem. (Refer Figure 7.19) The vascular supply from the stem enters a flower through **pedicel**. Pedicel may contain a single vascular cylinder or a ring of vascular bundles. The pedicel extends up to the region where the floral organs are borne. This region expands and is known as **receptacle**. The vascular cylinder also broadens, and the number of vascular bundles also increases. The vascular bundles then enter the different floral organs as traces. In some cases (for example in *Aquilegia*) the different organs and whorls of organs arise independently. While in some cases, the traces may fuse, generally fusion occurring in separate sectors. The organ traces arise from stele of receptacle in similar manner as leaf traces arise from stele of stem. In plant families with numerous and closely placed floral organs, the gap of traces breaks the receptacle stele forming a meshwork.

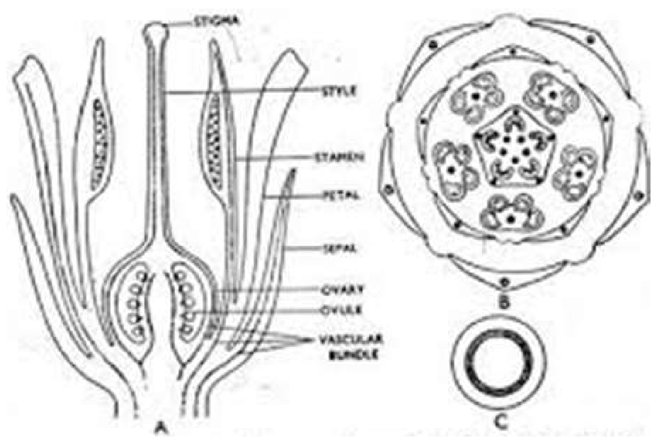

Fig. 7.19 *Hypogynous Flower showing Vascular Supply*

The sepals are anatomically very similar to leaves of the plants, except in few cases. A sepal usually receives three traces derived from the same or different vascular bundle. The sepals have been considered as equivalent to bracts or foliage leaves, morphologically. This view originated due to the similarity in the vascular pattern of sepals and foliage leaves or bracts of the same plant. The vascular supply of petals in some plants is somewhat similar to that of sepals but resembles more to stamens in majority of plants. Generally, there is single supply of vascular tissue. Stamens also generally receives a single trace. It remains unbranched throughout the filament till it reaches the anther, where it may undergo some branching. The number of traces entering the gynoecium vary in different families and is similar to the number of carpels. It may be one, three, five or more. Three traces carpel is most common with five trace carpel nearly as common.

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Check Your Progress

6. How is plant body formed?
7. What happens to the seedling formed after germination?
8. What is the age of shoot apex?
9. What happens to the vegetative shoot apices at the time of flower induction?
10. Give some characters of vegetative meristems.

7.4 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Vegetative growth is responsible for the development of vegetative organs, whereas reproductive growth gives rise to reproductive organs of plant like gynoecium, androecium and embryo.
2. Primary growth is initiated in apical region of shoot and root meristem. It results in the building of primary tissues of a plant which accounts for overall increase in the length of the plant axis at both stem and root tips, and in the development of the branching system of the stems and roots.
3. In gymnosperms and most dicotyledons, growth continues for many years (perennials). This extended growth pattern is known as secondary growth.
4. The stems and roots of such angiosperms and gymnosperms not only grow continuously by proliferation of the fundamental tissues of these organs but also increase in diameter as a result of the activity of the lateral meristem called as the 'vascular cambium'.
5. Various patterns of secondary growth that can be observed in herbaceous species are:
   - Very little or almost no cambial activity in some herbaceous dicots (annuals) consequently resulting into only primary growth, i.e., no prominent secondary growth,
   - Limited amount of secondary growth due to the cell division and differentiation activity of cambium within each vascular bundle in some dicots.

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- Parenchyma cells between the vascular bundles acquire meristematic character and form an interfascicular cambium that joins with the fascicular cambium to form a continuous ring leading to secondary vascular cylinders in some dicots (perennials).

6. The entire plant body is formed from two meristematic apical regions- Shoot Apical Meristem (SAM) and Root Apical Meristem (RAM).
7. The seedling formed after germination establishes itself and grows to enter juvenile stage
8. The shoot apex can grow for indefinite time period and hence shows indeterminate growth.
9. At the time of flower induction, the vegetative shoot apices undergo morphological changes
10. The vegetative meristems show the following characteristics:
    - Produce foliage leaves continuously.
    - Possess vacuolated cells.
    - The tunica cells contain very less ribonucleic acid in the cytoplasm.
    - The corpus cells have a small nucleolar volume.

7.5 SUMMARY

- Growth is by far the most intricate of all physiological processes. Several authors confine the term ‘growth’ as irreversible change in size and weight, i.e., cell division and cell growth process which eventually results in increase in height and size.
- Vegetative growth is responsible for the development of vegetative organs, whereas reproductive growth gives rise to reproductive organs of plant like gynoecium, androecium and embryo.
- Primary growth is initiated in apical region of shoot and root meristem. It results in the building of primary tissues of a plant which accounts for overall increase in the length of the plant axis at both stem and root tips, and in the development of the branching system of the stems and roots.
- Primary growth is the only type of growth in plants growing annually, i.e., only for one season. However, in gymnosperms and most dicotyledons, growth continues for many years (perennials). This extended growth pattern is known as secondary growth.
- In any plant, secondary growth is affected by the cell division activity of the vascular cambium. These growing layers in the cambium due to cell division activity continuously provide additional and renewed conducting and supporting elements of secondary xylem and phloem.
- Parenchyma cells between the vascular bundles acquire meristematic character and form an interfascicular cambium that joins with the fascicular

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cambium to form a continuous ring leading to secondary vascular cylinders in some dicots (perennials).

- The vascular cambium is primarily derived from procambial cells. The procambial cells differentiated acropetally from pre-existing promeristem strands into the apex of elongating primary shoot.
- The vascular cambium further generates the primary xylem and primary phloem tissues. Following the maturation of primary xylem and phloem, the cells located between primary xylem and phloem remains meristematic in nature called fascicular cambium.
- At the time of initiation of secondary growth, the cells located between the adjacent vascular bundles acquire meristematic nature and form interfascicular cambium.
- During the cell division activity, a single ring of cambium forms secondary xylem occurring centripetally (towards the center) and secondary phloem centrifugally (towards periphery). Such pattern of cell division is called as normal activity of cambium.
- Anomalous secondary growth is the term under which cambial confirmations, cambial products and cambial numbers have been grouped, which differ from the most common normal condition namely, a single cylindrical cambium that produce phloem externally and xylem internally.
- The term cambial variant is employed now days as a way of referring to the less common types as 'anomalous' may give the misleading impression of a disorderly action.
- Vascular cambia of this category function mostly in two ways. At some regions, the segments of cambia cease producing secondary xylem. In its place these segments produce secondary phloem only towards exterior.
- The newly formed wedges of phloem do not penetrate so deeply into the secondary xylem as the original wedges. More number of wedges of bast may be observed in the transverse section of stem at successive stages if the same phenomenon is repeated at frequent intervals.
- The four small segments of cambium located opposite to each other, become unidirectional after a brief period of activity, i.e., produce secondary phloem on the peripheral side only.
- Fascicular- and interfascicular cambium join with each other forming a continuous cambium ring. However, production of secondary vascular tissue is restricted to fascicular cambium only.
- The primary vascular bundles are arranged in a ring and surround central parenchymatous pith. Each vascular bundle is conjoint, collateral and open. The vascular bundles remain separated by wide parenchymatous interfascicular region.
- Some dicot stems appear as flat ribbon like at maturity, for example in *Prestonia macrocarpa*, *Bauhinia divaricata* and *B. sericella*. The stele is also flattened strap shaped.

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- The secondary xylem produced by the alternating segments of cambium is also different- the secondary xylem possessed small tracheary elements at the less active region of cambium, while wide lumened vessels were present in the xylem at the more active region of cambium.
- The cambial region of this category produces secondary vascular tissues in normal fashion, but their positions are anomalous. These cambia form discrete vascular cylinders and their arrangements differ according to species.
- The bundle rings possess permanent growth in girth by a ring of cambium present in them. At maturity, the divided xylem mass encloses the pith lacking central ring vascular cylinder.
- The stem of *Thinouia*, exhibits a central ring of vascular bundles surrounded by several peripheral rings. Each vascular cylinder possesses ring of cambium with phloem and xylem enclosing pith.
- The new strands of accessory cambia, though abnormal in position, produce normal phloem and xylem towards exterior and interior, respectively, enclosing pith at the centre.
- A cross-section of young stem shows the primary vascular bundles of different sizes, arranged in three rings. All vascular bundles are derived from procambial strands.
- The cambium divides tangentially, and the inner derivative cells differentiate into secondary xylem while the peripheral derivative cells form secondary phloem.
- As secondary growth continues, the primary phloem cells are crushed. The dead remnants of crushed phloem appear as cap over the later formed secondary phloem.
- The peripheral derivatives form parenchyma cells, whereas the inner derivatives differentiate into internally situated conjunctive tissue and storage parenchyma. The conjunctive tissue consists of elongated living cells that are later transformed to sclerenchyma by lignin deposition on their walls.
- After being active for some time, the function of new cambium stops. Then, another new additional cambium cylinder arises from the peripheral parenchyma cells produced by its predecessor.
- The entire plant body is formed from two meristematic apical regions- Shoot Apical Meristem (SAM) and Root Apical Meristem (RAM). These apices are recognized at 2-celled stage of developing embryo.
- The seedling formed after germination establishes itself and grows to enter juvenile stage. After a period of time the growing plant enters the vegetative phase of its life cycle.
- At the time of flowering, different floral organs or appendages are formed as a result of 'switching' of vegetative phase to reproductive phase.
- The shoot apex can grow for indefinite time period and hence shows indeterminate growth. On the other hand, when the vegetative apex transits

to reproductive phase, it is characterized with short and determinate growth.

- Flowers are determinate structures in annual plants, vegetative growth of the plants terminates with flowering.
- Asaki (2001) reported role of about 80 genes in regulating the transition from vegetative to floral state. This dramatic phase change in plant development is indicated by several forms of signal transduction, external environment factors (such as photoperiod and temperature) and internal factors (plant hormones).
- Development of floral organs is considered as a 'continuous succession of events- a cascade in which successive events build on initial events' (Tucker 1997).
- The vegetative shoot meristems show indeterminate (unlimited) growth, while flowering terminates this growth. The flower consists of an axis and lateral appendages arising from it. The axis is also known as receptacle and appendages as floral parts or floral organs.
- The floral organs consist of sterile organs and fertile productive organs. The floral parts are generally arranged in sequence beginning with sepals at the base and continuing through petals, stamens and carpels.
- The size, shape, position of ovary, style and stigmas vary greatly in different families.
- The ovary generally consists of an ovary wall enclosing the hollow chamber known as locule, bearing one or many ovules.
- The flower is considered as a determined shoot with appendages morphologically. The appendages are homologous with leaves. The anatomy of flower and floral appendages support this commonly accepted view. The vasculature of flower is more complex than that of leaves or stem.
- The pedicel extends up to the region where the floral organs are borne. This region expands and is known as receptacle.

7.6 KEY WORDS

- **Fascicular cambium:** The cells located between primary xylem and phloem remains meristematic in nature called fascicular cambium.
- **Anomalous secondary growth**: Deviation in the pattern of cell division and differentiation of its derivatives by the cambium is known as anomalous secondary growth.
- **Pericycle**: The perivascular fibre and the subjacent parenchyma are referred to as pericycle.
- **Perivascular** fibre: Cylinder of sclerenchymatous fibres present just below the endodermis are called perivascular fibre.

7.7 SELF ASSESSMENT QUESTIONS AND EXERCISES

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Short Answer Questions

1. What is cambial variant?
2. Write a note on *Bignonia.*
3. What is *Aristolochia*?
4. Distinguish between *Tinospora* and *Bauhinia*.
5. Brief a note on floral organs.

Long Answer Questions

1. Discuss about cambial variants due to abnormal positioning of cambium.
2. Elaborate a note on cambial variants due to abnormal activity.
3. What are accessory cambium? Explain.
4. Distinguish between inter-xylary phloem and intra-xylary phloem.
5. Write a note on floral vasculature.
6. What is transition of flowering and induction of flowering? Explain with example.

7.8 FURTHER READINGS

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NOTES

BLOCK - III
THE WOOD

UNIT 8 WOOD: STRUCTURE, CLASSIFICATION, IDENTIFICATION AND USES

Structure

8.0 INTRODUCTION

Wood is a porous and fibrous structural tissue found in the stems and roots of trees and other woody plants. It is an organic material, a natural composite of cellulose fibers that are strong in tension and embedded in a matrix of lignin that resists compression. Wood is sometimes defined as only the secondary xylem in the stems of trees, or it is defined more broadly to include the same type of tissue elsewhere such as in the roots of trees or shrubs. In a living tree it performs a support function, enabling woody plants to grow large or to stand up by themselves. It also conveys water and nutrients between the leaves, other growing tissues, and the roots. Wood may also refer to other plant materials with comparable properties, and to material engineered from wood, or wood chips or fiber.

Wood has been used for thousands of years for fuel, as a construction material, for making tools and weapons, furniture and paper. More recently it emerged as a feedstock for the production of purified cellulose and its derivatives, such as cellophane and cellulose acetate.

As of 2005, the growing stock of forests worldwide was about 434 billion cubic meters, 47% of which was commercial. As an abundant, carbon-neutral renewable resource, woody materials have been of intense interest as a source of renewable energy. In 1991 approximately 3.5 billion cubic meters of wood were harvested. Dominant uses were for furniture and building construction.

Heartwood (or duramen) is wood that as a result of a naturally occurring chemical transformation has become more resistant to decay. Heartwood formation is a genetically programmed process that occurs spontaneously. Some uncertainty exists as to whether the wood dies during heartwood formation, as it can still chemically react to decay organisms, but only once.

Heartwood is often visually distinct from the living sapwood, and can be distinguished in a cross-section where the boundary will tend to follow the growth rings. For example, it is sometimes much darker. However, other processes such as decay or insect invasion can also discolour wood, even in woody plants that do not form heartwood, which may lead to confusion.

Sapwood is the younger, outermost wood; in the growing tree it is living wood, and its principal functions are to conduct water from the roots to the leaves and to store up and give back according to the season the reserves prepared in the leaves. However, by the time they become competent to conduct water, all xylem tracheids and vessels have lost their cytoplasm and the cells are therefore functionally dead. All wood in a tree is first formed as sapwood. The more leaves a tree bears and the more vigorous its growth, the larger the volume of sapwood required. Hence trees making rapid growth in the open have thicker sapwood for their size than trees of the same species growing in dense forests. Sometimes trees (of species that do form heartwood) grown in the open may become of considerable size, 30 cm (12 in) or more in diameter, before any heartwood begins to form, for example, in second-growth hickory, or open-grown pines.

In this unit, you will study about structure, identification, classification and uses of wood in detail.

8.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the structure of wood
- Explain how to identify wood
- Discuss classification and uses of wood

8.2 WOOD: STRUCTURE, CLASSIFICATION, IDENTIFICATION AND USES

Wood is a complex biological structure, made up of many cell types having different chemical compositions. Wood is formed to meet the needs of the living tree. Wood evolved over the progression of millions of years to serve three main functions in plants:

- Conduction of water from the roots to the leaves.

- Mechanical support of the plant body.
- Storage and synthesis of biochemicals.

To accomplish these functions, wood must have specially designed and interconnected cells. These three functions have influenced the evolution of approximately 20,000 different species of woody plants. Each species has unique properties, uses, and capabilities, in both plant and human contexts. An understanding of the basic requirements dictated by these three functions and identifying the structures in wood that perform them, gives insight to the realm of wood and its products as a composite material.

Structure of Wood

A tree has two main spheres, the shoot and the roots. Roots are the underground structures responsible for water and mineral nutrient uptake, mechanical anchoring of the shoot, and the storage of biochemicals. The shoot is made up of the trunk, branches, and leaves. The trunk is composed of various materials present in concentric bands as visible in the trunk of a cutdown tree. From the outside of the tree to the inside are outer bark, inner bark, vascular cambium, sapwood, heartwood, and the pith (Refer Figure 8.1). Outer bark provides mechanical protection to the softer inner bark and helps to check water loss through evaporation. Inner bark is the tissue through which sugars produced by photosynthesis (photosynthate) are translocated within the tree. The vascular cambium is the layer between the bark and the wood that produces both these tissues each year. The sapwood is the active 'living' wood that conducts the water (or sap) from the roots to the leaves. It appears lighter as it has not yet accumulated the often-coloured chemicals, which are present in the darker non-conductive heartwood found as a core of most trees. The pith at the centre of the trunk is the residue of early growth, before wood was formed.

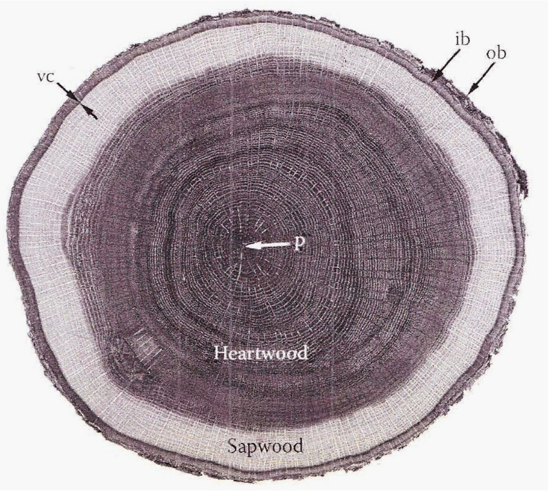

Fig. 8.1 *Macroscopic View of a Transverse Section of a Quercus alba Trunk*

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The above Figure 8.1 shows the macroscopic view of a transverse section of a *Quercus alba* trunk. Beginning at the outside of the tree is the Outer Bark (OB), next is the Inner Bark (IB) and then the Vascular Cambium (VC), which is too narrow to be seen at this magnification. Interior toward the vascular cambium is the sapwood. Which is easily differentiated from the heartwood that lies toward the interior. At the center of the trunk is the Pith (P), which is hardly visible in the center of the heartwood.

Wood: The Secondary Xylem

Vascular cambium produces secondary xylem towards the center of the stem and root. It also produces secondary phloem but the amount of phloem is usually less than the amount of xylem produced. The secondary xylem forms bulk of vascular tissue in woody plants. In woody plants (gymnosperms and dicotyledons) secondary xylem is more persistent than secondary phloem. As the tree matures, more secondary xylem is produced, which enables the plant to transport additional water required and also supports the increasing width of the stem. The elements of secondary xylem are tracheids, vessels, fibres, xylem parenchyma cells, xylem rays and sometimes secretory cells. The secondary xylem has two systems of elements which differ in the orientation of the plant. The vertical or longitudinal system is also known as axial system consists of vertical files of tracheary elements, fibres and wood parenchyma. The horizontal or transverse also known radial system consists of xylem rays or wood rays. The structure of secondary xylem is simpler and more homogenous in gymnosperms as compared to the angiosperms due to the absence of vessels (except in Gnetales) and presence of small amount of axial parenchyma (Refer Figure 8.2).

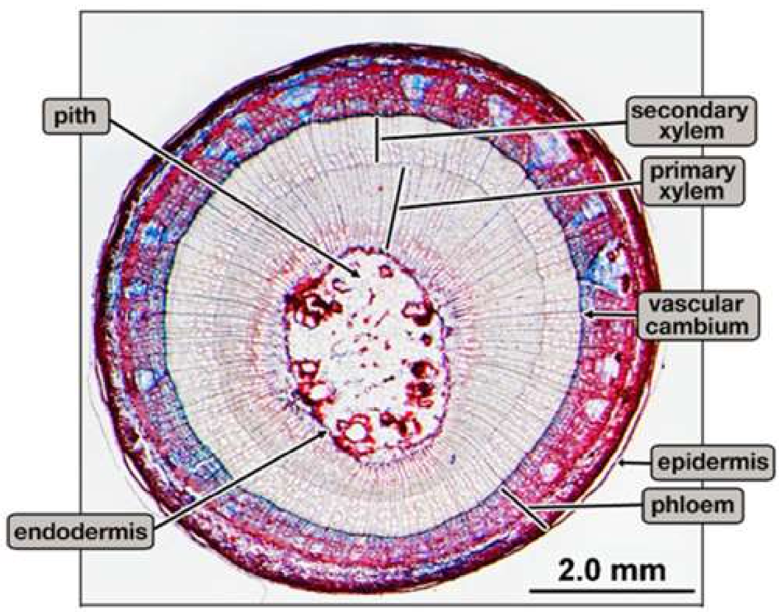

Fig. 8.2 *Cross Section of Two Year Old tilia Stem*

Secondary Xylem in Gymnosperms

Axially Oriented Elements in Gymnosperms

In gymnosperms, axially oriented derivatives of cambium consist of tracheids and parenchyma strands. Epithelial cells of axial resin ducts may also be present. In gymnosperms, tracheid provides mechanical support to the plant and helps in transportation of water. Tracheids are the derivatives of cambial cells and therefore resemble with these cells. The length of tracheids ranges between 0.5 mm-11 mm long depending upon the species and the part of the plant. The longest tracheids have been observed in the old stems of Sequoia and Araucaria. Because of this length, tracheids overlap one another with chisel-shaped ends and have bordered pit-pairs in their common walls. The number of pits per tracheids may vary from 50-300 (Refer Figure 8.3).

There is a great variation in size of pits, shape of the pit border and pit aperture in the different species and therefore, it is an important tool for the identification of gymnosperm wood. Pits are usually present on the radial walls, but they have also been observed on the tangential walls of the late wood.

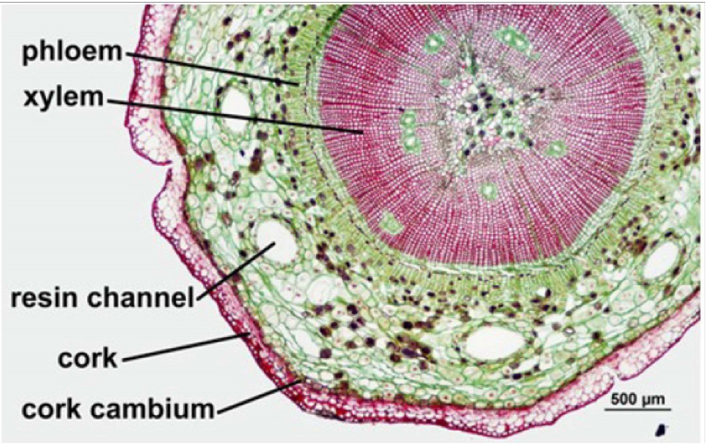

Fig. 8.3 *T.S of a Pinus Stem showing Tracheids, Parenchyma Strands and Epithelial Cells of the Resin Ducts*

The primary cell wall consists of some depressions which appear as beaded structures under electron microscope. These beaded structures are known as **primary pit fields**. In addition to these primary pit fields, the secondary walls are also provided with such depressions or cavities known as **pits**. Pits are the regions through which two adjacent cells maintain their cytoplasmic continuity (Refer Figure 8.4). Therefore, each pit has its complementary pit in the wall of the neighboring cell. The adjacent walls of two pits are known as **pit-pair**. The cavity formed by the breaking the secondary wall is called as **pit cavity** and the plasma membrane separating the two pit cavities of pit-pair is known as **closing membrane** or **pit membrane**. The opening through which the pit opens into the lumen of the cell is known as **pit aperture**.

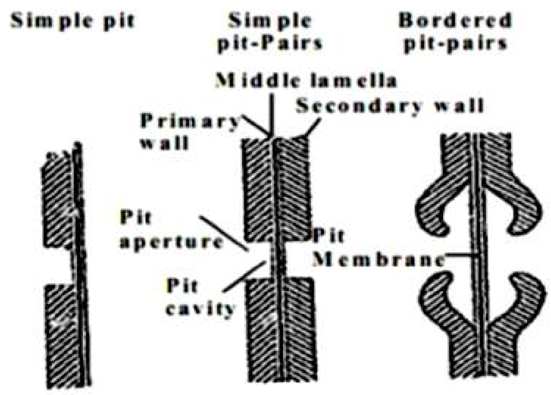

Fig. 8.4. *Types of Pits*

Pits are of two types: simple pits and bordered pits. **Simple pits** are usually present in libriform fibres and in sclereids. If both the pits of a pair are simple, it is known as simple pit-pair. Bordered pits are characterized by the overarching of the secondary wall over pit cavity. In simple pit, no such structure is developed. **Bordered pits** are mostly present in the tracheary elements (Pteridophytes, Gymnosperms and Angiosperms) and in fiber tracheids. When secondary wall forms a dome shaped structure on both sides of the pit, it is known as **bordered pit-pair**. When one of the pits of a pair is simple and other one is bordered, it is known as **half bordered pit-pair**. A pit without any complementary pit on the opposite cell wall is known as **blind pit** (Refer Figure 8.5).

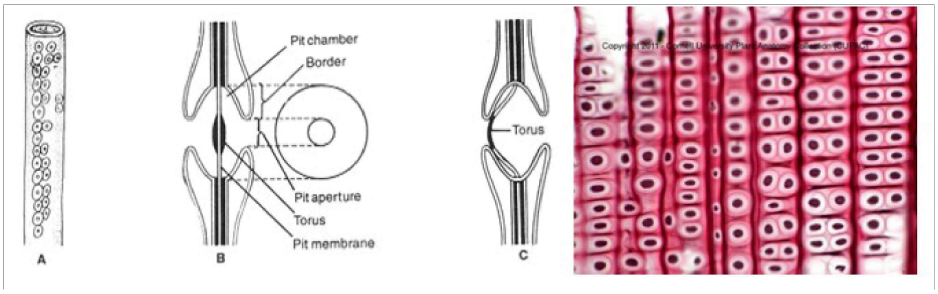

Fig. 8.5 *A) Bordered Pits on the Wall of Tracheids~ B) Bordered Pit pair (Presence of Torus, Pit Aperture, Pit Cavity) ~ C) Aspirated Pit~ D) Bordered Pits on Xylem Tracheids*

In Gymnosperms (*Ginkgo*, Gnetales and Coniferales), pit membrane of bordered pit-pair gets thickened in center and this thickened portion is known as **torus**. The diameter of torus is wider than that of the pit aperture. In tracheids of many conifers the marginal part of the pit membrane around the torus – '**the margo**' becomes porous while the central part, the torus remains solid. When the torus is in median position, water can easily pass from one tracheid to another. If the torus takes place the lateral position, specifically present against one of the pit apertures, it completely restricts the movement of water and known as **aspirated pits**. Aspirated pits are of common occurrence in heart wood or late wood.

Tracheids formed at the end of growing season (late wood) have relatively thick walls, small pit chambers, long canals and are more dense than early wood. Therefore, it becomes easy to distinguish the annual growth rings in gymnosperms (conifers), as late wood is darker in colour as compared to early wood. In gymnosperms, fibre tracheid with thin walls and bordered pits are present however, labriform fibres (thick walls and simple pits) are absent. The occurrence of trabeculae is another characteristic feature of gymnosperm wood. These are the rod-shaped outgrowths of the tangential cell walls and are usually arranged in long radial rows. Axial parenchyma is poorly developed in most of the gymnosperms (conifers). In *Podocarpaceae*, *Taxodiaceae* and *Cupressaceae* it is prominent, while poorly developed or absent in *Auracariaceae*, *Pinaceae* and *Taxaceae*. In *Pinus*, axial parenchyma is present only with the resin ducts.

Radial System in Gymnosperms

The radially oriented parenchymatous cell of wood consists of **xylem rays**. In most of the gymnosperms, the rays are uniseriate (one cell wide), except for those containing resin ducts. Ray parenchyma cells contain living protoplast. Ray tracheids are characterized by the absence of protoplast, presence of bordered pits and lignified secondary walls. There are two types of rays in gymnosperms~ **homocellular** rays (when rays comprise of only parenchyma) and **heterocellular** rays (when it consists of both parenchyma cells and tracheids). Ray tracheids occur singly or in rows and scattered among the ray parenchyma cells. In conifers, the walls of ray cells generally have simple pits, even if secondary wall is present, except in the cross-section which is an area of contact between ray parenchyma cell and single vertical tracheid. Here the pit pairs are of usually half-bordered. Variation in these types of pits, their number and distribution in the cross-section is an important feature in the identification of gymnosperm wood. In ray cells of some species of *Pinus*, large windowlike pits with extremely narrow borders occur which are known as **fenestriform pits** (Refer Figure 8.6).

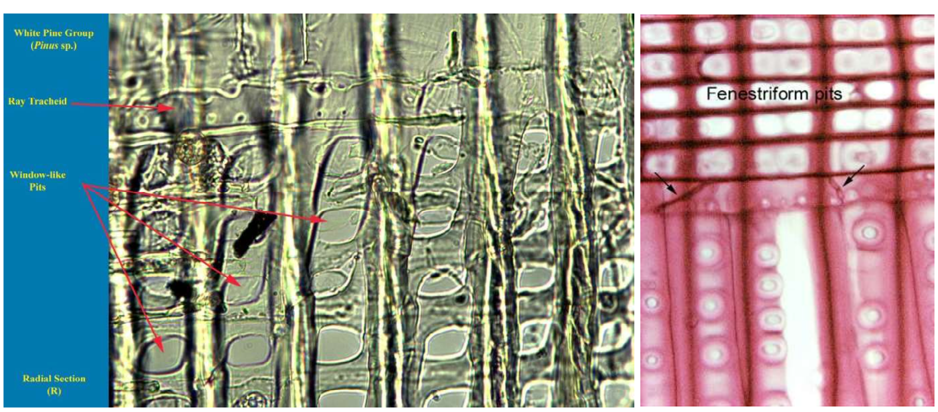

***Fig. 8.6** A) Radial Section of White Pine Group (Pinus Sp.) Showing 1 Row of Ray Tracheids and Fenestriform Pits B) Fenestriform Pits in Pinus Sp.*

Resin Ducts

In various physiological processes, a number of substances are produced in the cytoplasm and they are liberated outside the plant body through specialized cells. These specialized groups of cells are known as secretory tissue or idioblasts dispersed in ground parenchyma. A variety of contents of economic importance such as oil, resins, tannins, gums and mucilage are secreted by these cells. Some structures secrete water, nutrient, salt and nectar with the help of hydathodes, salt glands and nectaries. These are known as external secretory structures which may be epidermal or subepidermal in origin. Other structures secrete substances synthesized in their constituent cells. If substances are discharged onto the external plant surface, it is exo-secretion and if discharge is to an internal site stored in the protoplast, then it is endo-secretion (latex) (Refer Figure 8.7).

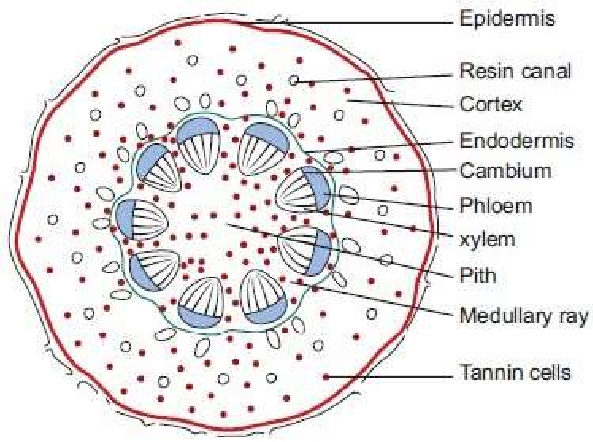

Fig. 8.7 *T.S. of Pine (Pinus sp.) Showing Resin Duct*

Resin ducts are internal secretory structures known as the best example of schizogenous ducts, which is a characteristic feature of gymnosperms (conifers). They may be present in both vertical and horizontal system. Resin ducts have long intercellular spaces lined with resin producing parenchyma cells, known as epithelial cells. Sometimes epithelial cells are enlarged so much that they block the cavity of resin ducts, these structures are known as **tylosoids**. Thickness and lignifications of epithelial cells varies in different genera of conifers. When the epithelial cells have thick and lignified cells, it remains functional only for one season and produces little resin (for example, *Abies* and *Cedrus*), while if are thin walled, they remain functional for several seasons and produces large amount of resin (for example, *Pinus*).

Although presence of resin duct is a normal anatomical feature, but in some species of conifers it can be produced under the stimulus of injury, such as wounding, pressure and frost. Therefore, for commercial production of resin, wounding is practiced. Location of the resin duct depends on the species and type of injury. Injuries resulting from pressure and frost result in the development of scattered ducts, whereas open wounding causes dense or scanty tangential groups of resin ducts around the wound. In *Cupressus* (conifers), resin ducts do not develop in the secondary xylem.

Secondary Xylem in Dicotyledons

Axially Oriented Elements in Dicotyledons: The secondary xylem of dicot is more complex than gymnosperms. Axial system of dicot comprises of tracheary elements, vessels, libriform fibres, fibre tracheids and wood parenchyma.

Tracheary Elements

Tracheids and vessels together constitute tracheary elements. Vessels are the major water conducting elements in the wood of dicots, though tracheids also help in the conduction of water. Presence of vessels is considered to be an advanced feature in angiosperms with the exception of some primitive families such as *Winteraceae* and *Trochodendraceae*. Vessels are characterized by the presence of perforation plate at their end walls. With the help of these perforation plates, vessel members are joined from one another to form a tube-like series of cells (syncytes), through which cell sap moves from one vessel to another.

In vessel elements, perforations are usually present on their end walls but sometimes these perforation plates are lateral or subterminal in position. The perforated areas of vessel member end walls are always much larger than pits. During cytodifferentiation of tracheary elements, cell wall material is partially hydrolysed and perforation plates are formed. The part of cell wall that bear perforations are called perforation plate. Area surrounding perforation plate is known as perforation rim. When perforation plate contains one large pore, it is known as simple perforation plate and when more than one pore is present, it is known as multiple perforation plate. Simple perforation plate is considered to be derived from multiple perforation plate by loss of secondary wall thickenings. In multiple perforation plate, pores can be arranged in multiple ways. When the pores are elongated and arranged in parallel series, it forms a scalariform perforation plate.

When the pores are arranged in a reticulate, i.e., separated by a network of secondary wall thickenings it is known as reticulate perforation plate. When the perforations are completely circular and grouped together, perforation plate is foraminate. Vessels with transverse end walls and simple perforations are considered to be the phylogenetically advanced features.

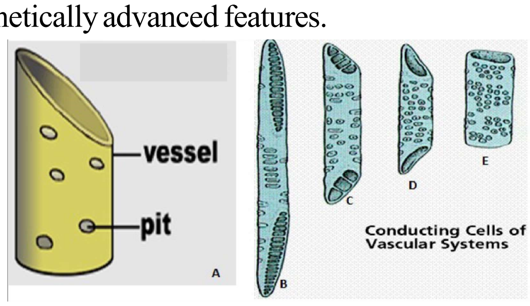

Fig. 8.8 *A) Vessel Showing Presence of Perforated End and Pits on Their Wall B) Evolution of Vessel Element; B) A Primitive, Tracheid like Vessel with Scalariform Perforation Plate*

Tracheids are nonperforated cells in which only bordered pit pairs are found in the areas of contact between them. In woody dicots, three types of tracheids are present:

- Vessel Tracheid
- Vasicentric Tracheids
- Fibre Tracheids

Vessel Tracheids

These are fusiform in shape and arranged in axial strands. These axial strands are interconnected by bordered pits, arranged in the scalariform manner on anticlinally oblique end walls. Walls of vessel tracheids usually have helical thickenings (for example, *Morus*, *Robinia*). Group of vessel tracheid strand resemble the clusters of small vessels, but these strands do not have the perforation plates like vessel elements. The length of vessel tracheids is nearly the same of the cambial fusiform initials as they are also derived from fusiform cells. Vessel tracheids are commonly located between vessels and provide a pathway for transport of water. As vessel tracheids are generally narrower and they are connected with the other neighbouring cells by pit connections only, they are less susceptible to embolism.

Vasicentric Tracheids

These are shorter than other tracheids, as during differentiation they divide through transverse or oblique division. These are present around the periphery of wider vessels and are in contact with other parenchyma cells with numerous pits. Vasicentric tracheids function as armour for vessel wall, damping shocks or vibrations that could break adhesive bonds between the sap solution and that wall.

Fibre Tracheids

These are considered to be the intermediate between tracheids and fibres. They are longer than tracheids and vessels, as their tips undergo appreciable growth during differentiation. They are characterized by the presence of relatively thin walls and bordered pits and therefore helps in the mechanical support (Refer Figure 8.9).

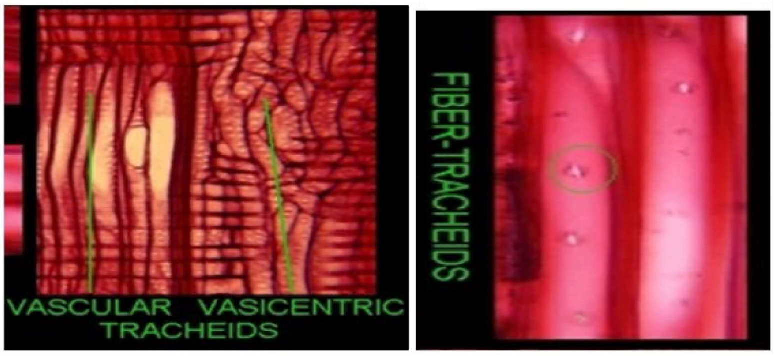

Fig. 8.9 *Type of Tracheids. A) Vasicentric Tracheids B) Fibre Tracheids*

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Fibres

The two major types of xylem fibres present in the wood of dicots living fibres and libriform fibres. Both kinds of fibres originate from the cambial cell derivatives.

Living Fibres

These fibres are septate, have protoplast, contain starch grains and therefore they cannot transport water through apoplasm. Their major function is to provide mechanical support. In *Tamarix aphylla*, these fibres live for about 20 years as long as xylem parenchyma.

Libriform fibres

These fibres are very long, characterized by the presence of thick walls and simple pits. They do not have living protoplast. Libriform fibres resemble phloem fibres. Libriform fibres are present in the species having short cambial fusiform initial. Sometimes these fibres are present in abundance that tracheary elements and parenchyma are embedded in the cellular matrix of libriform fibres. These fibres do not help in the super apoplasmic transport of water as they have narrow lumina and small pits.

Wood Parenchyma

They are differentiated into two types, axial parenchyma and ray parenchyma:

Axial Parenchyma: It develops from the long fusiform initials of the vascular cambium and is arranged parallel to the axis of the stem.

Ray Parenchyma: It initiates from short ray initials and arranged radially (Refer Figure 8.10).

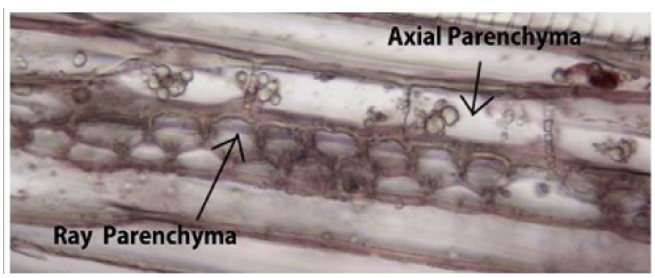

Fig. 8.10 *Axial and Ray Parenchyma*

The cells of axial parenchyma may be as long as fusiform initials or sometimes they become shorter because of transverse division before differentiation. Axial parenchyma cells which do not divide transversely forms fusiform parenchyma. Mature axial xylem parenchymatous cells retain living protoplast for many years. The amount of axial parenchyma shows considerable variation in different species of dicotyledons. In some hard wood axial parenchyma is completely absent (for example, *Sonnertia*), in some species it is present in less quantity (for example, *Boswellia serrata*). According to phylogenetic evolution, absence of the axial parenchyma is considered to be a primitive feature and the presence of terminal parenchyma an advanced feature, formed due to the reduction. Ray parenchyma cells of various shaped develops secondary thickenings in their wall. Parenchyma cells of the xylem help in the storage of reserve food material such as starch and fats, tannins, crystals and silica bodies. Axial parenchyma can be differentiated into: apotracheal and paratracheal parenchyma

In **Apotracheal parenchyma,** distribution of parenchyma is independent of vessels. It is divided into following subtypes (Refer Figure 8.11):

- **Diffuse or Scattered**: When apotracheal parenchyma is present in the form of isolated cells and is scattered irregularly among fibres.
- **Banded or Metatracheal Parenchyma**: When axial parenchyma is present in the form of concentric bands.
- **Terminal Parenchyma**: When single apotracheal parenchyma is arranged in more or less continuous layers at the end of a growth ring with variation in their width.
- **Initial Parenchyma**: When above parenchyma is formed at the beginning of the growth ring.

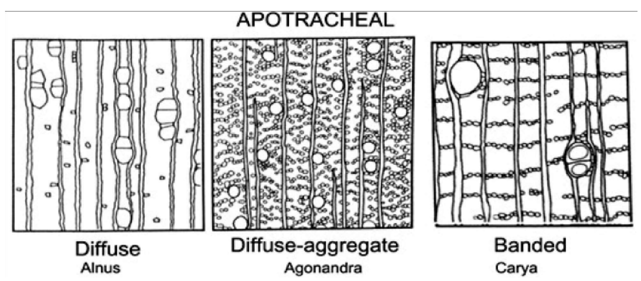

Fig. 8.11 *Distribution of Parenchyma in Apotracheal Pattern*

In **Paratracheal parenchyma**, the parenchyma is closely associated with vessels. It is divided into the following subtypes (Refer Figure 8.12):

- **Scanty parenchyma**: When paratracheal parenchyma does not form a continuous sheath (for example, *Acer*).
- **Unilaterally paratracheal parenchyma**: When paratracheal parenchyma is present on one side either externally or internally of the vessels
- **Vasicentric parenchyma**: When parenchyma forms a fairly uniform light-coloured sheath around the vessels (for example, *Tamarix*).
- **Aliform parenchyma**: When the parenchyma surrounds the vessels in such a way that wing like lateral projections are formed (for example, *Albizzia lebbek*).
- **Confluent parenchyma**: When wing like extensions of adjacent vessels are connected laterally (for example, *Acacia raddiana*).

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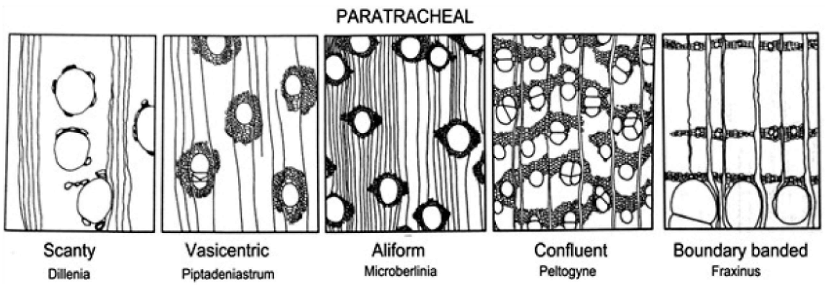

Fig. 8.12 *Distribution of Parenchyma in Paratracheal Pattern*

Tyloses

Tyloses are balloon like enlargement of parts of cell wall which projects into the adjacent cell lumina through pit cavities. In many plants, cells of both types of wood parenchyma (ray or axial parenchyma), penetrate into the vessel in the form of a short and blunt protuberances. The nucleus and parent cytoplasm of cell migrate into this peg like outgrowth. It gradually expands and takes the shape of a bladder penetrates into the vessel lumen. This protuberance is now known as tyloses (singular: tylosis). After certain stage of its development, it gets detached from the parenchyma cell through which it has been derived. Sometimes tylosis also undergoes repeated divisions to form a multicellular structure. This multicellular structure completely blocks the lumen of the vessel. This structure is common in wood of the angiosperm. Tyloses are also present in vessels of herbs such as *Cucurbita*, *Portulaca* and *Convolvulus*. In many species tyloses develop at the time of transformation of sap wood into heart wood. Tyloses are most abundant in heart wood, where wood parenchyma is scarce and tyloses are few.

Although tylosis formation is considered to be a normal phenomenon, but in some species, it is a common response to infection by vascular fungi (for example, *Fusarium*), or by bacteria (for example, *Pseudomonas*), flooding, freezing, mechanical injury or by any diseases. As the tyloses blocks the vessel lumina, it helps in preventing the rapid entrance of water, fungal or bacterial pathogens. Therefore, in some species, tyloses are of considerable economic importance. In some other species, like other parenchyma cells, tyloses also perform the function of storage of starch grains (Refer Figure 8.13).

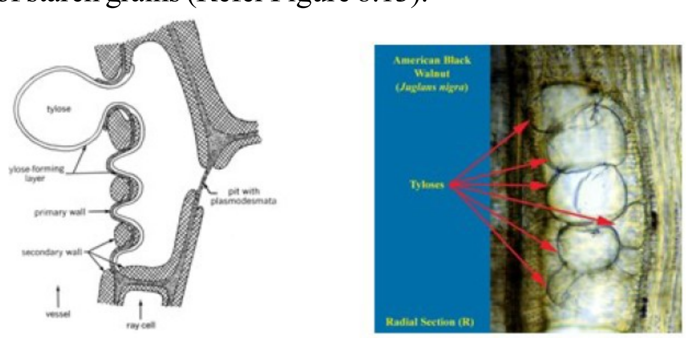

Fig. 8.13 *Line diagram of Tylosis Formation~ Entering Into The Vessel Lumina; Radial Section of American Black Walnut (Juglans nigra) Showing tyloses*

Gum Ducts

Intercellular gum ducts occur in dicotyledons wood similar to resin ducts in gymnosperms. Although these ducts are known as **gum ducts**~ they contain substances other than gums such as resins, oils and mucilage. Gum ducts may be either in axial or radial in position. Some taxa have only radial gum ducts and some have only axial gum ducts and a few have both. Radial ducts are located within rays. As dicots rays are wide and multiseriate, presence of ducts does not alter their shape. These ducts may arise normally in wood and can also be induced by giving some injury. Increased ethylene production is a factor in inducing the formation of traumatic gum ducts. A special type of duct, kino vein occurs in the wood of *Eucalyptus*. **Kino veins** differ from gum ducts in having polyphenols. Kino veins are formed by lysigenous breakdown of bands of parenchyma formed by the cambium.

Radially Oriented Elements

Xylem rays or wood rays are present in the radial system of secondary xylem. These are the sheets of parenchymatous cells which are arranged at right angle to longitudinal axis of plant. There is a great variation in the width and height of xylem rays in dicots than gymnosperms. The number of xylem rays in a trunk increases with the increase in girth. As the stem grows older, ray becomes distant due to the expansion of cambium as the axis also increases in its circumference. The length, width and height of the ray can be measured in cross-section, tangential section and in radial section respectively (Refer Figure 8.14).

There is a variation in the width and the cellular composition of the rays. When the ray is one cell wide, it is known as uniseriate ray~ when two cells wide, biseriate, and when more than two cells wide, multiseriate. In some plants aggregate rays are also present (for example, *Alnus*, *Corylus*). An aggregate ray consists of a group of small and narrow rays which appears to be a single large ray under low magnification. Uniseriate and mutiseriate rays can be present in the same species (for example, *Quercus*). Although some dicots have uniseriate rays (for example, *Populus*, *Salix*)~ but most of the dicots have multiseriate rays (for example, *Liriodendron*).

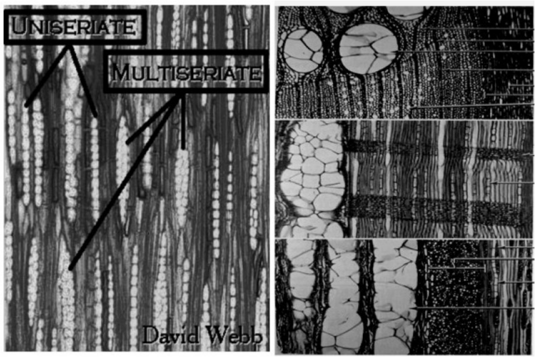

Fig. 8.14 *Tangential Section of Wood Showing Uniseriate and Multiseriate Rays*

In dicotyledons, parenchyma cells in xylem rays are morphologically of two types:

When all the ray cells are elongated in a radial direction, i.e., all the cells are procumbent, the ray is **homogenous** (homocellular). In most of the arborescent genera of temperate zones have homocellular rays (exception *Salix* (Refer Figure 8.15), *Cornus* and *Carpinus*).

- When medullary rays consist of radially elongated cells (procumbent cells) and upright/square or vertically elongated cells (erect cells), it is said to be **heterogenous** (heterocellular). Heterocellular rays are common in tropical trees.

These terms have different meanings for rays of dicots than for rays of gymnosperms.

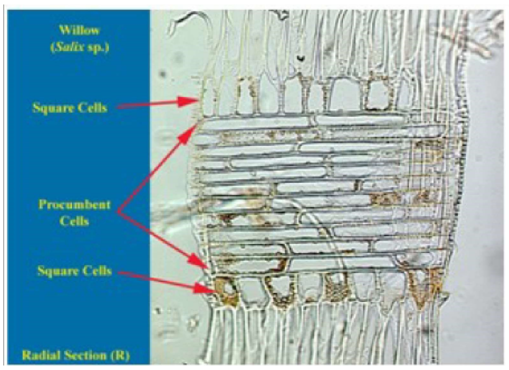

Fig. 8.15 *Radial Section of Willow (Salix sp.) Showing a Heterocellular Ray Composed of Procumbent Cells and Uprights*

Functionally, there are two kinds of ray cells. Contact ray cells have pit contacts with neighbouring tracheary elements and can release solutes directly into these elements. The pits of contact cells are relatively large and simple. Isolated ray cells do not have pit contacts with tracheary elements. They can symplasmically exchange solutes with other living cells but cannot release them directly into tracheary elements. Upright cells are always of the contact type, but procumbent cells may be either the contact or the isolated type (Refer Figure 8.16).

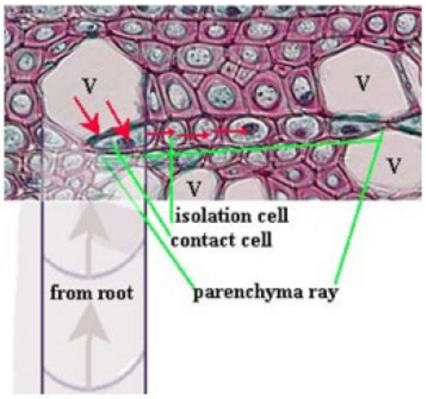

Fig. 8.16 *Transverse Section of Sambucus Secondary Xylem, Showing Flow from a Vessel*

Classification of Wood

Sapwood and Heartwood

In most of the woody plants, with the exception of few deciduous species, the outer light part of the secondary xylem is distinct from the inner dark coloured zone. The outer light coloured part is known as sapwood or alburnum. Sapwood contains living cells and outer rings of sapwood are involved in the conduction of water and inner rings function as storage of starch and fats. Presence of reserve food material in this zone invites the fungal or bacterial pathogen. Hence, sapwood is least durable and less economically important. Tyloses are of the rare occurrence in the sapwood. The inner darker zone is known as heartwood or duramen. It is composed of thick lignified dead cells impregnated with resins, oils, tannins, gums, coloured substances and various aromatic substances. Presence of all these substances makes heartwood more durable and commercially more important. Heartwood of some plants contains pigments of commercial importance such as **Hematoxylin** (*Hematoxylon campechianum*), **Brasilin** (*Caesalpinia sappan*) and **Santalin** (*Pterocarpus santalinus*).

As the plants grow older, rings of sapwood bordering heartwood are converted into heartwood. This is a gradual process~ accompanied by the disintegration of the protoplast, reduction of water content and removal of reserve materials from cells. Here, the vessels are completely occluded by the formation of tylosis. Cells become heavily lignified and develop coloured and various aromatic substances. The development of coloured substances is because of oxidation and polymerization of phenols, which is followed by disappearance of starch. The zone of wood in which these changes occur is known as transition zone. This zone is visible as a weakly pigmented band having lower moisture content than peripheral sapwood. The living, but senescent cells in the transition zone undergo increased metabolic activity during which flavonoids are produced. In angiosperms, vessels undergo embolism and neighboring parenchyma cells develop tyloses. All of these changes make the heart wood more resistant to decay.

The proportion of heartwood and sapwood is variable in different species and it is greatly influenced by climatic conditions. Heartwood and sapwood also vary in their colour The distinction of colour is sharp (*Pinus roxburghii*, *Dalbergia sissoo* and *Albizzia lebbek*)~ somewhat gradual (*Shorea robusta* and *Adina cordifolia*)~ or no colour distinction at all (*Abies pindrow* and *Picea smithiana*). Figure 8.17 shows the cross-section of yew wood (*Taxus baccata*).

Fig. 8.17 *Cross-Section of Yew Wood (Taxus baccata)*

Ring Porous Wood and Diffuse Porous Wood

The wood of dicotyledons has vessels in the xylem due to which it is known as **porous wood** and gymnosperm wood lacks vessels and therefore known as nonporous wood. Technically, the wood of angiosperm is called hard wood whereas wood of gymnosperms is called soft wood. Porous wood of *Bombax ceiba* and *Pterocymbium tinctorium* is soft whereas the nonporous wood of *Pinus* and *Cedrus,* although is very hard but considered as soft wood. The arrangement of vessels is an important diagnostic feature of wood, which is used in the identification of species. Environmental conditions and age of the plant also influence the arrangement of the vessels. On the basis of the arrangement of the vessels wood can be classified into ring porous and diffuse porous wood.

Wood contains vessels of different diameters. Vessels produced in the beginning of the season are distinctly larger than that of the late wood and are known as **ring porous wood** for example, *Morus alba* and *Toona ciliate* (Refer Figure 8.18). These vessels are arranged in the form of a ring or belt at the beginning of the growth ring. When the vessels are more or less equal in diameter and are uniformly distributed throughout the wood, the wood is known as **diffuse porous wood** for example, *Acer* spp., *Populus alba* and *Acacia cyanophylla*.

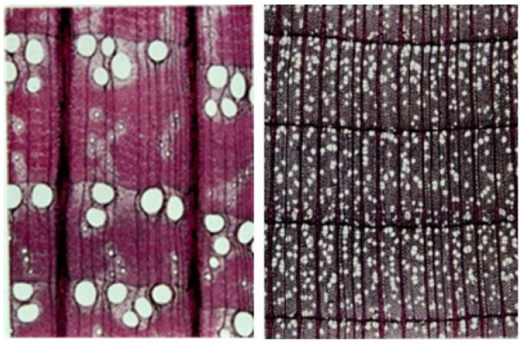

Fig. 8.18 *A) Ring Porous Wood in Red Oak (Quercus Rubra)*
B) Diffuse Porous Wood in Tulip Tree (Liriodendron Tulipifera)

Ring porous wood is relatively common in plants grown in arid habitats. It is considered to be more advanced than diffuse porous wood when compared phylogenetically Length of vessels in ring porous wood is longer than diffuse porous wood. In ring porous wood, the transport of water is restricted only to the outermost ring and flow is ten times more than the diffuse porous wood. The development of early ring porous wood is rapid and sudden, while that in diffuse porous wood is slow. In addition to the above two major patterns, there are some other patterns of vessel distribution:

- **Tangential Clusters**: When vessels tend to form tangentially aligned groups which may be either curved or arched for example, *Ulmus wallichiana*
- **Exclusively Solitary**: When vessels occur singly without any association with other pores for example, *Dipterocarpus, Xanthophyllum*
- **Long Radial Multiples**: When the vessels are arranged to form long radial rows for example, *Chloroxylon*
- **Oblique Groups**: When the vessels are arranged in long or short radially oblique groups to form the oblique pattern for example, *Quercus*
- **Flamelike**: When the vessels are arranged in small triangular patches which resemble with the flame of a candle. It is an uncommon feature for example, *Rhamnus.*

Early and Late Wood

In woody plants of temperate regions, the cambium shows marked variations in its activity in different season. There is an annual alteration of growing and quiescent seasons. The seasonal increments in the form of concentric rings are referred as growth rings or annual rings. Each growth ring denotes the growth of a single season but under certain environmental conditions more than one growth ring can be formed in one season. Each growth ring can be distinguished into spring and autumn wood on the basis of differences in shape, structure and distribution of homologous elements in the two regions. In the spring wood, the vessels are much wider and relatively thin walled than in the autumn wood. These differences in wood structure is to meet the varied requirements of the plant in spring and winter season. In the spring season, cambial activity is increased due to the various reasons such as longer duration of sunshine accompanied with the increase in temperature, maximum vegetative activity and more hormonal supply due to newly formed young leaves.

Cells of the cambium divide rapidly and, therefore, large amount of xylem tissue is produced. The vessels are comparatively broader, thin walled, lighter in colour and exhibits low density. The wood formed during the spring and summer is known as **spring wood** or **early wood**. In autumn, temperature is less, low relative humidity and shorter duration of sun which slows down the cambial activity and therefore lesser amount of xylem tissue is produced. Xylem elements are comparatively smaller in diameter, comparatively thick walled, darker in colour and has higher density. The wood formed during the autumn and winter is **late wood** or **autumn wood**. One light and one dark coloured zone comprise one year's growth and this is known as annual ring or growth ring. An annual ring consists of two parts~ inner layer or early wood and outer layer or late wood. Since each annual ring correspond to the growth of wood of one year, one can estimate the age of tree by counting the growth rings (Refer Figures 8.19 and 8.20).

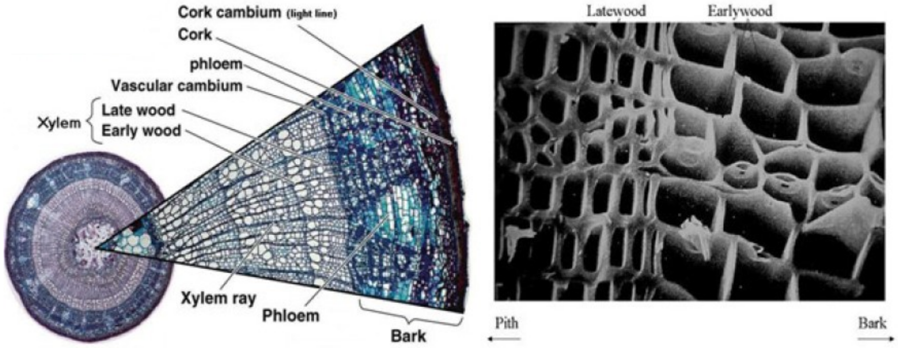

Fig. 8.19 *T.S. of Stem; A) Showing Secondary Growth and Variation in Early Wood and Latewood; B) Micrograph Showing Difference in Early Wood and Late Wood*

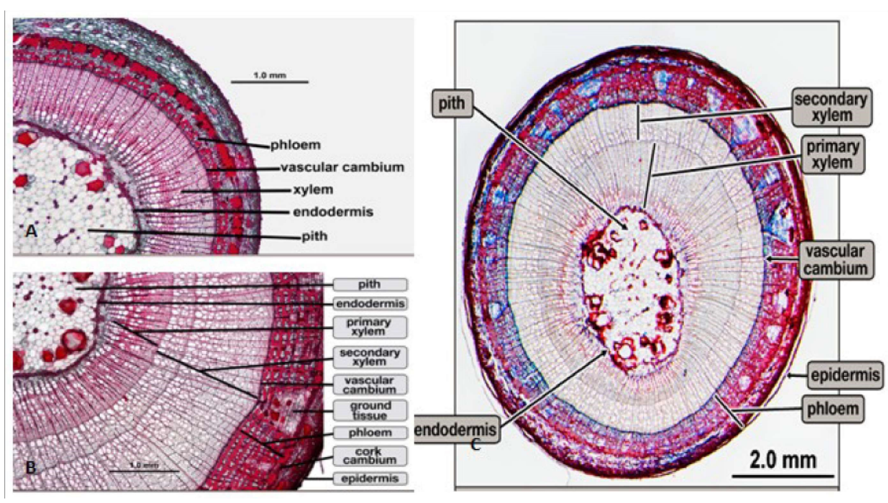

Fig. 8.20 *Comparison of Tilia Stem for Consecutive Three Years*

Identification of Wood

We can understand the degree of warmth and beauty that wood brings to our everyday décor by understanding the unique characteristics of wood and its source. Each furniture made of wood can be a unique piece due to particular grain pattern. Each grain pattern is a unique in design and texture. Even the structures which seem to be a defect, like a knot or other natural blemishes, can add more beauty and character to any given piece of furniture.

The classification of wood has historically always been either hard wood (any leaf bearing tree) or soft wood (any cone bearing tree). These terms can be confusing since some leaf bearing trees can have very soft wood and some coniferous trees can have very hard wood. There are two basic wood grades. The **select lumber** is of excellent quality is used when appearance and finishing are important, while **common lumber** that has defects is used for construction and general-purpose projects. The grades of the select lumber are:

- B- Better grade, which has minute or no blemishes;
- C- Select grade which has some minor defects such as small knots;
- D- select grade that has larger imperfections, which can be concealed by paint.

The grades of common lumber are:

- No. 1 grade containing tight knots and few blemishes.
- No. 2 grade that has more and larger knots and blemishes.
- No. 3 grade that has loose knots, knotholes, and other flaws.
- No. 4 grade that is low quality and
- No. 5 grade where the appearance is not important.

Identification of Hardwood

Oak: Oak is the most widely used hardwood. There are more than 600 extant species of oak grown worldwide. The most common oak species can be separated into two basic varieties; white and red. The red variety is also known as black oak (a reference to its bark). Oak is a heavy, strong, light coloured hardwood. It is ring porous, since more and larger conductive vessels are laid down early in the summer, rather than later. Prominent rings and large pores give oak a course texture and prominent grain. Oak also has conspicuous medullary rays which is visible as flakes in quarter sawed oak lumber.

Maple: Out of 128 species of maple only a few commercially important species are grown like hard rock maple and sugar maple. Maple is so hard and resistant to shocks that it is often used for bowling alley floors. Its diffuse evenly sized pores give the wood a fine texture and even grain. Maple that has a curly grain is often used for violin backs (the pattern formed is known as fiddleback figure). Burls, leaf figure, and birds-eye figures found in maple are used extensively for veneers. The Birds eye figure in maple is said to be the result of stunted growth and is quite rare.

Mahogany: Mahogany, also known as Honduras mahogany is a tropical hardwood indigenous to South America, Central America and Africa. There are many different grades and species sold under this name, which vary widely in quality and price. Mahogany which comes from the Caribbean is thought to be the hardest, strongest and best quality. Logs from Africa, though highly figured, are of slightly lesser quality. Mahogany is strong, with a uniform pore structure and poorly defined annual rings. It has a reddish - brown color and may display stripe, ribbon, broken stripe, rope, ripple, mottle, fiddleback or blister figures. Mahogany is an excellent carving wood and finishes well.

Cherry: It is sometimes called fruitwood. The term fruitwood is also used to describe a light brown finish on other wood. A moderately hard, strong, closed grain, light to red-brown wood, cherry resists warping and checking. It is easy to carve and polish.

Walnut: Walnut is one of the most versatile and popular cabinet making wood. It grows in Europe, America and Asia. There are many different varieties. Walnut is strong, hard and durable, without being excessively heavy. It has excellent woodworking qualities, and takes finishes well. The wood is light to dark chocolate brown in color with a straight grain in the trunk. Wavy grain is present toward the roots, and walnut stumps are often dug out and used as a source of highly figured veneer. Large burls are common. Walnut solids and veneers show a wide range of figures, including strips, burls, mottles, crotches, curls and butts. European walnut is lighter in color and slightly finer in texture than American black walnut, but otherwise comparable.

Rosewood: Very hard and has a dark reddish brown color. It is fragrant and close grained. It is hard to work and takes high polish. Used in musical instruments, piano cases, tool handles, art projects, veneers and furniture.

Teak: True teak is indigenous to Southeast Asia, but similar wood species also grow in Africa. Teak is a yellow to dark brown hardwood which is extremely heavy, strong and durable (Refer Figure 8.21).

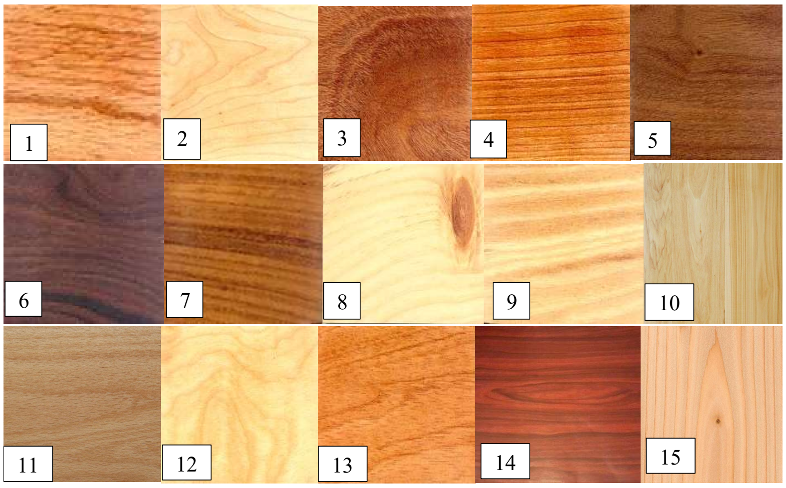

Fig. 8.21 *Identification of Hard Wood and Soft Wood*

The above Figure 8.21 shows the identification of Hard wood- 1. Oak. 2. Maple. 3. Mahogany. 4. Cherry. 5. Walnut. 6. Rosewood. 7. Teakwood. Soft wood- 8. Pine. 9. Ash. 10. Hickory. 11. Beech. 12. Birch. 13. Cedar. 14. Redwood. 15. Hemlock.

Identification of Softwood

Pine: Pine is a softwood which grows in most areas of the Northern Hemisphere. There are more than 100 species worldwide. Pine is a soft, white or pale-yellow wood which is light weight, straight grained and lacks figure. It resists shrinking and swelling. Knotty pine is often used for decorative effect.

Ash: There are about 58 species of ash which grow worldwide as evergreen temperate tree. Of these, the white ash is the largest and most commercially important. Ash is a hard, heavy, ring porous hardwood. It has a prominent grain that resembles oak, and a white to light brown colour. Ash can be differentiated from hickory (pecan) which it also resembles, by white dots in the darker summerwood which can be seen with the naked eye. Ash burls have a twisted, interwoven figure.

Hickory: There are 19 species of hickory, eight of which are commercially important. Hickory is one of the heaviest and hardest wood available. Pecan is a species of hickory sometimes used in furniture. It has a close grain without much figure.

Beech: about 15 species of beech wood are grown. Beech is a hard, strong, heavy wood with tiny pores and large conspicuous medullary rays, similar in appearance to maple. This relatively inexpensive wood has reddish brown heartwood and light sapwood.

Birch: There are many species of birch. The yellow birch is the most commercially important. European birch is fine grained, rare and expensive. Birch is a hard, heavy, close grained hardwood with a light brown or reddish coloured heartwood and cream or light sapwood. Birch is often rotary or flat sliced, yielding straight, curly or wavy grain patterns. It can be stained to resemble mahogany or walnut.

Cedar: cedar wood comes from different trees known as 'Cedars'. Cedar is a knotty softwood which has a red-brown colour with light streaks. Its aromatic and moth repellent qualities have made it a popular wood for lining drawers, chests and boxes.

Redwood: Indigenous to the Pacific United States, redwood trees grow to more than 300 feet tall and 2,500 years old. The best quality redwood comes from the heartwood which is resistant to deterioration due to sunlight, moisture and insects. It is used to craft outdoor furniture and decorative carvings. Redwood burls have a cluster of eye. They are rare and valuable.

Hemlock: Light in weight, uniformly textured. It machines well and has low resistance to decay and non-resinous.

Uses of Wood

After production, the lumber is generally treated with a preservative chemical to prevent attack by fungi and insects and is measured, graded, and piled to dry. Grading of lumber is usually visual and based on defects. The grading rules for softwood lumber differ from those for hardwood. Softwood grading is based on the kind, number, and size of defects; it does not take into account the further processing of the wood into final products. Most structural lumber is graded this way. Hardwood grading is based on the proportion of a board that is usable in smaller clear pieces (units) and requires only that one surface be clear. Such grading is made on the assumption that the lumber will be cut into smaller pieces for the manufacture of furniture or parts of other woodwork.

Veneer

Veneer is a thin sheet of wood of uniform thickness—commonly 0.5–1.0 mm (about 0.02–0.04 inch) and sometimes as much as 10 mm (about 0.4 inch). According to the method of production, it is classified as rotary-cut (cut on a lathe by rotating a log against a knife blade in a peeling operation), sliced (cut with a knife blade sheet by sheet from a log section, or flitch), or sawn (produced with a special tapered saw). More than 90 percent of all veneer is rotary-cut, but figured wood producing veneer for furniture and other decorative purposes are sliced. Sawn veneer is seldom produced, because it is a wasteful operation.

Logs of harder species of wood, intended for rotary-cut or sliced veneer, are first softened by submersion in hot water or treatment with steam. After production, the veneer is passed through specialized dryers, usually prefabricated metallic chambers where temperature, air circulation, and speed of transport are controlled. Rotary-cut veneer is "clipped," either before drying or afterward (when the continuous sheet goes directly to a dryer), by a guillotine-type knife to remove defects and produce individual sheets of acceptable size for the intended use. In some modern factories all operations, from handling the logs (bolts) to cutting, clipping, and drying, are automated by use of computers.

Veneers are used primarily for plywood and furniture, but they are also used in toys, various containers, matches, battery separations, and other products. The yield of veneer can be less than 50 percent of the original roundwood volume, but veneer sheets, especially decorative ones, are much more valuable than lumber.

Plywood

Plywood is a panel product manufactured by gluing one or more veneers to both sides of a central veneer layer or a lumber-strip core. Most plywood is all-veneer; lumber-core plywood is produced only in small quantities. Lumber cores are made by the lateral gluing of strips of wood. In both plywood products, the species, thickness, and grain direction of each layer are matched with those of its counterpart on the other side of the central layer. Consequently, the total number of layers is usually odd (three, five, or more), the exception being when the central veneer layer consists of two sheets glued together with their grains parallel. After the glue is spread, the panels are assembled and brought for pressing, usually in large, multistoried hot presses, where loading is automatic. Adhesives are thermosetting synthetic resins—phenol-formaldehyde for exterior-use plywood and ureaformaldehyde for interior-use plywood. Phenol-formaldehyde resin can produce joints more durable than the natural wood itself—highly resistant to weather, microorganisms, cold water, hot water, boiling water, seawater (marine plywood), steam, and dry heat. After pressing, the panels are stacked to cool and then are sanded, graded, and stored. Plywood ranges in thickness from 3 mm (about 0.12 inch) for all-veneer to 30 mm (1.2 inches) for lumber-core (Refer Figure 8.22).

Fig. 8.22 *Types of Plywood*

Plywood has many advantages over natural wood; among them are dimensional stability (the primary advantage), uniformity of strength, resistance to splitting, panel form, and decorative value. These characteristics make it adaptable to various uses. Plywood (and the panel products particleboard and fibreboard) serve in building construction, including walls, floors, roofs, and doors; exterior siding and interior finishing (for example,, wall paneling); furniture; shelving; shipbuilding; automobile manufacture; refrigeration cars; toys; concrete formwork; and many other applications. Special types combine decorative value with thermal- and sound-insulating properties.

In addition to being made into flat panels, plywood is manufactured in curved form (molded plywood), which is used for boats, furniture, and other products. Molded plywood is made by bending and gluing veneer sheets in one operation; the process employs curved forms in a press or fluid pressure applied with a flexible bag or blanket of impermeable material.

Some panels of special construction are overlaid with aluminum or reinforced plastics; others are made with hollow cores (parallel or crossed wooden strips, planer shavings, undulating veneer, honeycombed paperboard, or foamed plastic) or cores of particleboard or fibreboard. Many of these products are not plywood by definition, because they lack the characteristic crossing of wood grain in alternate layers.

Laminated Wood

Laminated wood is usually built by the parallel gluing of lumber boards in a variety of sizes and shapes according to intended use. The main products are load-carrying members, such as beams and arches. Parallel-glued veneers are sometimes used to produce specialized items (for example, furniture, sporting goods, and novelties).

Laminated wood possesses several advantages over solid wood. It can be used to fabricate large members that are impossible to make from solid wood. The individual boards used in laminated wood, because of their relative thinness, can be properly dried without checking (cracking), and defects, such as knots, can be removed. Structures can be designed with laminated wood on the basis of required strength, and wood of low grade can be positioned accordingly. In addition, because laminated wood is glued, wood of small dimensions can be used, thus reducing waste.

Particleboard

Particleboard, another panel product, is manufactured of particles of wood glued together. Particles are flakes or flakelike forms such as wafers and strands, planer shavings, slivers (or splinters), and fines produced from wood by cutting, breaking, or friction. Sources of particles include residues from sawmills (including sawdust) and other wood-using industries, small-diameter roundwood, defective logs, and harvesting residues. Bark is tolerated in limited amounts, and debarking is not necessary if the bark is thin and the particles are placed in the interior of the panel. Particle production or delivery to the factory is followed by screening, drying, classification of particles, mixing with resin adhesive and such additives as water repellents and preservatives, board formation (either in batches or in a continuous process), and pressing (Refer Figure 8.23).

Fig. 8.23 *Three Types of Particleboard (Left To Right): Single-Layer Particleboard, Waferboard, and Oriented Strand Board (OSB)*

Particleboard is made in several forms—single-layer, in which particle size is practically homogeneous throughout; three-layer, in which particle size is different in core and surface layers; and graded, in which there is a gradual, symmetrical reduction of particle size from the centre of a board to its surface layers. Particle grain is usually parallel to the surfaces, and panels are produced as separate boards, as in plywood manufacture. Perpendicular arrangement of particle grain exists only in so-called extruded boards, made from a continuous supply of particles and simultaneous pressing; the continuous product is sectioned to desired lengths as it exits a special press. Variation in such characteristics as particle morphology and arrangement, method of production, board thickness (2–40 mm [about 0.08–1.6 inches]), presence of perforations, and type and amount of adhesive allow the production of particleboards with different properties. They are classified as low-density (used for insulation), medium-density, and high-density. Low- and high-density boards are rare.

Particleboard is made for interior use (for example, for furniture, panelling, and doors) or for structural purposes (to support loads). Interior-type boards are usually overlaid with veneer or plastic laminate (such as melamine). Two relatively new products, waferboard and **Oriented Strand Board** (**OSB**), belong to the structural type. Waferboard is made with large, nearly square flakes, whereas OSB is a three-layer product in which the particles (strands) of surface layers are parallel to the direction of panel production and those of the middle layer are crosswise. Both products are used as non-veneered panels.

Strands are also employed in making certain structural, lumber-type products—Parallel Structural Lumber (PSL), Laminated Strand Lumber (LSL), and Oriented Strand Lumber (OSL). PSL, or paralam, is produced from oriented long strands of veneer, LSL from shorter strands, and OSL from strands similar to those in OSB. Another structural product, made of thin lumber and veneer and called Lumber-Veneer-Lumber (LVL), is used to produce a variety of I-beam products in combination with OSB.

In addition to being produced in its flat-board form, particleboard is sometimes moulded under high pressure and temperature to various shapes. Some forms of particleboard are consolidated with mineral binders, such as cement or gypsum, rather than synthetic resins; the wood in this product is usually in the form of excelsior (long, thin ribbons), although particles also can be used.

Fibreboard

The panel product fibreboard is made of wood fibres. In the pulp, paper, and fibreboard industry fibre refers to all cells of wood and is not limited to the specific cell type found in hardwood. A resin adhesive is not always used in fibreboard manufacture; in some cases, the boards are held together by physical forces, like hydrogen bonding, the flow of the natural lignin present among the fibres or interweaving of the fibres. As in the case of particleboard, residues and wood of low quality can be used, and bark is usually tolerated (Refer Figure 8.24).

Fig. 8.24 *Two Common Types of Compressed Fibreboard: Hardboard (Left) and Medium-Density Fibreboard (MDF, Right)*

Production of fibreboard involves reduction of the wood to particles, pulping, sheet (mat) formation, pressing, and finishing treatment. Pulping is mechanical; the main method is the thermomechanical process, in which wood particles are steamed and then reduced to fibres by the action of special mills. Some factories use a so-called explosion (Masonite) process, in which steamed chips are transformed into fibres by the application and sudden release of pressure. Before sheet formation, the pulp is blended with certain materials to improve water resistance, strength, and other properties. Either of two basic processes, dry or wet, is employed in the formation of the fibre mat. In dry (or air) forming, fibres are transported by air, and a synthetic resin is added. In wet forming, the fibres are carried in a water suspension, and a resin adhesive is not used. Because dry forming consumes no water and is less polluting, it is preferred over the wet process. Pressing is considered either wet or dry depending on the moisture content of the fibre mat. The properties of wet-pressed boards are improved by tempering treatments (exposure to heat or application of drying oils). The appearance of fibreboard can be enhanced by overlays or patterns of perforations, tiles, simulated leather, and other designs.

There are two types of fibreboard- **insulation** and **compressed** (represented mainly by hardboard); the distinction is based on density and the method of production. Insulation board is used in construction as insulation and cushioning; hardboard has a wide variety of uses, including furniture, house siding, wall panelling, and concrete forms. A relatively new compressed product is **Medium-Sensity Fibreboard** (MDF). MDF is manufactured in a range of thicknesses (6–40 mm), usually by the dry process, and it is less dense than hardboard. It can be machined as solid wood and has many uses, including furniture, panelling, and siding.

Pulp and Paper

Wood is the main source of pulp and paper. Preliminary production steps are debarking and chipping. Pulping processes are of three principal types: mechanical, or grinding; chemical, or cooking with added chemicals; and semi-chemical, or a combination of heat or chemical pre-treatment with subsequent mechanical reduction to fibres. The yield of pulp ranges from about 40 percent by chemical methods to 95 percent by mechanical ones. Chemical processes are based on either acids (i.e., sulfite pulping) or alkalies (alkaline pulping, including soda and sulfate processes). The pulp so produced is washed, screened, thickened by the removal of most of the water, and bleached. Paper manufacture involves beating or refining (defibring) the pulp, sizing and filling or loading (introducing various additives) and running the pulp into the proper machine to make paper.

Check Your Progress

1. What are the main functions of wood?
2. What is axially oriented elements in dicotyledons?
3. Write a note on tracheary elements.
4. What are vasicentric tracheids?
5. What are fibre tracheids?
6. What are living fibers?

8.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Wood evolved over the progression of millions of years to serve three main functions in plants:
    - Conduction of water from the roots to the leaves.
    - Mechanical support of the plant body.
    - Storage and synthesis of biochemicals.
2. The secondary xylem of dicot is more complex than gymnosperms. Axial system of dicot comprises of tracheary elements, vessels, libriform fibres, fibre tracheids and wood parenchyma.
3. Tracheids and vessels together constitute tracheary elements. Vessels are the major water conducting elements in the wood of dicots, though tracheids also help in the conduction of water. Presence of vessels is considered to be an advanced feature in angiosperms with the exception of some primitive families such as *Winteraceae* and *Trochodendraceae*. Vessels are characterized by the presence of perforation plate at their end walls. With the help of these perforation plates, vessel members are joined from one another to form a tube-like series of cells (syncytes), through which cell sap moves from one vessel to another.
4. Vasicentric tracheids are shorter than other tracheids, as during differentiation they divide through transverse or oblique division. These are present around the periphery of wider vessels and are in contact with other parenchyma cells with numerous pits. Vasicentric tracheids function as armour for vessel wall, damping shocks or vibrations that could break adhesive bonds between the sap solution and that wall.
5. Fibre tracheids are considered to be the intermediate between tracheids and fibres. They are longer than tracheids and vessels, as their tips undergo appreciable growth during differentiation. They are characterized by the presence of relatively thin walls and bordered pits and therefore helps in the mechanical support.

6. Living fibres are septate, have protoplast, contain starch grains and therefore they cannot transport water through apoplasm. Their major function is to provide mechanical support. In *Tamarix aphylla*, these fibres live for about 20 years as long as xylem parenchyma.

8.4 SUMMARY

- Wood is a complex biological structure, made up of many cell types having different chemical compositions. Wood is formed to meet the needs of the living tree.
- Wood evolved over the progression of millions of years to serve three main functions in plants: Conduction of water from the roots to the leaves, Mechanical support of the plant body, Storage and synthesis of biochemicals.
- A tree has two main spheres, the shoot and the roots. Roots are the underground structures responsible for water and mineral nutrient uptake, mechanical anchoring of the shoot, and the storage of biochemicals.
- The shoot is made up of the trunk, branches, and leaves. The trunk is composed of various materials present in concentric bands as visible in the trunk of a cutdown tree.
- Inner bark is the tissue through which sugars produced by photosynthesis (photosynthate) are translocated within the tree.
- The vascular cambium is the layer between the bark and the wood that produces both these tissues each year.
- The sapwood is the active ‘living’ wood that conducts the water (or sap) from the roots to the leaves.
- The pith at the centre of the trunk is the residue of early growth, before wood was formed.
- Vascular cambium produces secondary xylem towards the center of the stem and root.
- The secondary xylem forms bulk of vascular tissue in woody plants. In woody plants (gymnosperms and dicotyledons) secondary xylem is more persistent than secondary phloem.
- In gymnosperms, axially oriented derivatives of cambium consist of tracheids and parenchyma strands. Epithelial cells of axial resin ducts may also be present.
- In gymnosperms, tracheid provides mechanical support to the plant and helps in transportation of water.
- Pits are usually present on the radial walls, but they have also been observed on the tangential walls of the late wood.
- The primary cell wall consists of some depressions which appear as beaded structures under electron microscope. These beaded structures are known as primary pit fields.

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- In addition to these primary pit fields, the secondary walls are also provided with such depressions or cavities known as pits.
- Pits are the regions through which two adjacent cells maintain their cytoplasmic continuity
- In Gymnosperms (*Ginkgo*, Gnetales and Coniferales), pit membrane of bordered pit-pair gets thickened in center and this thickened portion is known as torus.
- If the torus takes place the lateral position, specifically present against one of the pit apertures, it completely restricts the movement of water and known as aspirated pits.
- The radially oriented parenchymatous cell of wood consists of xylem rays. In most of the gymnosperms, the rays are uniseriate (one cell wide), except for those containing resin ducts.
- Ray parenchyma cells contain living protoplast. Ray tracheids are characterized by the absence of protoplast, presence of bordered pits and lignified secondary walls.
- A variety of contents of economic importance, such as oil, resins, tannins, gums and mucilage are secreted by these cells.
- Axial system of dicot comprises of tracheary elements, vessels, libriform fibres, fibre tracheids and wood parenchyma.
- The two major types of xylem fibres present in the wood of dicots living fibres and libriform fibres. Both kinds of fibres originate from the cambial cell derivatives.
- Libriform fibres fibres are very long, characterized by the presence of thick walls and simple pits. They do not have living protoplast. Libriform fibres resemble phloem fibres.
- In apotracheal parenchyma, distribution of parenchyma is independent of vessels.
- Tyloses are balloon like enlargement of parts of cell wall which projects into the adjacent cell lumina through pit cavities.
- Kino veins differ from gum ducts in having polyphenols. Kino veins are formed by lysigenous breakdown of bands of parenchyma formed by the cambium.
- Xylem rays or wood rays are present in the radial system of secondary xylem. These are the sheets of parenchymatous cells which are arranged at right angle to longitudinal axis of plant.
- The number of xylem rays in a trunk increases with the increase in girth. As the stem grows older, ray becomes distant due to the expansion of cambium as the axis also increases in its circumference.
- Heartwood of some plants contains pigments of commercial importance such as Hematoxylin (*Hematoxylon campechianum*), Brasilin (*Caesalpinia sappan*) and Santalin (*Pterocarpus santalinus*).

- The wood of dicotyledons has vessels in the xylem due to which it is known as porous wood and gymnosperm wood lacks vessels and therefore known as nonporous wood.
- The seasonal increments in the form of concentric rings are referred as growth rings or annual rings.
- In the spring wood, the vessels are much wider and relatively thin walled than in the autumn wood.
- In the spring season, cambial activity is increased due to the various reasons such as longer duration of sunshine accompanied with the increase in temperature, maximum vegetative activity and more hormonal supply due to newly formed young leaves.
- The wood formed during the spring and summer is known as spring wood or early wood.
- Mahogany, also known as *Honduras mahogany* is a tropical hardwood indigenous to South America, Central America and Africa. There are many different grades and species sold under this name, which vary widely in quality and price.
- Cherry is sometimes called fruitwood. The term fruitwood is also used to describe a light brown finish on other wood. A moderately hard, strong, closed grain, light to red-brown wood, cherry resists warping and checking. It is easy to carve and polish.

8.5 KEY WORDS

- **Wood:** Wood is a complex biological structure, made up of many cell types having different chemical compositions.
- **Primary pit fields**: The primary cell wall consists of some depressions which appear as beaded structures under electron microscope. These beaded structures are known as primary pit fields.
- **Pits**: Pits are the regions through which two adjacent cells maintain their cytoplasmic continuity.
- **Pit-pair**: The adjacent walls of two pits are known as pit-pair**.**
- **Pit cavity**: The cavity formed by the breaking the secondary wall is called as pit cavity.
- **Pit membrane**: The plasma membrane separating the two pit cavities of pit-pair is known as closing membrane or pit membrane.
- **Pit aperture**: The opening through which the pit opens into the lumen of the cell is known as pit aperture.

8.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

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Short Answer Questions

1. What is secondary xylem?
2. Write short note on axially oriented elements.
3. Give short note on radially oriented elements.
4. Define resin ducts.
5. What are gum ducts?
6. What is tension wood?
7. Distinguish between veneer and plywood.

Long Answer Questions

1. Briefly discuss the structure of wood.
2. Explain secondary xylem in gymnospermms.
3. Discuss about secondary xylem in angiosperms.
4. Give in detail the classification of wood system giving examples.
5. Explain how identification of wood can be done.
6. Elaborate a note on uses of wood.

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UNIT 9 PHYSICAL, CHEMICAL AND MECHANICAL PROPERTIES OF WOOD

NOTES

Structure

9.0 INTRODUCTION

Wood is a porous and fibrous structural tissue found in the stems and roots of trees and other woody plants. It is an organic material, a natural composite of cellulose fibers that are strong in tension and embedded in a matrix of lignin that resists compression. Wood is sometimes defined as only the secondary xylem in the stems of trees, or it is defined more broadly to include the same type of tissue elsewhere such as in the roots of trees or shrubs. In a living tree it performs a support function, enabling woody plants to grow large or to stand up by themselves. It also conveys water and nutrients between the leaves, other growing tissues, and the roots. Wood may also refer to other plant materials with comparable properties, and to material engineered from wood, or wood chips or fiber.

Wood has been used for thousands of years for fuel, as a construction material, for making tools and weapons, furniture and paper. More recently it emerged as a feedstock for the production of purified cellulose and its derivatives, such as cellophane and cellulose acetate. As of 2005, the growing stock of forests worldwide was about 434 billion cubic meters, 47% of which was commercial. As an abundant, carbon-neutral renewable resource, woody materials have been of intense interest as a source of renewable energy. In 1991 approximately 3.5 billion cubic meters of wood were harvested. Dominant uses were for furniture and building construction.

The main physical properties of wood include: color, luster, texture, macro-structure, odor, moisture, shrinkage, internal stresses, swelling, cracking, warping, density, sound - electro - thermal conductivity. Ñolor, shine, texture and macrostructure determine the appearance of wood. Macrostructure is characterized by the width of annual rings - the number of annual rings per 1 cm of segment, measured in the radial direction in cross section. Softwood have good physical - mechanical features when the number of layers varies from 3 to 25. The percentage of late wood in timber is determined by softwood samples. The higher late wood content in timber, the more the density and better mechanical wood characteristics.

Essential oils, resins, tannins and other substances, founded in certain tree species, give them a smell. Humidity - is the ratio of moisture mass in a given wood volume to the weight of absolutely dry wood, expressed as a percentage. Moisture, soaking the cell membrane, named the bound or hygroscopic, and moisture that fills the cavity of the cells and intercellular spaces, named free or capillary.

In this unit, you will study about physical, chemical and mechanical properties of wood in detail.

9.1 OBJECTIVES

After going through this unit, you will be able to:

- Discuss about physical properties of wood
- Analyse chemical properties of wood
- Explain mechanical properties of wood

9.2 WOOD: PHYSICAL, CHEMICAL AND MECHANICAL PROPERTIES

Physical properties of wood refer to density, moisture and shrinkage relations that affect its use. Chemical properties of wood are governed by the chemical composition of the cell walls like cellulose, pectin and lignin, and secondary metabolites stored in secretory structures including resin ducts, cavities and tylosis. Mechanical properties refer to the strength related characteristics of wood.

9.2.1 Physical Properties of Wood

Wood is one of the most versatile and widely used materials in the world. It can be used in anything from wood carving and creating small wooden items, such as chairs and rocking horses, to building timber structures and sheds.

It also has a lot of scientific properties associated with it, and every type of wood that is available can exhibit similar, and also different, properties. As such, it is important to understand how different types of wood can be used, so you can make sure that you don’t use the wrong type of wood in your project.

The main physical properties of wood include: colour, luster, texture, macro-structure, odour, moisture, shrinkage, internal stresses, swelling, cracking, warping, density, sound - electro - thermal conductivity. Colour, shine, texture and macrostructure determine the appearance of wood.

Wood of different breeds have different colour - from white - aspen, spruce to black - ebony. Tannins, resin and pigments, founded in cells cavities, make wood more colourful.

Timber gloss is the ability to reflect light beam pointedly. It depends on wood density, size and location of medullary rays, which reflect light rays pointedly, thereby creating the shine on the radial aspect. Beech wood, maple, oak, elm have the most characteristic luster. Aspen, poplar and linden has a matte surface due to a very narrow medullar rays, and thin cells walls. Wood gloss surface is enhanced and preserved for long periods of time by creating transparent protective - decorative coatings.

Texture is a peculiar pattern formed by the medullary rays, fibers, and yearly layers of wood in different contexts. Texture saturation is determined by anatomical features of arboreous breeds structure and the section direction, and by the colour of early and late wood, rippling and by mixed up fibre arrangement.

Density: Wood is a porous material made up of cells of several types. Depending on the nature of these cells, some woods have variation in solid wood substance per unit volume. The amount of wood substance for a given volume determines density. Woods with more weight for a given volume have a higher density than woods with less weight. Units for density are typically expressed as grams per cubic centimetre (g cm^{-3}) or kilograms per cubic meter (kg m^{-3}). Both weight and volume of wood are affected by the amount of moisture it contains. Therefore, moisture conditions must be stated while specifying density. For example, the density of air-dried balsam fir is 430. This means it weighs 430 kg. per m^3, at 12 percent moisture content - a standard for strength testing and density measurement. On the other hand, the density of red spruce is 450; and sugar maple, is 740, again both in the air-dry condition. Density is an excellent indicator of wood strength- the higher the density the stronger the wood. However, a wood with a density of 600 may not be twice as strong as one with a density of 300.

Wood structure determines the wood specific gravity- softwoods in which latewood is abundant in proportion to earlywood have higher specific gravity, for example 0.59 specific gravity in longleaf pine, *Pinus palustris*. The reverse is true when there is more earlywood than latewood, for example 0.35 specific gravity in eastern white pine, *Pinus strobus*. To say it another way, specific gravity increases as the proportion of cells with thick cell walls increases. In hardwoods, specific gravity is dependent not only on fiber wall thickness, but also on the amount of void space occupied by vessels and parenchyma. In balsa, vessels are large (typically >250 ìm in tangential diameter) and there is an abundance of axial and ray parenchyma. Fibers that are present are thin walled, and the specific gravity may be <0.20. In dense woods, the fibres are thick walled, lumina are virtually absent, and fibres are abundant in relation to vessels and parenchyma. Some tropical hardwoods have specific gravities >1.0.

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Moisture Content: Wood has a porous structure due to presence of tracheary elements. Consequently, it can absorb water as a liquid, if in contact with it as well as vapour from the surrounding atmosphere. This property of wood is known as **hygroscopicity**. Because of its hygroscopicity, wood, either as a part of the living tree or as a material, always contains moisture. Moisture affects all wood properties, but only moisture contained in cell walls is important, as moisture in the cell cavities hardly adds weight. The amount of moisture held in cell walls varies from about 20 to 40 percent, but for practical purposes it is taken to be 30 percent and is expressed as percentages of the oven-dry weight of wood. The theoretical point at which cell walls are completely saturated and cell cavities are empty is known as the **fibre saturation point**. Beyond this point, moisture goes into the cavities, and, when they are entirely filled, the maximum moisture content that wood can hold is attained. This maximum can be very high and depends mainly on density. For example, a very light wood, such as balsa, can hold as much as 800 percent moisture, pine 250 percent, and beech 120 percent.

The moisture content of the wood of living trees varies from about 30 to 300 percent. It depends on the species, position of the wood in the tree, and season of the year. When green wood is exposed to the atmosphere, its moisture content gradually decreases. Moisture in the cell cavities is lost first. Gradually, moisture content falls, to various degree in different plant species. For instance, it drops to levels ranging from about 6 to 25 percent, average 12 to 15 percent for temperate-zone localities and under shelter. Local conditions of air temperature and relative humidity control the final moisture level. Species and dimensions of wood have no practical impact on the final moisture level, although refractory species and wood of larger dimensions require more time to reach it. However, because of hygroscopicity, the moisture content of air-dry wood does not remain unchanged, even when the wood is kept under shelter. In contrast, it is subject to continuous change, within certain limits, as a result of changing air temperature and relative humidity.

The moisture content of a sample of wood is calculated on the basis of its current and oven-dry weight. It can also be determined directly with portable electric moisture meters, which measure the change of electrical properties of wood as a function of changing moisture content. Hygroscopicity is of primary importance because moisture in wood affects all wood properties. For example, moisture content can increase weight 100 percent or more, with consequent effects on transportation costs. Variation in moisture content causes wood to shrink or swell, altering its dimensions. Resistance to decay and insects is greatly affected. The working, gluing, and finishing of wood and its mechanical, thermal, and acoustic properties are all influenced by moisture content. Also affected are processing operations, such as drying, preservative treatment, and pulping.

Shrinkage and Swelling: Wood undergoes dimensional changes when its moisture varies below the fibre saturation point. Loss of moisture results in shrinkage while increase of moisture causes swelling. It is characteristic that these dimensional changes are **anisotropic**—different in axial, radial, and tangential directions. Average values for shrinkage are roughly 0.4 percent for axial, 4 percent for radial and 8 percent for tangential directions. Shrinkage in volume averages 12 percent, but large variations are exhibited among species. These values refer to changes from green to oven-dry condition and are expressed in percentage of green dimensions. The differential shrinkage and swelling in different growth directions is attributed mainly to cell wall structure. The difference between axial and the two lateral (radial and tangential) directions can be explained on the basis of respective orientation of cellulose microfibrils in the layers of the secondary cell wall, but the reasons for the differences between radial and tangential directions are not well understood.

Various kinds of **distortions** occur in sawn wood due to shrinkage and swelling like warping, at right, may result from differential shrinkage and swelling or from differences in the distribution of moisture content in the wood. In general, the factors that affect shrinkage and swelling are moisture content, density, content of extractives, mechanical stresses, and abnormalities in wood structure. The amount of shrinkage or swelling that occurs is approximately proportional to the change in moisture content. The higher the density of wood, the greater is its shrinkage and swelling, because denser (heavier) woods contain more moisture in their cell walls. Dimensional changes in wood caused by shrinkage and swelling can result in opening or tightening of joints, change of cross-sectional shape, warping, checking (formation of cracks), case-hardening (release of stresses in resawing or other machining, with consequent warping), honeycombing (internal checking), and collapse (distortion of cells, causing a corrugated appearance of the surface of lumber). Thus, the fact that wood shrinks, and swells constitutes a great obstacle to its utilization.

9.2.2 Chemical Properties of Wood

Wood is a complex, heterogenous aggregate of cell wall fibres composed primarily of cellulose and hemicellulose. These fibres are joined by polymers of lignin to form rigid lignocellulosic matrix. Further, symbiont and enzyme degraded cellulosic polysaccharides provide the principal carbohydrate component in the diets of wood feeding termites. Also, lignin and other chemical extractives, such as alkaloids, phenols, resins, terpenes, essential oils, quinones, silica, etc. play a dynamic role in preventing the degradation of wood by termites. They act as toxicants, feeding deterrents, repellents, or as non-preferred substrates. Chemical constituents, such as cellulose, lignin, and total phenolic content, of wood influenced the rate of degradation. It was found that the higher the cellulose content, the higher the susceptibility to termite attacks. However, the higher the lignin and total phenolic content, the higher the resistance of wood species. Cellulose is one of the factors that drive termites towards wood species, as it is a primary food source for termites, which explains the significant positive correlation of cellulose content and wood degradation. Lignin acts as a physical barrier, which is unpalatable to termites.

Extractives and other phenolic compounds of wood also impart higher resistance to termite attack. Wood species with lower amounts of cellulose and higher amounts of lignin and total phenol were termite resistant, while the wood with higher amounts of cellulose and lower amounts of lignin and total phenol were susceptible to termite damage.

Wood consists mainly of organic substances- about 99% of the total mass. Although, elemental chemical composition of wood of different species is practically the same, absolutely dry wood on average contains 49% of carbon, 44% of oxygen, 6% of hydrogen, 0.1-0.3% of nitrogen. When wood is burnt, its inorganic part remained behind is known as **ash**. The composition of the ash includes calcium, potassium, sodium, magnesium and other elements. Th most dynamic chemical elements which form the basic organic substances of wood include cellulose, lignin and hemicelluloses.

Cellulose: Cellulose is a natural polymer, a polysaccharide with a long chain molecule. The basic unit of cellulose is glucose, The cellulose formula $(C_6H_{10}O_5)_n$, where **n** represents the degree of polymerization, generally 6000-14000 monomeric units. This is a very persistent substance, insoluble in water and ordinary organic solvents like alcohol, ether, etc. Rays of macromolecules of cellulose - the finest fibres are called **microfibrils**. They comprise the main component of primary and secondary cell wall of the plant cells. Microfibrils are oriented mainly along the long axis of the cell, cemented together by lignin, and interconnected by hemicelluloses and water.

Lignin: Lignin is a polymer of an aromatic polyphenol of complex structure, however, contains more carbon and less oxygen than cellulose. The process of **lignification** of the young cell wall is associated with lignin. It is chemically unstable, easily oxidized natural macromolecule. It reacts with chlorine and dissolves when heated in alkalis, aqueous solutions of sulfuric acid and its acid salts.

Hemicellulose: Hemicellulose is a group of polysaccharides, which includes pentose $(C_5H_8O_4)$ and hexoses $(C_6H_{10}O_5)$. Although, the hexo-form formula is identical to the cellulose formula. However, the degree of polymerization in all hemicelluloses is much smaller and amounts to 60-200 monosaccharide units. This indicates a shorter chain of molecules and a lower resistance of these substances compared to cellulose.

Degradation: Wood is subject to degradation by bacteria, fungi, insects, marine borers, and factors like-climatic, mechanical, chemical, and thermal factors. Degradation can affect wood of living trees, logs, or products, causing changes in appearance, structure, or chemical composition. These changes range from simple discoloration to alterations that render wood completely useless. It should be noted that wood can last for hundreds or thousands of years, as demonstrated, for example, by furniture and other wooden items found in excellent condition in the tombs of ancient Egyptian pharaohs. Wood is degraded or destroyed only under the action of external factors, not with the passage of time.

Bacteria are considered to be the cause of discolorations in the form of darker-coloured heartwood in living trees, a phenomenon called **wet-wood** in fir and **black heartwood** in hybrid poplars. The colour lightens on exposure to air, although the properties of the wood are not really affected. Bacteria also appear during prolonged storage of wood in water, including seawater, for instance in the case of old sunken ships. Acting in combination with physical and chemical factors related to submersion, they can cause considerable structural changes, leading to breakdown of the wood after exposure to air.

Fungi that attack wood are responsible for discoloration also known as **stain** or decay. **Blue stain** or **sap stain** of pines is the most common and serious consequence of attack by stain fungi. The sapwood becomes bluish or blackish, usually in wedge-shaped patches. Blue stain may appear very quickly in warm weather, sometimes within hours or days after the tree is felled or the green wood is sawed or otherwise processed. The degradation is mainly aesthetic with a large reduction in the market value of the wood, among properties only toughness appears to be affected.

Decay fungi are, by far, the most important cause of wood loss. Decay is not an innate property of wood, however; it takes place only if the conditions of exposure-namely, moisture, air, and temperature- are suitable for growth and activity of fungi. A moisture content below 20 percent inhibits growth of fungi, as do temperatures lower than 10°C and higher than 30°C. If wood is kept under water, it cannot be attacked by fungi, because of insufficient oxygen. Toxic substances contained in wood are a delaying factor and are the main reason for differences in resistance to decay among species, but no wood is immune.

Insects, like fungi, can attack the wood of living trees, logs, or products. Insects bore holes and tunnels, and some reduce the interior of wood to dust, leaving only a thin outer layer. Conditions of exposure are the same as for fungi—suitable temperature, moisture, and air. Infested wood can be rendered free of insects at temperatures of 50–60°C, by the introduction of insecticides, or by exposure to toxic gases. Marine borers attack wooden structures in seawater and cause severe damage.

Wood is also subject to degradation by changing climatic conditions, for instance, by rain and sunlight causing repeated wetting and drying; mechanical stresses like imposed on railroad ties; and exposure to chemicals acids and alkalies. Furthermore, wood is destroyed by fire. Large-dimension timbers (such as glued laminated beams) offer more resistance for a certain time, and fire-retardant treatments are also available.

9.2.3 Mechanical Properties of Wood

The mechanical, or **strength**, properties of wood are measures of its ability to resist applied forces that might tend to change its shape and size. Resistance to such forces depends on their magnitude and manner of application and to various

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characteristics of the wood such as moisture content and density. It is important to note that wood has drastically different strength properties parallel to the grain, i.e., in the axial direction, then it does across the grain- in the transverse direction.

The mechanical properties of wood include **strength in tension** and **compression** (as measured in axial and transverse directions), **shear**, **cleavage**, **hardness**, **static bending**, and **shock** (impact bending and toughness). Respective tests determine-

- Stresses per unit of loaded area (at the elastic limit and maximum load).
- The modulus of elasticity (a criterion of stiffness).
- The modulus of rupture (bending strength).
- Toughness.

Tests are normally conducted with small, clear specimens, usually 2 × 2 cm or 2 × 2 inches in cross section. Laboratory data are analyzed to produce working values of stresses, which are made available for use by engineers and architects in designing wooden structures. Tests are sometimes conducted with structural components of actual size. Individual cells (tracheids and fibres) also are subject to testing, since their strength relates to the strength of products—paper, for example.

Strength: Density is the best index of the strength of clear wood; higher density indicates greater strength. The strength of wood is also influenced by its moisture content when it fluctuates below the fibre saturation point. Generally, a decrease in moisture content is accompanied by an increase in most strength properties. Temperature and duration of loading also affect strength. In general, strength falls as temperature rises. Wood loaded permanently will support a smaller maximum load than that indicated by short-term laboratory tests. The most important strength-reducing factors are wood defects, such as knots, compression and tension wood, and grain deviations. Their adverse effect depends on the kind and extent of the defects, their position, and the manner in which the wood is loaded.

Defects constitute the basis for rules by which lumber and other wood products are visually graded. These rules set limits on sizes of defects and other wood characteristics that affect strength—for example, rate of growth, which is expressed as rings per centimetre or inch. Also available are non-destructive grading techniques based on vibration, sound transmission, and mechanics. The latter technique makes use of a correlation established between the modulus of rupture and the modulus of elasticity. This relationship allows the strength of a wooden member, for example a lumber board to be determined with fair accuracy simply by passing it through a machine that applies a bending force. The less the deflection, the higher the predicted strength. Use of such machines in industry is still limited, however, and the main method remains the visual inspection of wood by skilled graders. Grading leads to more efficient utilization of wood and is essential in order to achieve adequate standards of safety in wooden structures.

Check Your Progress

1. What does physical properties of wood refer to?
2. What governs the chemical properties of wood?
3. What does mechanical properties of wood refer to?
4. Give the main physical properties of wood.
5. What does wood structure determines?
6. What does degradation effect?
7. What is the major cause of decay of woods?

9.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Physical properties of wood refer to density, moisture and shrinkage relations that affect its use.
2. Chemical properties of wood are governed by the chemical composition of the cell walls like cellulose, pectin and lignin, and secondary metabolites stored in secretory structures including resin ducts, cavities and tylosis.
3. Mechanical properties refer to the strength related characteristics of wood.
4. The main physical properties of wood include: colour, luster, texture, macro-structure, odour, moisture, shrinkage, internal stresses, swelling, cracking, warping, density, sound - electro - thermal conductivity.
5. Wood structure determines the wood specific gravity- softwoods in which latewood is abundant in proportion to earlywood have higher specific gravity, for example 0.59 specific gravity in longleaf pine, *Pinus palustris.*
6. Degradation can affect wood of living trees, logs, or products, causing changes in appearance, structure, or chemical composition.
7. Decay fungi are, the most important cause of wood loss. Decay is not an innate property of wood, however; it takes place only if the conditions of exposure- namely, moisture, air, and temperature- are suitable for growth and activity of fungi.

9.4 SUMMARY

- Physical properties of wood refer to density, moisture and shrinkage relations that affect its use.
- Chemical properties of wood are governed by the chemical composition of the cell walls like cellulose, pectin and lignin, and secondary metabolites stored in secretory structures including resin ducts, cavities and tylosis.
- Mechanical properties refer to the strength related characteristics of wood.

NOTES

- Wood is one of the most versatile and widely used materials in the world. It can be used in anything from wood carving and creating small wooden items, such as chairs and rocking horses, to building timber structures and sheds.
- Wood also has a lot of scientific properties associated with it, and every type of wood that is available can exhibit similar, and also different, properties.
- The main physical properties of wood include: colour, luster, texture, macro-structure, odour, moisture, shrinkage, internal stresses, swelling, cracking, warping, density, sound - electro - thermal conductivity.
- Wood of different breeds have different colour - from white - aspen, spruce to black - ebony.
- Tannins, resin and pigments, founded in cells cavities, make wood more colourful.
- Timber gloss - is the ability to reflect light beam pointedly. It depends on wood density, size and location of medullary rays, which reflect light rays pointedly, thereby creating the shine on the radial aspect.
- Beech wood, maple, oak, elm have the most characteristic luster. Aspen, poplar and linden has a matte surface due to a very narrow medullar rays, and thin cells walls.
- Wood gloss surface is enhanced and preserved for long periods of time by creating transparent protective - decorative coatings.
- Texture is a peculiar pattern formed by the medullary rays, fibers, and yearly layers of wood in different contexts.
- Wood is a porous material made up of cells of several types. Depending on the nature of these cells, some woods have variation in solid wood substance per unit volume.
- Wood structure determines the wood specific gravity- softwoods in which latewood is abundant in proportion to earlywood have higher specific gravity, for example 0.59 specific gravity in longleaf pine, *Pinus palustris*.
- Wood has a porous structure due to presence of tracheary elements. Consequently, it can absorb water as a liquid, if in contact with it as well as vapour from the surrounding atmosphere. This property of wood is known as hygroscopicity.
- The amount of moisture held in cell walls varies from about 20 to 40 percent, but for practical purposes it is taken to be 30 percent and is expressed as percentages of the oven-dry weight of wood.
- The theoretical point at which cell walls are completely saturated and cell cavities are empty is known as the fibre saturation point. Beyond this point, moisture goes into the cavities, and, when they are entirely filled, the maximum moisture content that wood can hold is attained.
- Moisture in the cell cavities is lost first. Gradually, moisture content falls, to various degree in different plant species.
- The moisture content of a sample of wood is calculated on the basis of its current and oven-dry weight.

- Hygroscopicity is of primary importance because moisture in wood affects all wood properties.
- Variation in moisture content causes wood to shrink or swell, altering its dimensions.
- Cellulose is one of the factors that drive termites towards wood species, as it is a primary food source for termites, which explains the significant positive correlation of cellulose content and wood degradation. Lignin acts as a physical barrier, which is unpalatable to termites.
- When wood is burnt, its inorganic part remained behind is known as ash.
- Rays of macromolecules of cellulose - the finest fibres are called microfibrils. They comprise the main component of primary and secondary cell wall of the plant cells.
- Microfibrils are oriented mainly along the long axis of the cell, cemented together by lignin, and interconnected by hemicelluloses and water.
- Lignin is a polymer of an aromatic polyphenol of complex structure, however, contains more carbon and less oxygen than cellulose. The process of lignification of the young cell wall is associated with lignin.
- Wood is subject to degradation by bacteria, fungi, insects, marine borers, and factors like-climatic, mechanical, chemical, and thermal factors.
- Degradation can affect wood of living trees, logs, or products, causing changes in appearance, structure, or chemical composition.
- Wood is degraded or destroyed only under the action of external factors, not with the passage of time.
- Insects, like fungi, can attack the wood of living trees, logs, or products. Insects bore holes and tunnels, and some reduce the interior of wood to dust, leaving only a thin outer layer.
- Wood is also subject to degradation by changing climatic conditions, for instance, by rain and sunlight causing repeated wetting and drying; mechanical stresses like imposed on railroad ties; and exposure to chemicals acids and alkalies.
- The mechanical properties of wood include strength in tension and compression (as measured in axial and transverse directions), shear, cleavage, hardness, static bending, and shock (impact bending and toughness).
- Density is the best index of the strength of clear wood; higher density indicates greater strength. The strength of wood is also influenced by its moisture content when it fluctuates below the fibre saturation point.

9.5 KEY WORDS

- **Timber gloss**: Timber gloss is the ability to reflect light beam pointedly. It depends on wood density, size and location of medullary rays, which reflect light rays pointedly, thereby creating the shine on the radial aspect.

- **Texture**: Texture is a peculiar pattern formed by the medullary rays, fibers, and yearly layers of wood in different contexts.
- **Ash**: When wood is burnt, its inorganic part remained behind is known as ash.
- **Microfibrils**: Rays of macromolecules of cellulose - the finest fibres are called microfibrils.

9.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. What is density of wood.
2. Write about moisture content of wood.
3. Define cellulose.
4. What is lignin?
5. What is degradation and decay of fungi?

Long Answer Questions

1. Briefly discuss about the physical properties of wood.
2. Distinguish between shrinkage and swelling giving examples.
3. Discuss about chemical properties of wood.
4. Write a note on hemicellulose.
5. Give the mechanical properties of wood.

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UNIT 10 NATURAL DEFECTS, KNOTS AND WOOD TYPES

NOTES

Structure

10.0 INTRODUCTION

A defect is simply an abnormality or irregularity found in wood. There are many different types of defects arising from many different causes. For instance, there are natural and acquired defects caused by a broken limb or other injury, insect and fungal attack, or rapid tree growth. There are innate defects caused by the natural characteristic of wood to shrink or expand in response to water vapor in the air. And, there are artificial and mechanical defects caused by incorrect sawing or machining, improper drying, or improper handling and storage.

Defects may be responsible for reducing wood's economic value, lowering its strength, durability and usefulness, marring its appearance, and in some cases, causing its decay. During its lifetime, a tree is subjected to many natural forces that cause defects in the wood. Woodworkers are quite familiar with these defects – knots, splits, ugly dark streaks or stains, worm holes, even decay.

Reaction wood is the characteristic wood formed as part of the gravitropic response of trees and shrubs, and generally occurs in leaning stems including branches. In conifers, reaction wood is known as compression wood while in hardwoods it is known as tension wood. Reaction wood formed on the lower sides of branches and leaning trunks and characterized by darker color, glassy appearance, relatively wide and eccentric annual rings, shorter vascular elements, and excessive and uneven shrinkage — compare tension wood. Tension wood is a type of reaction wood in response to bending or leaning stem as a corrective growth process. Tension wood is formed by both natural and man-made processes. Most attractively, tension wood contains higher glucan content and undergoes higher enzymatic conversion to fermentable sugars.

NOTES

In this unit, you will study about natural defects, knots, reaction wood, compression wood, tension wood in detail.

10.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand what natural wood defects are
- Explain knots in wood
- Discuss about reaction wood
- Explain compression wood and tension wood

10.2 NATURAL WOOD DEFECTS

During its lifetime, a tree is subjected to many natural forces that cause defects in the wood. These defects include – knots, splits, ugly dark streaks or stains, worm holes, even decay. Some of the more common wood defects include:

Bark Pockets: These are formed when a small piece of the bark protrudes into the lumber. This area is generally considered defective.

Bird Pecks: These are caused by birds, especially woodpeckers, which peck on trees mainly to cause panic to the insects living in or under the bark and in the wood of the tree. This causes the insects to come out enabling the birds to eat them. Bird pecking can cause small injuries to the tree, resulting in grain changes that later show up as various forms or figure in the wood. Figure is the 'look' or appearance of a piece of wood.

Burls: Burls are a deformed growth formed when a tree receives a shock or injury in its young age. Due to its injury, the tree's growth is completely disturbed, and irregular projections appear on the body of the timber. Continued tree growth follows the contour of the original burl deformity, producing all manner of twists, swirls and knots in the wood fiber. Usually, this results in spectacular patterns in the wood that can be used to great effect in woodworking. Burl wood is normally darker than the rest of the tree and, in some cases, may be a significantly different color altogether.

Coarse Grain: When the tree grows rapidly, the annual rings are widened. It is known as coarse grain timber and possesses less strength.

Fungal Damage: Fungi generally damages timber or wood by discoloration and/ or decay. The resulting wood is generally weaker or of a different color than is typical for that species. The more common effects of fungal damage include:

- **Blue Stain**: Common in pine, maple, and many other woods, blue stain (also called '**sapstain**') is caused by a fungus that feeds on the sap. It does not live in live trees due to lack of oxygen. The bluish color (sometimes gray or dark gray) is the fungus itself. The color does not degrade the cellular structure and does not count against wood in the grading process.

- **Brown Rot**: A form of wood decay found only in softwoods that destroys the wood's cellulose, eventually causing cracks across the grain. Advanced brown rot tends to leave the wood more brown than normal. It is a precursor to dry rot.
- **Dry Rot**: After the wood infected with brown rot dries out, the cell walls of the remaining wood turns into dry powder when crushed. This is called dry rot.
- **Heart Rot**: This is formed when a branch has come out of the tree. The heart wood is exposed to an attack of atmospheric agents. Ultimately, the tree becomes weak and it gives a hollow sound when struck with a hammer.
- **Wet Rot**: Some kinds of fungi cause chemical decomposition of a wood's timber and in doing so converts timber into a grayish brown powder known as wet rot. Alternative wet and dry conditions favor the development of wet rot. If unseasoned or improperly seasoned timber is exposed to rain and wind, it easily becomes vulnerable to wet rot attack.
- **White Rot**: This is just the opposite of brown rot. In this type of fungi attack, the wood's lignin and the wood itself assumes the appearance of a white mass consisting of cellulose compounds. Some of the white rots during their early stages of development form what is commercially termed '**spalted wood**'. This wood has a unique color and figure and therefore sometimes highly prized.

Insect Defects: There are a number of insects that eat wood. Many other insects use wood as a nesting place for their larvae which results in holes and tunnels in the wood. The damage they cause ranges from minor to catastrophic. Some of the more common insects include:

- **Wood Boring Beetles:** Wood boring beetles, such as buprestid, powder post, ambrosia, furniture, and longhorn, tunnel through wood to deposit their larvae. Some larvae eat the starchy part of the wood grain. Many species attack live but usually stressed trees, while others prefer recently dead hosts.
- **Pin-Hole Borers:** They damage fresh-cut logs and unseasoned lumber, but also attack weakened, stressed, dying trees, and healthy trees with bark injuries.
- **Termites:** Termites not only tunnel through wood in various directions, but eat away the wood from the cross-section core. They usually do not disturb the outer shell or cover. In fact, the timber piece attacked by termites may look sound until it completely fails.

NOTES

Raised Grain: Anything that gives the wood a corrugated feel. Typically, this is caused by the harder summerwood rising above the softer springwood in the growth ring. The growth rings do not separate.

Shake: A lengthwise crack or separation of the wood between the growth rings, often extending along the board's face and sometimes below its surface. Shakes may either partly or completely separate the wood fibers. The separations make the wood undesirable when appearance is important. Although this is a naturally occurring defect possibly caused by frost or wind stress, shakes can also occur on impact at the time of felling and because of shrinkage in the log before conversion. There are two types of shakes:

- **Star Shake**: A group of splits radiating from the pith or center of the tree in the form of a star. It is wider on the outside ends and narrower on the inside ends. Star shakes are usually formed due to extreme heat or severe frost during the tree's growth. Also referred to as heart shake.
- **Ring Shake**: Also known as 'cup shake' or 'wind shake', this rupture runs parallel to the growth rings. A ring shake is not easily detected in green logs and lumber, but only becomes apparent after drying. It is caused by any one of numerous factors, including bacteria, tree wounds, tree age, and environmental conditions such as excessive frost action on the sap when the tree is young.

Split: A split is a rupture or separation in the wood grain which reduces a board's appearance, strength, or utility. One of the more typical ruptures of this type is called ring shake. In a ring shake (also known as cup shake or wind shake), the rupture runs parallel to the growth rings. It is not easily detected in green logs and lumber, but only becomes apparent after drying. It is caused by any one of numerous factors, including bacteria, tree wounds, tree age, and environmental conditions.

Stains: Stains are a discoloration that penetrate the wood fiber. They are caused by a variety of conditions and can be any color other than the natural color of the wood. A number of fungi can cause stains or discoloration although do not destruct it. Some stains may indicate decay or bacteria are present.

Spalting: Any form of wood discoloration caused by fungi. It is typically found in dead trees, so if the wood is not stabilized at the right time it will eventually become rotten wood. There are three types of spalting that are typically incorporated into woodworking as design elements: pigmentation (sapstain), white rot, and zone lines.

Twisted Fibers: These are known as wandering hearts and caused by twisting of young trees by fast blowing wind. The timbers with twisted fibers are unsuitable for sawing.

NOTES

Figure 10.1 shows various natural defects of the wood.

Fig. 10.1 *Some Natural Defects in Wood*

The above Figure 10.1 shows some natural defects in wood, in which; 1. Twisted Fibers; 2. Rind Galls; 3. Burls; 4. Dead Wood; 5. Coarse Grain; 6. Druxiness; 7. Dry Rot; 8. Wet Rot; 9. Brown Rot; 10. White Rot; 11. Blue Stain; 12. Heart Rot; 13. Sap Stains; 14. Splits.

10.2.1 Knots

A knot is the base of a branch or limb that was broken or cut off from the tree. The portion of the remaining branch receives nourishment from the stem for some time and it ultimately results in the formation of dark hard rings known as knots. As the continuity of wood fibers are broken by knots, they form a source of weakness. In simple words, these are common blemishes in trees, which are known to often cause holes or lumps within the trunk of the tree in question. There are several types of knots (Refer Figure 10.2):

- **Sound** knots (or tight knots) are solid and cannot be knocked loose because they are fixed by growth or position in the wood structure. They are partially or completely intergrown with the growth rings.
- **Unsound Knots** (or loose knots) are knots which fall out of the lumber when pushed or have already fallen out. They are caused by a dead branch that was not fully integrated into the tree before it was cut down.
- **Encased Knots** are those which are not intergrown with the surrounding wood.
- **Knothole** is a hole left where the knot has been knocked out.
- **Spike Knots** are limbs which have been cut across or cut lengthwise, showing the endwise or lengthwise section of the limb or knot. These knots generally have splits and severe grain deviations near them.

NOTES

(a) *(b)*

Fig. 10.2 *A. Knot in a Plank. B. Knot in a Tree Trunk*

Effects of Knots: Knots are known to affect the technical properties of the wood. They are very hard to cut through themselves, but also reduce the local strength of the wood that surrounds them. However, they may not affect the stiffness of structural timber, as elastic strength and stiffness are more dependent on the sound wood than upon localized defects. Knots are not always bad though; they are often exploited for visual effect. In some cases, knots on trunks add to the aesthetic appeal of the planks that are sawn from those trees.

Dealing with Defects: Generally, it is preferred to avoid wood with defects because they detract from the beauty or value of the finished product. Sometimes, though, defects are highly prized. For example, several wood microphone makers often seek wood with certain defects because they believe they add character to the wood and ultimately their final product. However, the easiest way to deal with natural defects is to simply avoid using the defected wood. Defects can also play a supporting role – provided they enhance the beauty of a piece.

10.2.2 Reaction Wood

Environmental factors may also induce the production of a special type of wood which is different from normal wood in its structure and properties. This special type of wood is called as reaction wood, which is considered to be developed in response to the stimulus of gravity. Gravity affects the distribution of hormones (auxin/IAA) in inclined stems which causes the formation of eccentric radial growth. There are specific differences in the place of development, nature, and shape of the reaction wood between gymnosperms (conifers) and dicotyledons. Reaction wood also helps in the recovery of the organs. The reaction wood of conifers is called compression wood which is produced on the underside of leaning trunk or branch, whereas in dicotyledons it is developed on the upper side of branches and is known as tension wood. High concentration of IAA is required for the formation of compression wood in conifers, and low concentration of IAA promotes the development of tension wood in dicotyledons.

Tilted tree produces reaction wood in an effort to strengthen up gymnosperms produce compression wood on the tilt side of the tree, where angiosperms produce tension wood on the side opposite the tilt (Fritts, 1979).

10.2.3 Compression Wood

Compression wood is developed on the lower side of the stem of conifers due to the activity of vascular cambium. It is characterized by eccentric growth rings, highly lignified cell wall and is 1540% heavier than the normal wood. In compression wood, the tracheids are shorter, rounder with some intercellular spaces between them. These intercellular spaces are filled with an amorphous water absorbing substance. As being heavier than normal wood, compression wood is more brittle and capable of unusually high and irregular longitudinal shrinkage but of less transverse shrinkage.

Tension Wood: Tension wood is developed on the upper side of dicotyledons stems. It also has eccentric growth rings. It is characterized by the presence of gelatinous fibres which have a thick, highly refractive gelatinous layer in cell wall. It is because of the gelatinous wall layer (Glayer) which causes the contraction of the tension wood. This gelatinous layer can replace the S2 or S3 layer. In tension wood, the vessels are less in number and reduced in width. The amount of lignin is less in tension wood as compared to normal wood, but cellulose is in higher amount. Although the phloem fibres are less lignified, their walls are thicker than the normal phloem fibres (Refer Figure 10.3).

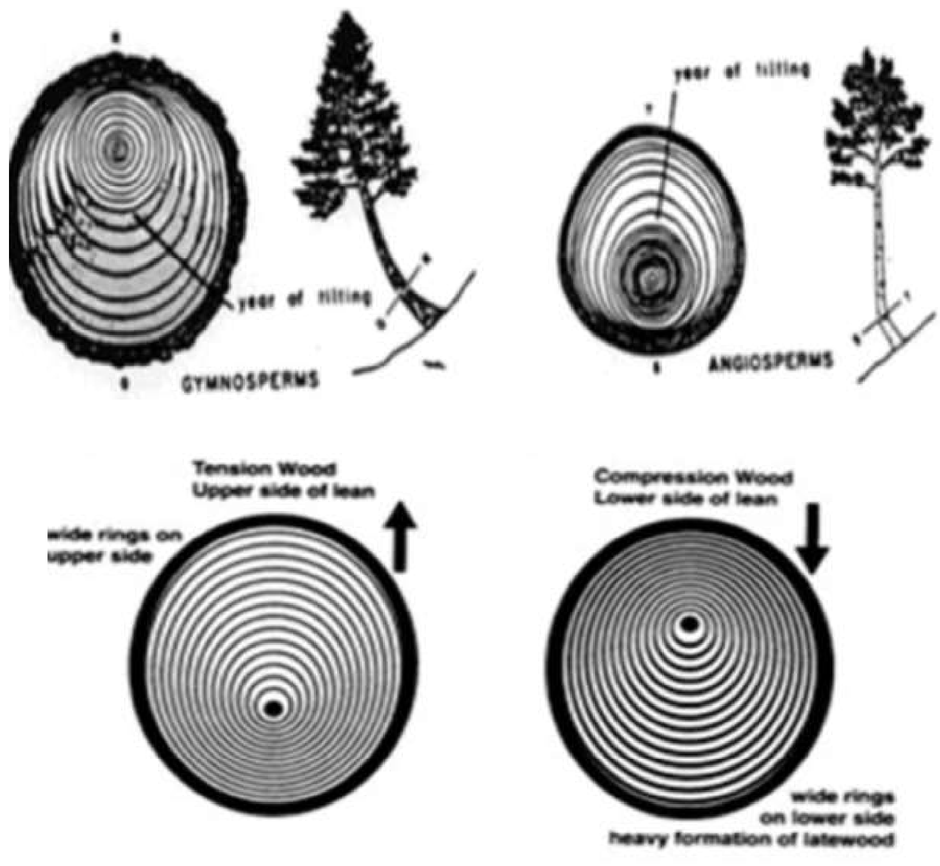

Fig. 10.3 *Diagrammatic Illustration Showing A) Compression Wood and B) Tension Wood.*

NOTES

On the basis of the arrangement of the gelatinous fibres, there are two types of tension wood:

- **Compact Tension Wood**: The gelatinous fibres form continuous regions (for example, *Acer*)
- **Diffuse Tension Wood**: The gelatinous fibres are scattered in the single or in the groups among the normal fibres (for example, *Acacia*).

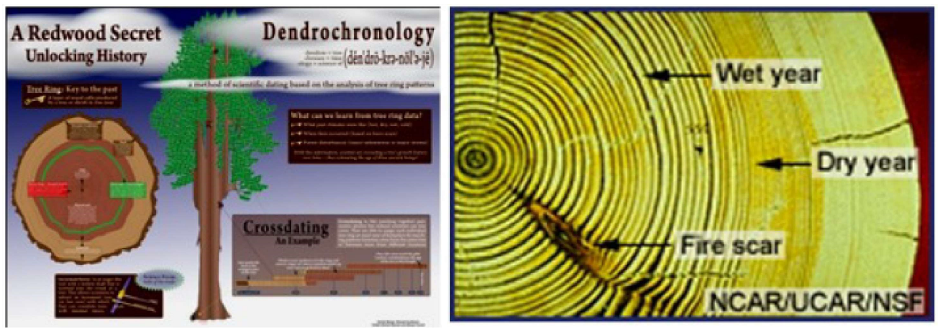

Fig. 10.4 *Reaction Wood in Gymnosperms and Angiosperms*

Check Your Progress

1. How are bark pockets formed?
2. What does fungi damage?
3. Define dry rot.
4. How is heart rot formed?
5. What is white rot?
6. Write in brief about ring shake.
7. Distinguish between sound and unsound knot.

10.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Bark Pockets are formed when a small piece of the bark protrudes into the lumber. This area is generally considered defective.
2. Fungi generally damages timber or wood by discoloration and/or decay. The resulting wood is generally weaker or of a different color than is typical for that species.
3. After the wood infected with brown rot dries out, the cell walls of the remaining wood turns into dry powder when crushed called dry rot.
4. Heart rot is formed when a branch has come out of the tree. The heart wood is exposed to an attack of atmospheric agents. Ultimately, the tree becomes weak and it gives a hollow sound when struck with a hammer.

5. White rot is just the opposite of brown rot. In this type of fungi attack, the wood's lignin and the wood itself assumes the appearance of a white mass consisting of cellulose compounds. Some of the white rots during their early stages of development form what is commercially termed 'spalted wood'. This wood has a unique color and figure and therefore sometimes highly prized.
6. Ring shake known as 'cup shake' or 'wind shake', this rupture runs parallel to the growth rings. A ring shake is not easily detected in green logs and lumber, but only becomes apparent after drying. It is caused by any one of numerous factors, including bacteria, tree wounds, tree age, and environmental conditions such as excessive frost action on the sap when the tree is young.
7. Sound knots (or tight knots) are solid and cannot be knocked loose because they are fixed by growth or position in the wood structure. They are partially or completely intergrown with the growth rings.

   Unsound Knots (or loose knots) are knots which fall out of the lumber when pushed or have already fallen out. They are caused by a dead branch that was not fully integrated into the tree before it was cut down.

10.4 SUMMARY

- During its lifetime, a tree is subjected to many natural forces that cause defects in the wood. These defects include – knots, splits, ugly dark streaks or stains, worm holes, even decay.
- Bark pockets are formed when a small piece of the bark protrudes into the lumber. This area is generally considered defective.
- Bird pecks are caused by birds, especially woodpeckers, which peck on trees mainly to cause panic to the insects living in or under the bark and in the wood of the tree. This causes the insects to come out enabling the birds to eat them.
- Burls are a deformed growth formed when a tree receives a shock or injury in its young age. Due to its injury, the tree's growth is completely disturbed, and irregular projections appear on the body of the timber.
- When the tree grows rapidly, the annual rings are widened. It is known as coarse grain timber and possesses less strength.
- Fungi generally damages timber or wood by discoloration and/or decay. The resulting wood is generally weaker or of a different color than is typical for that species.
- Blue Stain is common in pine, maple, and many other woods, blue stain (also called 'sapstain') is caused by a fungus that feeds on the sap. It does not live in live trees due to lack of oxygen. The bluish color (sometimes gray or dark gray) is the fungus itself. The color does not degrade the cellular structure and does not count against wood in the grading process.

NOTES

- Brown rot is a form of wood decay found only in softwoods that destroys the wood's cellulose, eventually causing cracks across the grain. Advanced brown rot tends to leave the wood more brown than normal. It is a precursor to dry rot.
- After the wood infected with brown rot dries out, the cell walls of the remaining wood turns into dry powder when crushed. This is called dry rot.
- Heart rot is formed when a branch has come out of the tree. The heart wood is exposed to an attack of atmospheric agents. Ultimately, the tree becomes weak and it gives a hollow sound when struck with a hammer.
- White rot is just the opposite of brown rot. In this type of fungi attack, the wood's lignin and the wood itself assumes the appearance of a white mass consisting of cellulose compounds.
- There are a number of insects that eat wood. Many other insects use wood as a nesting place for their larvae which results in holes and tunnels in the wood.
- Wood boring beetles, such as buprestid, powder post, ambrosia, furniture, and longhorn, tunnel through wood to deposit their larvae.
- Pin-hole borers damage fresh-cut logs and unseasoned lumber, but also attack weakened, stressed, dying trees, and healthy trees with bark injuries.
- Termites not only tunnel through wood in various directions, but eat away the wood from the cross-section core.
- A lengthwise crack or separation of the wood between the growth rings, often extending along the board's face and sometimes below its surface. Shakes may either partly or completely separate the wood fibers.
- Star shake is a group of splits radiating from the pith or center of the tree in the form of a star. It is wider on the outside ends and narrower on the inside ends. Star shakes are usually formed due to extreme heat or severe frost during the tree's growth.
- A split is a rupture or separation in the wood grain which reduces a board's appearance, strength, or utility.
- Stains are a discoloration that penetrate the wood fiber. They are caused by a variety of conditions and can be any color other than the natural color of the wood.
- Twisted fibers are known as wandering hearts and caused by twisting of young trees by fast blowing wind. The timbers with twisted fibers are unsuitable for sawing.
- A knot is the base of a branch or limb that was broken or cut off from the tree. The portion of the remaining branch receives nourishment from the stem for some time and it ultimately results in the formation of dark hard rings known as knots.

- Sound knots (or tight knots) are solid and cannot be knocked loose because they are fixed by growth or position in the wood structure. They are partially or completely intergrown with the growth rings.
- Encased knots are those which are not intergrown with the surrounding wood.
- Knothole is a hole left where the knot has been knocked out.
- Generally, it is preferred to avoid wood with defects because they detract from the beauty or value of the finished product. Sometimes, though, defects are highly prized.
- Environmental factors may also induce the production of a special type of wood which is different from normal wood in its structure and properties. This special type of wood is called as reaction wood, which is considered to be developed in response to the stimulus of gravity.
- Gravity affects the distribution of hormones (auxin/IAA) in inclined stems which causes the formation of eccentric radial growth.
- Compression wood is developed on the lower side of the stem of conifers due to the activity of vascular cambium. It is characterized by eccentric growth rings, highly lignified cell wall and is 1540% heavier than the normal wood.
- Tension wood is developed on the upper side of dicotyledons stems. It also has eccentric growth rings. It is characterized by the presence of gelatinous fibres which have a thick, highly refractive gelatinous layer in cell wall.

10.5 KEY WORDS

- **Burls:** Burls are a deformed growth formed when a tree receives a shock or injury in its young age.
- **Coarse grain:** When the tree grows rapidly, the annual rings are widened. It is known as coarse grain timber and possesses less strength.
- **Shake:** A lengthwise crack or separation of the wood between the growth rings, often extending along the board's face and sometimes below its surface.
- **Star shake**: A group of splits radiating from the pith or center of the tree in the form of a star.
- **Split:** A split is a rupture or separation in the wood grain which reduces a board's appearance, strength, or utility.
- **Stains:** Stains are a discoloration that penetrate the wood fiber.
- **Knot:** A knot is the base of a branch or limb that was broken or cut off from the tree.

10.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

NOTES

Short Answer Questions

1. What are bark pockets?
2. Define the term bird pecks.
3. Give short note on:
   - Burls
   - Raised Grain
4. Distinguish between shake and split.
5. What are stains?
6. What is tension wood?

Long Answer Questions

1. Discuss briefly about the natural wood defects giving example.
2. Distinguish between fungal damage and insect defects in wood.
3. What is coarse grain? Explain.
4. Write the differences between compression wood and tension wood.
5. What are knots? Explain.

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NOTES

UNIT 11 MOLECULAR ASPECTS ON WOOD DIFFERENTIATION AND COMMERCIAL WOOD OF SOUTH INDIA

Structure

11.0 INTRODUCTION

Wood (also termed secondary xylem) is the most abundant biomass produced by plants, and is one of the most important sinks for atmospheric carbon dioxide. The development of wood begins with the differentiation of the lateral meristem, vascular cambium, into secondary xylem mother cells followed by cell expansion, secondary wall deposition, programmed cell death, and finally heartwood formation. Significant progress has been made in the past decade in uncovering the molecular players involved in various developmental stages of wood formation in tree species. Hormonal signalling has been shown to play critical roles in vascular cambium cell proliferation and a peptide-receptor-transcription factor regulatory mechanism similar to that controlling the activity of apical meristems is proposed to be involved in the maintenance of vascular cambium activity. It has been demonstrated that the differentiation of vascular cambium into xylem mother cells is regulated by plant hormones and HD-ZIP III transcription factors, and the coordinated activation of secondary wall biosynthesis genes during wood formation is mediated by a transcription network encompassing secondary wall NAC and MYB master switches and their downstream transcription factors. Most genes encoding the biosynthesis enzymes for wood components, i.e., cellulose, xylan, glucomannan, and lignin have been identified in poplar and a number of them have been functionally characterized. With the availability of genome sequences of tree species from both gymnosperms and angiosperms, and the identification of a suite of wood-associated genes, it is expected that our understanding of the molecular control of wood formation in trees will be greatly accelerated.

NOTES

Wood has been of service to mankind through the ages. The most unique feature of wood, unlike other natural materials, is its high degree of structural variability. Even, two pieces of wood belonging to the same timber species may not be exactly alike. Even though the basic wood structure of the species is more or less similar; every fragment of it may show some difference. This attracts a unique fascination and attraction for this material. At the same time, it makes timber identification a tricky business. One has to learn to isolate those features that are characteristic of a certain timber, from others that many kinds of woods share.

Due to ignorance about the identity of timbers, usage of inferior and often unsuitable timber species, such as Malaysian Sal, Pynkado, Merbau, Kusia and different species of acacias, eucalyptus and even conifers from temperate regions, such as pines, have found their way into the timber market and have become popular for various end uses. However, the timber dealers, officials and the common man are left wondering as to the correct identification and utility of such species. Many instances of substitution of popular and traditional species by less costly and inferior species is happening in timber trade in the country, leading to litigations which have been reported from governmental as well as from other quarters.

There are a large number of indigenous timbers whose identification poses problems to even professionals in the field. Reliable anatomical key differentiators of important timber species used by the Wood Based Handicrafts Industry (WBHI) in the states of Uttar Pradesh, Rajasthan and Kerala, which could help in their accurate identification, are currently not available. Also, very accurate identification techniques requiring elaborate laboratory facilities may not be possible to practice, especially under field conditions. Hence field relevant key indicators based on general and gross anatomical features that can be observed using a hand held lens is the need of the hour.

In this unit, you will study about molecular aspects on wood differentiation and commercial wood of South India in detail.

11.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the molecular aspects on wood differentiation
- Discuss about commercial wood of South India

11.2 MOLECULAR ASPECTS ON WOOD DIFFERENTIATION

Terrestrial plants fix about 56 billion metric tons of carbon every year and about half of that is stored in tree species. Wood, being the bulk of tree biomass, is an important reservoir of fixed carbon and, therefore, carbon storage in wood is crucial for balancing the atmospheric carbon dioxide level. Wood is also an abundant source of raw materials for a numerous uses for humans, such as burning for energy, pulping, paper-making, construction, and potentially lignocellulosic biofuel production. To modify wood for our use, it is critical to dissect the molecular and biochemical mechanisms controlling wood formation. Knowledge gained from such studies can be applied to genetically modify wood quantity and quality.

Wood, also termed secondary xylem, is produced from the activity of vascular cambium that is composed of two meristematic initials: fusiform initials and ray initials. Fusiform initials generate axially oriented woody cells, termed tracheids, in gymnosperms, and vessels, fibres, and parenchyma in angiosperms, which provide mechanical strength to the plant body. Tracheids and vessels are also responsible for longitudinal conduction. Ray initials produce transversely oriented ray parenchyma, which is responsible for transverse conduction and nutrient storage. Wood formation is a sequential developmental process, including differentiation of vascular cambium cells into secondary xylem mother cells, cell expansion, massive deposition of secondary walls, programmed cell death, and finally formation of heartwood. A number of genes involved in vascular tissue differentiation and secondary wall biosynthesis have been uncovered using the herbaceous *Arabidopsis* model.

Molecular Studies of Wood Formation

Transcriptome analyses in tree species have revealed that a suite of genes, including receptor kinases, transcription factors, and secondary wall biosynthesis genes, are highly expressed in wood-forming cells. These studies provide valuable resources for identifying putative genes involved in wood formation. Of particular note is the *Populus* Gene Expression (PopGenExpress) data set, which is generated by whole genome transcriptome profiling of different tissues/organs of *Populus trichocarpa*, including secondary xylem, seedlings, young and mature leaves, roots, and male and female catkins.

With the sequencing of the genomes of increasing numbers of tree species from both gymnosperms and angiosperms, it is now possible to uncover the molecular mechanisms controlling the formation of both softwood and hardwood. So far, the genome sequences of four tree species have been released; these are the angiosperms *Populus trichocarpa* and *Eucalyptus grandis*, and the gymnosperms *Picea abies* and *Picea glauca* (white spruce). The availability of these tree genome sequences together with an improvement of the methodologies used for generation of transgenic trees will enable researchers to directly employ tree species as models for studying wood formation.

Control of Activity of Vascular Cambium

Since wood is differentiated from the vascular cambium, the activity of vascular cambium largely determines the rate of wood formation. It has been shown that vascular cambium activity is regulated by several plant hormones, including auxin, cytokinin, and ethylene. Perturbation of auxin signaling by overexpression of a mutant form of PttIAA3 in transgenic poplar results in a reduction in cell division activity in vascular cambium. The mutant form of PttIAA3 is presumably resistant to auxin-mediated degradation and thus constitutively represses the activation of auxin-responsive genes mediated by Auxin Responsive Factor (ARF). This finding indicates that auxin-mediated signaling is essential for vascular cambium activity. Several cytokinin receptor genes from poplar (PtHK3a/ Histidine Kinase 3 and PtHK3b) and birch (BpCRE1/ Cytokinin Receptor1) exhibit a high level of expression in vascular cambium zones, and a reduction in cytokinin level by overexpression of a cytokinin catabolic gene, *Arabidopsis* cytokinin oxidase 2, in transgenic poplar leads to a decrease in the number of cambium cells and concomitantly a reduced stem diameter. Similarly, simultaneous mutations of four cytokinin biosynthesis genes encoding ATP/ADP isopentenyltransferases cause a loss of vascular cambium activity and a lack of secondary xylem in the hypocotyls of *Arabidopsis*. These results demonstrate that cytokinins are also critical regulators of vascular cambium activity. It has been shown that exogenous application of ethylene stimulates vascular cambium activity, and that this stimulation is inhibited in transgenic poplar overexpressing a dominant negative mutant allele of the *Arabidopsis* ethylene receptor ETR1 (Ethylene Responsive1), which is insensitive to ethylene.

Consistent with a role of ethylene in stimulating vascular cambium activity, an ethylene biosynthesis gene, ACC oxidase (PttACO1), is highly expressed in developing secondary xylem of poplar, and its overexpression in transgenic poplar results in increased wood formation. Because auxin, cytokinin, and ethylene all stimulate vascular cambium activity, it is likely that these hormones crosstalk to coordinate their activities or that their signaling pathways converge to regulate common targets that control cell division in the vascular cambium. In *Arabidopsis*, it has been shown that auxin, cytokinin, and ethylene crosstalk to coordinate their regulation of various developmental processes. For example, both cytokinin and ethylene are involved in modulating auxin transport during lateral root development.

Studies of vascular cambium-associated genes have revealed a conservation of the genetic mechanisms controlling the proliferation and maintenance of shoot apical meristem and vascular cambium (a lateral meristem). In Arabidopsis shoot apical meristem, WUSCHEL (WUS) together with the signaling peptide CLAVATA3 (CLV3) and the receptor kinase CLV1 form a peptide–receptor–transcription factor feedback regulatory loop that maintains the dynamic balance between meristematic cell division and differentiation. In addition, several other transcription factors, such as SHOOT MERISTEMLESS (STM), KNOX proteins (KNAT1 and KNAT6), and AINTEGUMENTA (ANT) also play important roles in the maintenance of shoot apical meristem.

Regulation of Secondary Xylem Differentiation

Vascular cambium cells undergo anticlinal divisions; the daughter cells produced on the inner side of the cambium differentiate into secondary xylem mother cells, and those produced towards the outside differentiate into secondary phloem mother cells. The molecular mechanism underlying the precise spatial control of secondary xylem differentiation is not well understood. It has long been known that auxin, cytokinin, and brassinosteroid could induce xylem differentiation in cultured cells, indicating that the signaling pathways mediated by these hormones are involved in the initiation of secondary xylem differentiation. In addition, gibberellin signaling has been suggested to be involved in stimulating secondary xylem differentiation, because overexpression of the gibberellin receptor GIBBERELLIN INSENSITIVE DWARF1 (PttGID1) results in increased wood formation in transgenic poplar. It remains to be investigated how these hormonal signals are integrated to promote the differentiation of vascular cambium cells into secondary xylem mother cells.

Regulation of Cell Expansion and Secondary Wall Biosynthesis

After differentiation of vascular cambium cells into secondary xylem mother cells, they undergo cell expansion followed by a massive deposition of secondary walls that are mainly composed of cellulose, hemicelluloses, and lignin. The plant hormone gibberellin plays an important role during the expansion of secondary xylem cells in poplar. It has been shown that the bioactive gibberellins GA1 and GA4 are predominantly concentrated in the zone of expanding xylem cells in poplar stems, as is the expression of the gibberellin signaling and response genes DELLA-like1 and GID-like1. GID1 is a gibberellin receptor and, upon activation by gibberellin, it targets the gibberellin signaling suppressor DELLA for degradation, which leads to transduction of gibberellin signals and gibberellin-stimulated responses. A role of gibberellin in xylem cell expansion in poplar wood was further demonstrated by overexpression of GA 20-oxidase, a key enzyme in controlling gibberellin biosynthesis, which results in a significant increase in plant height and fibre length in wood.

Deposition of secondary walls during wood formation requires coordinated expression of secondary wall biosynthesis genes, which is controlled by a secondary wall transcriptional network that is conserved in vascular plants. In this transcriptional network, secondary wall NAC and secondary wall MYB transcription factors act as the top-level and second-level master switches, respectively, and together they activate a battery of downstream transcription factors and secondary wall biosynthesis genes. Wood-associated NAC master switches from poplar (PtrWNDs), *Eucalyptus* (EgWND1), and spruce (PgNAC-7) have been functionally characterized These findings further demonstrate that these wood associated NACs are master transcriptional switches activating secondary wall biosynthesis during wood formation in trees.

Phylogenetic analysis of secondary wall NAC master switches in tree species indicates an expansion in the number of these genes in angiosperms (six in *Eucalyptus* and six pairs of duplicated ones in poplar) compared to gymnosperms (two in pine and spruce, respectively), which correlates with the increased complexity of wood structure in angiosperms (composed of vessels and fibres) compared to that in gymnosperms (composed of tracheids).

Regulation of secondary wall biosynthesis during wood formation not only involves transcriptional activators but also entails transcriptional repressors. Eucalyptus EgMYB1, an *Arabidopsis* MYB4 orthologue, represses the expression of secondary wall biosynthesis genes and inhibits secondary wall thickening in fibres when overexpressed in *Arabidopsis* and poplar, suggesting that it is a transcriptional repressor of secondary wall formation.

Biosynthesis of Wood Components

Wood is mainly composed of cellulose, hemicelluloses (xylan and glucomannan), and lignin, the proportion of which varies among different species. For example, wood from *Populus tremuloides* consists of 48% cellulose, 24% glucuronoxylan, 3% glucomannan, and 21% lignin, and wood from *Pinus strobus* is made of 41% cellulose, 9% arabinoglucuronoxylan, 18% galactoglucomannan, and 29% lignin. It is predicted that the deposition of secondary walls in the developing wood requires the catalytic activities of all the biosynthesis enzymes involved in the biosynthesis of wood components and, therefore, their genes must be coordinately expressed.

Transcriptome profiling of developing secondary xylem of poplar led to the identification of a number of xylem-specific glycosyltransferases, many of which have been demonstrated to participate in the biosynthesis of cellulose, xylan, and glucomannan. Among them, cellulose synthase (CesA) genes, which are orthologues of the three Arabidopsis secondary wall CesAs, are highly expressed in developing secondary xylem, and overexpression of one of them causes co-suppression of the expression of wood-associated CesAs and a drastic reduction in cellulose content in transgenic poplar wood. Several other proteins, such as sucrose synthases and cellulases, have been implicated in cellulose biosynthesis.

Overexpression of a cotton sucrose synthase results in a slight elevation in cellulose content and an increased cellulose crystallinity in transgenic poplar wood, suggesting a possible association of sucrose synthase with cellulose biosynthesis. Downregulation of sucrose synthase activities in transgenic poplar appears not to support a direct role of sucrose synthase in cellulose biosynthesis; instead, it is proposed that sucrose synthase is involved in supplying carbon for overall wood polymer biosynthesis. Downregulation of a poplar cellulase, PttCel9A1, which is an orthologue of Arabidopsis Korrigan1, has been shown to cause a defect in cellulose biosynthesis in poplar wood.

The biosynthesis of glucomannan is catalysed by members of cellulose synthase-like A (CslA) family of glycosyltransferases, the functions of which are conserved in vascular plants

Xylan is the predominant hemicellulose in wood of angiosperms and it is made of a linear chain of β-1,4-linked xylosyl residues substituted with α-1,2-

linked 4-O-methylglucuronic acid (MeGlcA) residues and acetylated at O-2 and/ or O-3. The reducing end of xylans from wood of gymnosperms and angiosperms contains a unique tetrasaccharide sequence composed of β-d-Xylp-(1→3)-α-l-Rhap- (1→2)-α-d-GalpA-(1→4)-d-Xylp. Among the xylem-specific glycosyltransferase genes identified from transcriptome profiling of developing wood of poplar, PoGT47C, PoGT8D, and PoGT8E/PoGT8F are orthologues of Arabidopsis FRA8 (Fragile Fiber8), IRX8 (Irregular Xylem8) and PARVUS, respectively, which are involved in the biosynthesis of xylan reducing end sequence.

Lignin is a polyphenolic polymer produced via oxidative polymerization of three monolignols, p-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol. Monolignols are synthesized through the phenylpropanoid biosynthesis pathway involving at least 10 enzymes. Comprehensive expression analysis in poplar of all candidate genes potentially participating in phenylpropanoid biosynthesis has shown that 18 of them are highly expressed in developing wood, and they are considered to be the core genes responsible for monolignol biosynthesis during wood formation. The kinetic properties of these core monolignol pathway enzymes have been comprehensively characterized and their endogenous amounts in developing wood have been quantitated, the data of which were used to construct a kinetic metabolic-flux model that could predict how perturbation of monolignol pathway enzymes may affect lignin content and composition

Studies of monolignol transport in developing pine wood indicate that membrane transporters are involved in exporting monolignols from the cytosol into the cell wall for polymerization, which is consistent with the finding in *Arabidopsis* that ABC transporter activities mediate the transport of monolignols.

Programmed Cell Death and Heartwood Formation

After deposition of secondary walls, tracheids (gymnosperms), and vessels and fibres (angiosperms), in wood undergo programmed cell death. A number of genes encoding proteases, nucleases, and autophage-related proteins have been shown to be upregulated during secondary xylem maturation in poplar, indicating their potential roles in regulating programmed cell death during wood formation. Cytological analysis of poplar wood has revealed that cell death in fibres involves a gradual degradative process in both the nucleus and the cytoplasm before the loss of vacuolar integrity, a process different from that of vessels in which cell death is initiated by the loss of vacuolar integrity. Eventually, cell death of wood ray parenchyma together with tylosis formation, wood dehydration, and accumulation of heartwood substances converts sapwood into heartwood. The mechanism controlling heartwood formation is not well understood; several reports have shown upregulation of a number of genes during the transition from sapwood to heartwood, indicating that heartwood formation is a genetically controlled developmental process.

Reaction Wood Formation

In a vertically grown tree stem, the vascular cambium undergoes uniform cell division and differentiation, which gives rise to the concentricity of wood. When a tree stem leans, the vascular cambium exhibits asymmetric activity, which results in the eccentricity of stems due to formation of reaction wood. Reaction wood in gymnosperms, termed compression wood, forms on the lower side of a leaning stem, and that in angiosperms, termed tension wood, forms on the upper side. Ethylene has been shown to be involved in tension wood formation. Several Ethylene Response Factors (ERFs), which mediate ethylene signaling, are induced in responsive to tension wood formation in poplar and, when overexpressed, they alter wood formation in transgenic trees. Disruption of ethylene signaling in transgenic poplar by overexpression of a dominant negative mutant allele of the Arabidopsis ethylene receptor ETR1 leads to inhibition of tension wood formation, demonstrating an essential role of ethylene in controlling the asymmetric activity of vascular cambium and formation of tension wood. Transcriptome profiling of tension wood in poplar has uncovered a number of genes, including transcription factors and cell wall-related genes, that are upregulated in tension wood-forming tissues compared with normal woody tissues Because tension wood is enriched in cellulose due to the deposition of a cellulose-rich gelatinous layer in fibres, uncovering the molecular mechanism controlling its formation may provide novel tools for generating cellulose-enriched wood tailored for biofuel production.

Check Your Progress

1. What does wood provide us?
2. How is wood produced?
3. How wood formation occurs?
4. What happens after differentiation of vascular cambium cells into secondary xylem?
5. What is the composition of wood?

11.3 COMMERCIAL WOOD OF SOUTH INDIA

Hardwood trees are the ones whose wood comes from deciduous trees. They are sturdy and stand the test of time. Hardwood trees are best attested for their strong durability and strength. Softwood is another classification of wood that offers fine timber for many purposes. They are a product of coniferous trees and their wood is not as costly as the hardwood ones.

Oak: The Oak is a hardwood, of which the northern red oak is the most expensive one. It belongs to the angiosperm group of plants and is a native to the Northern hemisphere, that include America, Asia, Europe and North Africa. Oak trees have a deep brown and copper colour. Identify your oak tree by simply looking for the acorns. If you spot acorns, that sure is an oak tree. The bark of the tree comes in small, hard and scaly bits of bark with leaves that have pointed knobs that will extend out from the centre line. It has been used as a hardwood timber for many years. Flooring, homewares, wine barrels are some of the objects made of oak wood or where oak wood is suitable (Refer Figure 11.1).


Fig. 11.1 *Oak Tree and Oak Wood Log*

Maples: Maples belong to the angiosperm category and are native to Asia. They are about 128 variants of it. They grow to a height of 10-45metres and are deciduous. Maples are most commonly known for their autumn leaf colour. They can be quickly understood by their opposite leaf arrangement and flower in late winter or early spring. Their colour ranges from white to off-white cream colour. It can be quite tricky identifying a maple tree given the many variants. However, it is most often spotted using its leaves. Maple wood is the one that is used as the butcher's block, pool cue shafts, bowling alley lanes and also in the limbs of the bow for its stiffness (Refer Figure 11.2).


Fig. 11.2 *Maple Tree and Maples Wood*

Mahogany: The mahogany wood is straight -grained with a reddish-brown timber. It is indigenous to America and is a hardwood. Identifying mahogany is a little easy. Feel the wood to understand if it is soft or hard. Mahogany is hard. The corners of the wood have to be soft. If it is not, then it is a veener. The grain has to be long and also fine. The best indicator of mahogany is the dark fine lines to the grain. Lastly, observe the colour. If it is reddish-brown it is mahogany. If it is young, the wood is pink in colour. Mahogany is used to make furniture, boat, musical instruments and for panelling. They are best known for their beauty.

Rosewood: Rosewood is strong and tough. It takes high polish and looks beautiful on completion. It is available in large dimensions and is used for superior furniture making. It is also used in making cabinets and other ornamental objects. Rosewood is considered very valuable. It is commonly found in Madhya Pradesh, Karnataka, Kerala and Orissa (Refer Figure 11.3).

Fig. 11.3 *Rosewood Tree and Rosewood Wood Log*

Teak: Teak wood is moderately hard and is valuable. However, it can be easily worked on and stands strong against white ants and termites. The wood is durable and is fire resistant. It is also known to not corrode on iron and is used for heavy superior work only. Teak timber is considered as the most prized wood in the entire classification of woods. While teak furniture could burn your pocket a little, it however lasts a very long time. It is commonly found in Central and Southern India (Refer Figure 11.4).

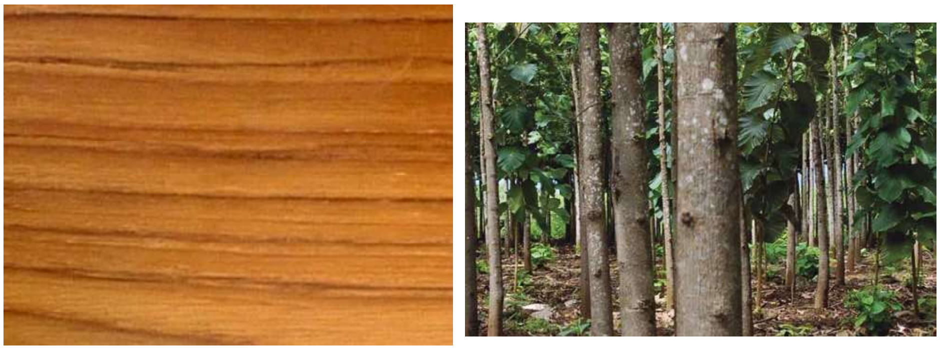

Fig. 11.4 *Teak Wood and Teak Tree*

Beech: Beech is native to Europe, Asia and North America. Beech has strong and sturdy wood that has tiny pores and look similar to maple tree wood. The wood is pale cream colour and is comparatively inexpensive. To identify them, look for beech nuts that are very small, which has a triangular shape. The colour of the leaves tends to be green in summer and have shades of yellow in winter. The bark of the tree is smooth and slightly gritty when touched. It is used for making veener plywood, flooring and other railroad ties. It is also used as a fuel because of its high density along with good burning ability (Refer Figure 11.5).

Fig. 11.5 Beech Tree and Beech Wood

Sissoo: The Sissoo or Sheesham wood is very strong and durable. It is known to maintain its shape and can be seasoned easily. It is often considered as a good wood for decorative items. Sissoo wood is used in the making of fine quality furniture and cabinets. Sissoo wood is common in Uttar Pradesh, Bengal, Assam, Mysore, Maharashtra and Orissa (Refer Figure 11.6).

Fig. 11.6 Sissoo Wood and Sissoo Tree

Sal: Sal wood is found in Kerala, Karnataka, Madhya Pradesh, Tamil Nadu and Orissa. It has close grain and is very sturdy combined with toughness. The wood is vulnerable is used in making of superior quality furniture, cabinet and other decorative pieces. It is known to maintain its shape well and lasts a very long time (Refer Figure 11.7).

NOTES


Fig. 11.6 *Sal Tree and Sal Wood*

Check Your Progress

6. What is hardwood?
7. What is oak?
8. Write in short about teak.
9. Brief about mahogany wood.
10. What is the specialty of sissoo wood?

11.4 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. Wood is also an abundant source of raw materials for a numerous uses for humans, such as burning for energy, pulping, paper-making, construction, and potentially lignocellulosic biofuel production.
2. Wood, also termed secondary xylem, is produced from the activity of vascular cambium that is composed of two meristematic initials: fusiform initials and ray initials.
3. Wood formation is a sequential developmental process, including differentiation of vascular cambium cells into secondary xylem mother cells, cell expansion, massive deposition of secondary walls, programmed cell death, and finally formation of heartwood.
4. After differentiation of vascular cambium cells into secondary xylem mother cells, they undergo cell expansion followed by a massive deposition of secondary walls that are mainly composed of cellulose, hemicelluloses, and lignin.

5. Wood is mainly composed of cellulose, hemicelluloses (xylan and glucomannan), and lignin, the proportion of which varies among different species. For example, wood from *Populus tremuloides* consists of 48% cellulose, 24% glucuronoxylan, 3% glucomannan, and 21% lignin, and wood from *Pinus strobus* is made of 41% cellulose, 9% arabinoglucuronoxylan, 18% galactoglucomannan, and 29% lignin.
6. Hardwood trees are the ones whose wood comes from deciduous trees. They are sturdy and stand the test of time.
7. The 'Oak' is a hardwood, of which the northern red oak is the most expensive one.
8. Teak wood is moderately hard and is valuable. However, it can be easily worked on and stands strong against white ants and termites. The wood is durable and is fire resistant. It is also known to not corrode on iron and is used for heavy superior work only. Teak timber is considered as the most prized wood in the entire classification of woods. While teak furniture could burn your pocket a little, it however lasts a very long time. It is commonly found in Central and Southern India.
9. The mahogany wood is straight -grained with a reddish-brown timber. It is indigenous to America and is a hardwood. Identifying mahogany is a little easy. Feel the wood to understand if it is soft or hard. Mahogany is hard. The corners of the wood have to be soft. If it is not, then it is a veener. The grain has to be long and also fine. The best indicator of mahogany is the dark fine lines to the grain. Lastly, observe the colour. If it is reddish-brown it is mahogany. If it is young, the wood is pink in colour. Mahogany is used to make furniture, boat, musical instruments and for panelling. They are best known for their beauty.
10. The 'Sissoo or Sheesham' wood is very strong and durable. It is known to maintain its shape and can be seasoned easily. It is often considered as a good wood for decorative items. Sissoo wood is used in the making of fine quality furniture and cabinets. Sissoo wood is common in Uttar Pradesh, Bengal, Assam, Mysore, Maharashtra and Orissa.

11.5 SUMMARY

- Terrestrial plants fix about 56 billion metric tons of carbon every year and about half of that is stored in tree species.
- Wood, being the bulk of tree biomass, is an important reservoir of fixed carbon and, therefore, carbon storage in wood is crucial for balancing the atmospheric carbon dioxide level.

- Wood is also an abundant source of raw materials for a numerous uses for humans, such as burning for energy, pulping, paper-making, construction, and potentially lignocellulosic biofuel production.
- Wood, also termed secondary xylem, is produced from the activity of vascular cambium that is composed of two meristematic initials: fusiform initials and ray initials.
- Fusiform initials generate axially oriented woody cells, termed tracheids, in gymnosperms, and vessels, fibres, and parenchyma in angiosperms, which provide mechanical strength to the plant body.
- Tracheids and vessels are also responsible for longitudinal conduction. Ray initials produce transversely oriented ray parenchyma, which is responsible for transverse conduction and nutrient storage.
- Wood formation is a sequential developmental process, including differentiation of vascular cambium cells into secondary xylem mother cells, cell expansion, massive deposition of secondary walls, programmed cell death, and finally formation of heartwood.
- A number of genes involved in vascular tissue differentiation and secondary wall biosynthesis have been uncovered using the herbaceous *Arabidopsis* model.
- Transcriptome analyses in tree species have revealed that a suite of genes, including receptor kinases, transcription factors, and secondary wall biosynthesis genes, are highly expressed in wood-forming cells.
- It has been shown that exogenous application of ethylene stimulates vascular cambium activity, and that this stimulation is inhibited in transgenic poplar overexpressing a dominant negative mutant allele of the *Arabidopsis* ethylene receptor ETR1 (Ethylene Responsive 1), which is insensitive to Ethylene.
- Vascular cambium cells undergo anticlinal divisions; the daughter cells produced on the inner side of the cambium differentiate into secondary xylem mother cells, and those produced towards the outside differentiate into secondary phloem mother cells.
- The molecular mechanism underlying the precise spatial control of secondary xylem differentiation is not well understood.
- After differentiation of vascular cambium cells into secondary xylem mother cells, they undergo cell expansion followed by a massive deposition of secondary walls that are mainly composed of cellulose, hemicelluloses, and lignin.
- A role of gibberellin in xylem cell expansion in poplar wood was further demonstrated by overexpression of GA 20-oxidase, a key enzyme in controlling gibberellin biosynthesis, which results in a significant increase in plant height and fibre length in wood.

- Deposition of secondary walls during wood formation requires coordinated expression of secondary wall biosynthesis genes, which is controlled by a secondary wall transcriptional network that is conserved in vascular plants.
- Phylogenetic analysis of secondary wall NAC master switches in tree species indicates an expansion in the number of these genes in angiosperms (six in *Eucalyptus* and six pairs of duplicated ones in poplar) compared to gymnosperms (two in pine and spruce, respectively), which correlates with the increased complexity of wood structure in angiosperms (composed of vessels and fibres) compared to that in gymnosperms (composed of tracheids).
- Regulation of secondary wall biosynthesis during wood formation not only involves transcriptional activators but also entails transcriptional repressors.
- Wood is mainly composed of cellulose, hemicelluloses (xylan and glucomannan), and lignin, the proportion of which varies among different species. For example, wood from *Populus tremuloides* consists of 48% cellulose, 24% glucuronoxylan, 3% glucomannan, and 21% lignin, and wood from *Pinus strobus* is made of 41% cellulose, 9% arabinoglucuronoxylan, 18% galactoglucomannan, and 29% lignin.
- Transcriptome profiling of developing secondary xylem of poplar led to the identification of a number of xylem-specific glycosyltransferases, many of which have been demonstrated to participate in the biosynthesis of cellulose, xylan, and glucomannan.
- Overexpression of a cotton sucrose synthase results in a slight elevation in cellulose content and an increased cellulose crystallinity in transgenic poplar wood, suggesting a possible association of sucrose synthase with cellulose biosynthesis.
- A number of genes encoding proteases, nucleases, and autophage-related proteins have been shown to be upregulated during secondary xylem maturation in poplar, indicating their potential roles in regulating programmed cell death during wood formation.
- Cytological analysis of poplar wood has revealed that cell death in fibres involves a gradual degradative process in both the nucleus and the cytoplasm before the loss of vacuolar integrity, a process different from that of vessels in which cell death is initiated by the loss of vacuolar integrity.
- The mechanism controlling heartwood formation is not well understood; several reports have shown upregulation of a number of genes during the transition from sapwood to heartwood, indicating that heartwood formation is a genetically controlled developmental process.
- Hardwood trees are the ones whose wood comes from deciduous trees. They are sturdy and stand the test of time. Hardwood trees are best attested for their strong durability and strength.

NOTES

- Softwood is another classification of wood that offers fine timber for many purposes.
- The 'Oak' is a hardwood, of which the northern red oak is the most expensive one. It belongs to the angiosperm group of plants and is a native to the Northern hemisphere, that include America, Asia, Europe and North Africa.
- Oak trees have a deep brown and copper colour. Identify your oak tree by simply looking for the acorns. If you spot acorns, that sure is an oak tree. The bark of the tree comes in small, hard and scaly bits of bark with leaves that have pointed knobs that will extend out from the centre line. It has been used as a hardwood timber for many years.
- Maples belong to the angiosperm category and are native to Asia. They are about 128 variants of it. They grow to a height of 10-45metres and are deciduous. Maples are most commonly known for their autumn leaf colour.
- Maple wood is the one that is used as the butcher's block, pool cue shafts, bowling alley lanes and also in the limbs of the bow for its stiffness.
- The mahogany wood is straight -grained with a reddish-brown timber. It is indigenous to America and is a hardwood. Identifying mahogany is a little easy. Feel the wood to understand if it is soft or hard. Mahogany is hard.
- Rosewood is strong and tough. It takes high polish and looks beautiful on completion. It is available in large dimensions and is used for superior furniture making.
- Teak wood is moderately hard and is valuable. However, it can be easily worked on and stands strong against white ants and termites.
- Beech is native to Europe, Asia and North America. Beech has strong and sturdy wood that has tiny pores and look similar to maple tree wood. The wood is pale cream colour and is comparatively inexpensive.
- The 'Sissoo or Sheesham' wood is very strong and durable. It is known to maintain its shape and can be seasoned easily. It is often considered as a good wood for decorative items. Sissoo wood is used in the making of fine quality furniture and cabinets.

11.6 KEY WORDS

- **Hardwood tree:** Hardwood trees are the ones whose wood comes from deciduous trees. They are sturdy and stand the test of time.
- **Oak:** The Oak is a hardwood, of which the northern red oak is the most expensive one.

NOTES

11.7 SELF ASSESSMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. Write about the molecular studies of wood formation.
2. Explain the control of activity of vascular cambium briefly.
3. How is regulation of secondary xylem differentiation carried out?
4. What is the procedure of regulation of cell expansion and secondary wall biosynthesis?
5. Write short note on the following:
   - Oak
   - Maple
   - Rosewood

Long Answer Questions

1. Discuss in detail about the molecular aspects on wood differentiation.
2. Explain the biosynthesis of wood components.
3. Write a note on programmed cell death and heartwood formation.
4. Discuss about regulations of wood formation.
5. Write a detailed note on commercial wood of South India.

11.8 FURTHER READINGS

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BLOCK - IV
THE DEVELOPMENTAL BIOLOGY

UNIT 12 ANTHER DEVELOPMENT AND POLLEN MORPHOLOGY

Structure

12.0 INTRODUCTION

Anther development and pollen production are particularly sensitive to abiotic stresses such as heat, leading to severe reductions in crop. The sensitivity of the anther to abiotic stresses varies throughout the development of the anther. An understanding of the effects of these stresses on pollen and anther development requires an accurate and efficient method to identify the various anther developmental stages.

Morphological developmental staging schemes have been previously published for Arabidopsis and rice A 10 stage model of anther development has also been described for the model monocot Brachypodium distachyon and several wheat stages have also been and provide general descriptions of plant development and the Zadoks Scale has been adapted to correlate node number and flag leaf elongation with spike length in barley developed a scoring system for both barley and wheat which correlated spike development with anther length, spike length, awn length, and spikelet number. Floret size and anther length have been correlated with stages of anther development in rice. Generally, anther and pollen stages appear to be tightly linked to spike size in barley and wheat.

Pollen is a fine to coarse powdery substance comprising pollen grains which are male microgametophytes of seed plants, which produce male gametes. Pollen grains have a hard coat made of sporopollenin that protects the gametophytes during the process of their movement from the stamens to the pistil of flowering plants, or from the male cone to the female cone of coniferous plants. If pollen lands on a compatible pistil or female cone, it germinates, producing a pollen tube that transfers the sperm to the ovule containing the female gametophyte. Individual pollen grains are small enough to require magnification to see detail. The study of pollen is called palynology and is highly useful in paleoecology, paleontology, archaeology, and forensics. Pollen in plants is used for transferring haploid male genetic material from the anther of a single flower to the stigma of another in cross-pollination. In a case of self-pollination, this process takes place from the anther of a flower to the stigma of the same flower.

In this unit, you will study about anther development, pollen morphology and pollen stigma compatibility in detail.

12.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand anther development
- Discuss about pollen morphology
- Explain pollen stigma compatibility

12.2 ANTHER DEVELOPMENT

The male reproductive part of a flower is known as stamen, collectively known as androecium. Each stamen has a lower sterile thread like structure filament and upper fertile two pollen sacs known as anther. The median sterile portion of anther is called connective (Refer Figure 12.1).

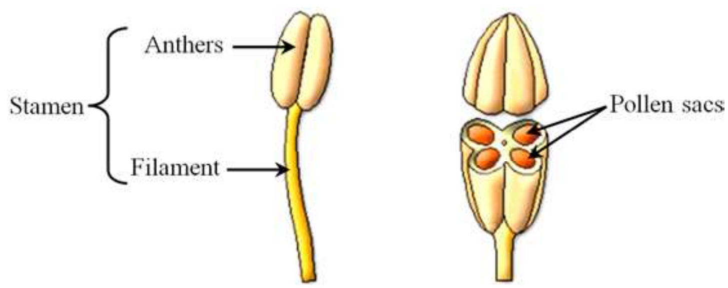

Fig.12.1 *Structure of Stamen*

Each anther is a bilobed and tetrasporangiate structure. In young anther, a single layer of epidermis is surrounded by meristematic cells. In each lobe, some cells below the epidermis (hypodermal cells), become more evident because of their larger size than neighbouring cells and prominent nuclei. These cells are known as archesporial cells, which are arranged in a plate like or crescent shaped manner.

In Malvaceae and Asteraceae a single vertical row of archesporial cells is present whereas in Lamiaceae a layer of archesporial cells are present at each corner. These archesporial cells divide by a periclinal division forming parietal cells towards outer side and primary sporogenous tissue towards inner side. The cells of parietal layer undergo anticlinal and periclinal divisions forming 2-5 anther wall layers. Primary sporogenous tissue either directly behaves as microspore mother cell or after few mitotic divisions it behaves as micropsore mother cells (Refer Figure 12.2).

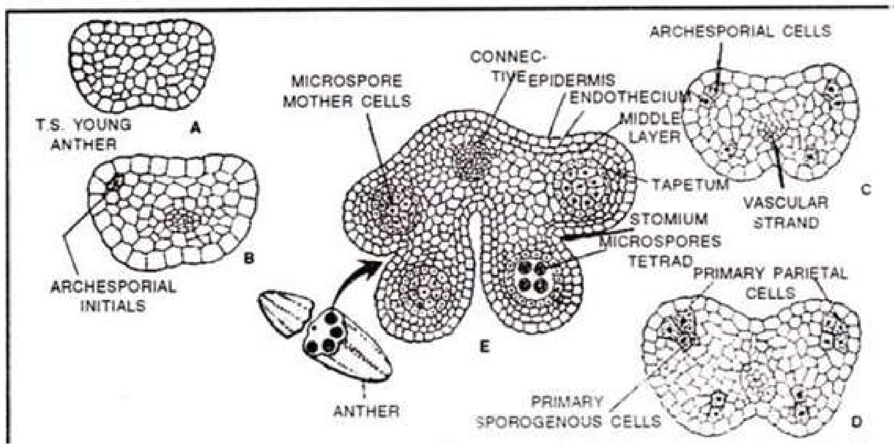

Fig. 12.2 *Stages in the Development of Anther*

Anther Wall

The mature anther consists of four wall layers, i.e., as follows: (Refer Figure 12.3):

- Epidermis
- Endothecium
- Middle Layer
- Tapetum

Epidermis: It is the outermost layer of anther and protective in nature. In *Alangium* stomata may occur in the epidermis.

Endothecium: It is the subepidermal layer of the anther. Usually it is single layered but in some plants it becomes multilayered. In *Coccinia indica*, it is two layered. The cells are radially elongated and develop thickenings at maturity. These thickenings are made up of β-cellulose and slightly lignified. Thickenings help in the dehiscence of anther because of its hygroscopic nature. These thickenings are absent at the junction of two sporangium. This layer attains its maximum development when anther is ready to dehisce. These fibrous bands are absent in cleistogamous flowers and in some members of Hydrocharitaceae. In some plants such as *Musa*, *Sesamum*, *Annona* and *Ipomoea* the epidermis of anther develops the deposition of cutin and lignin, where the endothecium lacks the thickenings.

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Middle layer: The cells of middle layer are short-lived and degenerate before the anther dehiscence. In *Momordica charantia*, soon after the meiosis middle layer degenerates. The exact function of this layer is not clear but some scientists consider that it may be the storage centre of starch and other reserve food material.

Tapetum: It is the innermost layer of anther which provides the nourishment to the developing pollen grains and therefore also known as the nutritive layer. It achieves its maximum development at the tetrad stage of microsporogenesis. Tapetum is composed of single layer of cells characterized by the presence of dense cytoplasm and prominent nuclei. Sporogenous tissue is completely surrounded by tapetum. As tapetum provides the nourishment to the developing pollen grains, therefore it degenerates before the dehiscence of anther. In some plants tapetal cells show pigmentation such as in *Anemone*, tapetal cells having the violet pigments whereas in apple red-brown pigments are present.

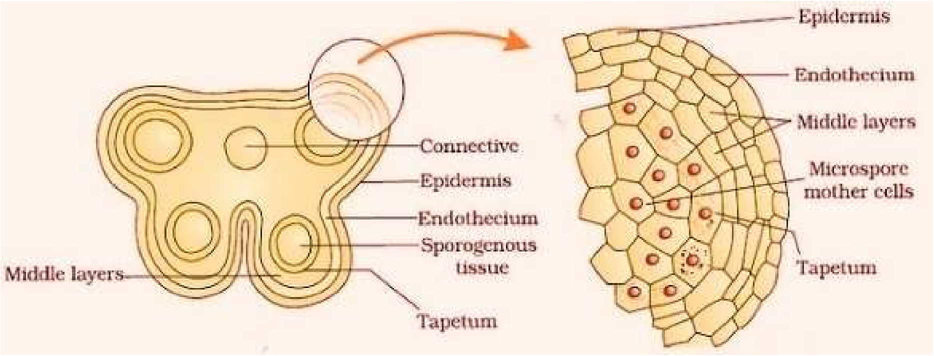

Fig.12.3 *T.S. of Mature Anther and Enlarged View of One Lobe Showing Anther Wall Layers*

Tapetum cell is of two types:

- Amoeboid Tapetum
- Secretory Tapetum

Amoeboid Tapetum: This is also known as invasive or periplasmodial tapetum. This tapetum is characterized by the early degeneration of inner and radial walls of its cells. The masses of protoplast move into anther cavity, protoplast fused to form a tapetal periplasmodium closely surrounding the microspore mother cell. This mass provides the nourishment to the pollen grains till they get mature. Besides providing the nourishment to pollen grains, periplasmodium also contributes in the formation of exine by providing sporopollenin precursors. It is considered that dictyosomes in tapetal cells secrete hydrolytic enzymes which are responsible for early break down of these cells. This type of tapetum is considered to be primitive type and found in *Alisma, Typha, Tradescantia, Sagittaria* or *Potamogeton.*

Secretory Tapetum: This is also known as parietal or glandular tapetum. Secretory tapetum is present in most of the angiosperms. Here the tapetum remains in its original position till the development of pollen grains. At the pre-meiotic stage of microspore mother cell, tapetal cells are thin and all cell organelles such as mitochondria, ribosomes, plastids and dictyosomes are present. The cell walls are also thin composed of middle lamella with a small amount of cellulosic primary wall. Some special kind of spherical cells are also present known as pro-ubisch bodies. These cells are present only in secretory tapetum and not in any other cell. At the tetrad stage, there is an increase in the number of ribosomes and pro-ubisch bodies. The number of plastids and microtubules are reduced. At this stage pro-ubisch bodies pass into anther locule from tapetal cells and now they are known as ubisch bodies. These ubisch bodies are involved in the formation of sculpturing of exine.

Nuclear Divisions in Tapetal Cells

The nucleus of the tapetal cells divide by the following methods:

- **Endomitosis Type**: It is the replication of chromosomes and separation of chromatids within the intact nuclear membrane without spindle formation. Therefore, it results into the formation of large number of nuclei within a cell.
- **Formation of Restitution Nucleus**: Here, a single nucleus formed following the failure of the chromosomes to separate properly at anaphase stage. Therefore, tetraploid nucleus is formed, known as restitution nucleus.
- **Multinucleate Condition**: This situation comes when karyokinesis (nuclear division) is not followed by cytokinesis (wall formation). Therefore, the number of nuclei depends on the nuclear division, it may be 2, 4, 8 or more. It is the most common method of nuclear divisions in tapetal cells.

Functions of Tapetum

Following are the functions of tapetum:

- Tapetum plays an important role in pollen wall formation. Exine chiefly composed of sporopollenin is mainly contributed by tapetum.
- During tetrad formation it is the only channel through which nutrients are transported inside the anther locule.
- Tapetum is also concerned with the synthesis of callase enzyme which is responsible for the dissolution of callose wall around the microspore tetrad.
- Non-functional or faulty development of tapetum is associated with non-viable pollen grains.

Sporogenous Tissue

Primary sporogenous tissue either directly behaves as microspore mother cell or divides by several mitotic divisions to form microspore mother cells. Each microspore mother cell divides by a meiotic division to form microspore tetrads (Refer Figure 12.4). The development of microspore from sporogenous tissue is called as microsporogenesis.

Pollen grains or micropsores represent the first cell of male gameophyte. Pollen grains are formed due to the meiotic division in the Microspore Mother cell. This division is completed in two steps. Stimule for the reductional division arises in the vegetative shoots of the plant. All the pollen mother cells in an anther locule are connected through thread like connections known as plasmodesmata and therefore all the tetrads are in the same stage. As the Pollen mother cell enters into the meiotic stage, it is all plasmodesmatal connections with the tapetal cells are broken. A thick callose wall is formed around each microspore mother cell contributed by the dictyosomes during meiosis. In those plants where compound pollen grains are present callose wall is not formed either before or after meiosis.

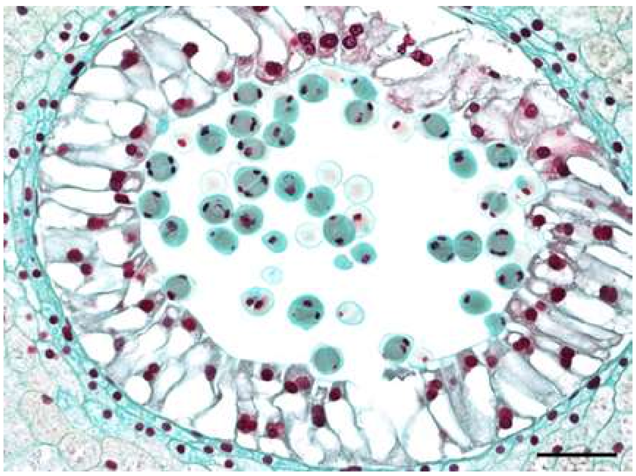

Fig. 12.4 *T.S. of an Anther Lobe Showing Meiotic Division in Microspore Mother Cell*

After the meiotic division, cytokinesis is of two types (Refer Figures 12.5 A and B):

- Successive Type
- Simultaneous Type

Successive Type: After the first meiotic division, a cell wall is formed between the two daughter nuclei, results in the formation of a dyad. This wall gradually extends towards the periphery. The two cells of a dyad undergo second meiotic division which results in the formation of a microspore tetrad. The second meiotic division may not be synchronous in both the cells of a diad. This type of cytokinesis is present in monocotyledons.

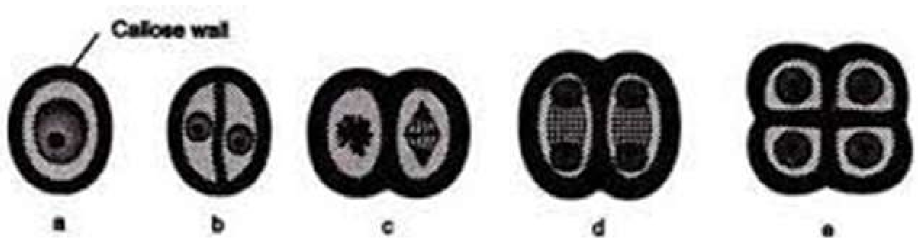

Fig. 12.5 (A) *Successive Type of Cytokinesis in Commelina subulata*

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The above Figure 12.5 A shows the successive type of cytokinesis in *Commelina subulata*. The dark zone around the cells represents the callose wall, in which; a). premeiotic microspore mother cell; b). dyad stage; c). Metaphase II; d). Telophase II, e). Tetrad stage

Simultaneous Type: This type of cytokinesis is present in dicotyledons. In this type, no wall formation takes place between the two daughter nuclei after meiosis I. Now these two daughter nuclei undergo II meiotic division which gives rise to four microspore tetrad. A synchrony has been observed because all the microspores are present in a common cytoplasm. Here the wall formation takes place after second meiotic division and it is centripetal, i.e., from periphery towards centre.

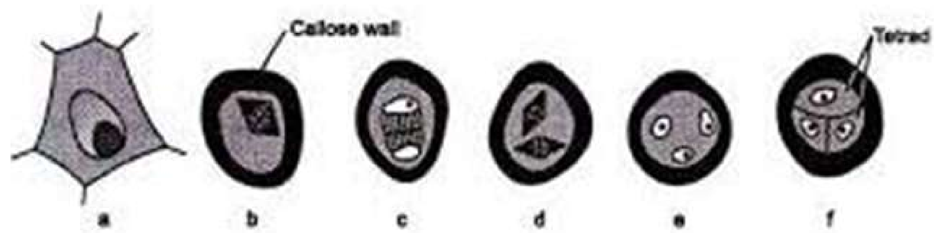
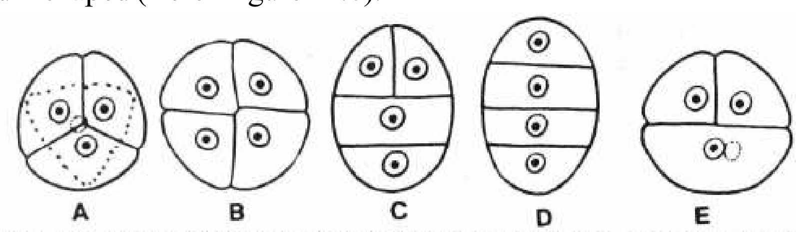


Fig. 12.5 (B) *Simultaneous Type of Cytokinesis in Drimys winteri*

The above Figure 12.5 B shows the simultaneous type of cytokinesis in *Drimys winteri*. The dark zone around the cells represents the callose wall, in which a. premeiotic microspore mother cell. The callose wall has not appeared as yet. b. Metaphase I. c. binucleate cell d. Metaphase II e. 4-nucleate stage f. tetrad stage

After the meiosis, the microspores of a tetrad are separated from each other by callose wall. The microspores of different tetrads in anther locule are not interconnected with each other. Later on, a callase enzyme is released which dissolves the callose wall and all the microspores present in a tetrad get released. Now, there is no interconnection exists between the microspores of a tetrad. The arrangement of microspores in a tetrad is tetrahedral, isobilteral, decussate, linear and T-shaped (Refer Figure 12.6).



Types of microspore tetrads : **A.** Tetrahedral, **B.** Isobilateral, **C.** T-shaped, **D.** Linear, **E.** Decussate.

Fig. 12.6 *Arrangement of Microspore Tetrads in Different Manner*

Out of these five, the most common arrangements are tetrahedral and isobilateral. In *Aristolochia elegans*, all five types of tetrads have been observed (Refer Figure 12.7) (Bhojwani *et al*., 2015).

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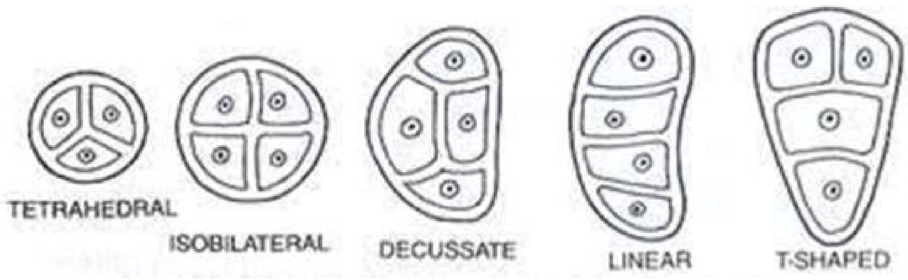

Fig.12.7 *Different Types of Microspore Tetrads in Aristolochia elegans*

In some plants these microspores do not get separated but they remain together in tetrads and develop into compound pollen grains. These compound pollen grains are known as pollinium, found in *Asclepiadaceae* and *Orchidaceae* (Refer Figure 12.8). In some plants, as an abnormality, more than four spores have been observed in a tetrad known as polyspory.

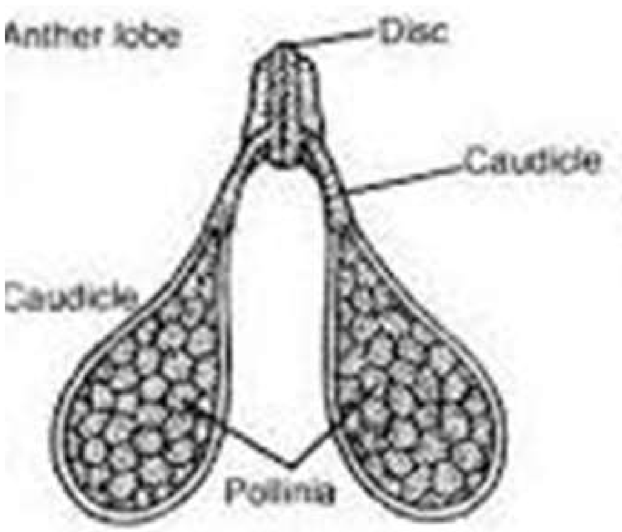

Fig. 12.8 *Pollinia of Calotropis*

As a rule, from each microspore mother cell divides by a meiotic division and therefore four microspores are formed but in Cyperaceae, MMC divides meiotically to form four microspores but out of four, only one is functional and other three degenerates. So in this family, from one MMC only one pollen grain is formed.

Development of Male Gametophyte

Microspore or pollen grains represent the first generation of male gametophyte. After releasing from the tetrads, each microspore is a uninucleate structure. The first mitotic division of pollen grain results in two unequal cells, larger vegetative cell and smaller generative cell. In the early development, the generative cell remains attached to the intine of the pollen wall but later on, it comes freely in the cytoplasm of the vegetative cell. In most of the plants growing in the tropical regions, there is

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a short time gap between the second meiotic division of microsporogenesis and first division of pollen grain whereas the plants growing in the temperate regions this interval may be of several months. As all the pollen grains in an anther locule are not interconnected therefore, no synchrony exists during the mitotic division of pollen nucleus of an anther locule. In some families such as Orchidaceae and Asclepiadaceae where microspores do not get separated from tetrad and remain united, a complete synchrony may exist.

Before the mitotic division of pollen grain starts, some changes occur in the protoplast of pollen:

- Its nucleus migrates from centre to the periphery and its migration marks the position of generative cell (position of generative cell is a genetic character).
- Vacuolation occurs between the cytoplasm of pollen wall and nucleus on one side where vegetative cell is to be formed (Refer Figure 12.9).

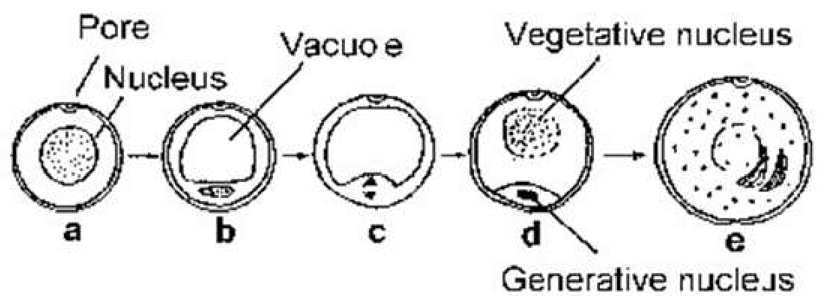

Fig. 12.9 *Diagram Showing Vacuolation in the Pollen Cytoplasm before Pollen Mitosis*

The spindle formation during mitotic division is asymmetrical. It is short and blunt towards the pollen wall and long and acute towards inner side. The two nuclei formed after mitotic division, one lying towards the pollen wall is the generative nucleus and other forms the vegetative nucleus. In initial stages, both vegetative and generative nucleus are separated through a membrane later on which separates by a cell wall formation (Refer Figure 12.10).

The nucleus of the vegetative cell is spherical, with thin chromatin material and one or two nucleoli. The cell organelles increase in number as well as RNA and protein also increases. The vegetative cell does not divide, although it is capable of DNA synthesis.

After separating from the pollen wall the generative cell is spherical. It takes the different shapes during its development. In mature stages it becomes elongated to facilitate its movement into the pollen tube. It consists of all cell organelles except plastids. In *Oenothera hookeri* and *Medicago sativa* plastids are present but without starch.

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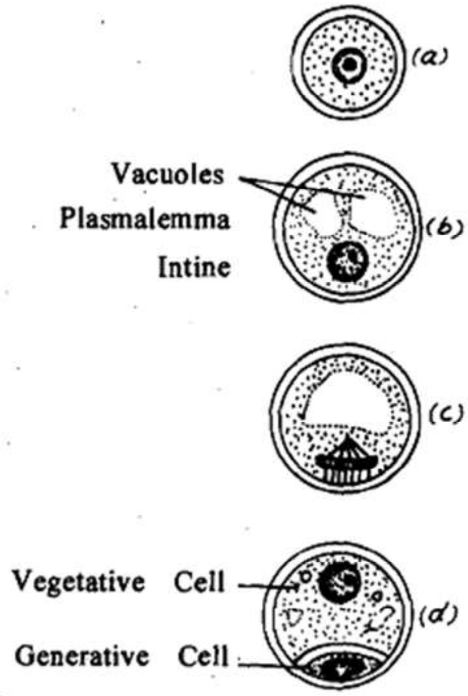

Fig. 12.10 *Formation of Vegetative and Generative Cells*

Male Gametes

Generative cell divides by mitotic division forming 2 male gametes (Refer Figure 12.11). In some plants pollen grains are shed at 2-celled stage whereas in others pollen grains shed at 3-celled stage. In 2-celled stage generative cell divides after its release from anther. In 3-celled stage generative cell divides when pollen is still present inside the anther. Approximately in 70% species pollen grains are bicellular and in 30% pollen grains are tricellular. Two-celled pollen grains remain viable for a longer period and can be easily grown on culture medium. Tricellular pollen grains show higher metabolic activity than bicellular pollen grains and therefore remain viable for a short time and cannot be grown on culture medium. Whether it is bicellular or tricellular both types of pollen grains have vegetative nucleus, also known as tube nucleus later on it forms pollen tube. The generative nucleus either before germination or after germination divides to form 2 non-motile male gametes. Each male gamete consists of a large nucleus surrounded by a thin sheath of cytoplasm, surrounded by a cell membrane. The cytoplasm of male gametes contains all cell organelles such as mitochondria, dictyosomes, ribosomes and microtubules. Plastids are absent in male gametes. The two male gametes are directly associated with each other by a common cell wall with plasmodesmata.

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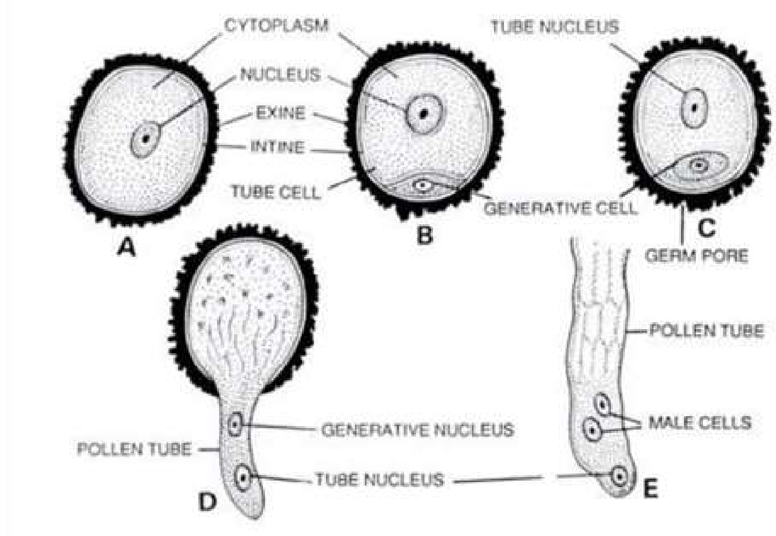

Fig. 12.11 *Development of Male Gametophyte*

Pollen Wall

Pollen wall consists of two wall layers. Outer wall layer is known as exine and the inner one as intine. Exine is chiefly composed of sporopollenin. Sporopollenin is the oxidative polymer of carotenoids. The substance is very tough and therefore resistant to any kind of biological and physical decomposition and because of this character pollen grains can be preserved for long periods in fossil deposits. Exine consists of several sculpturing pattern which are synthesized from tapetum. These patterns are used in the taxonomic classification as well as to solve many forensic cases also. Exine further differentiates into outer ektexine and inner endexine. The ektexine further divided into three layers, upper tectum, middle bacula and basal foot layer (Refer Figure 12.12 A and B).

Intine is made up of pectin and cellulose. The characteristic feature of intine is the presence of beads, ribbons or plates which are of proteinaceous in nature.

In entomophilous plants, an oily layer is formed on the outer surface of pollen grains known as pollen kitt. Sticky nature, colour and odour of pollen grains are due to its presence in insect-pollinated species. Pollen kitt is made up of carotenoid or flavonoid pigments and therefore imparts yellow or orange colour to the pollen grains. The substances required for the formation of pollen kitt are synthesized in tapetal cells. Although the exact function of pollen kitt is not clear but it is believed that it helps in attracting the insects and also protects the pollen grains from harmful UV-radiations.

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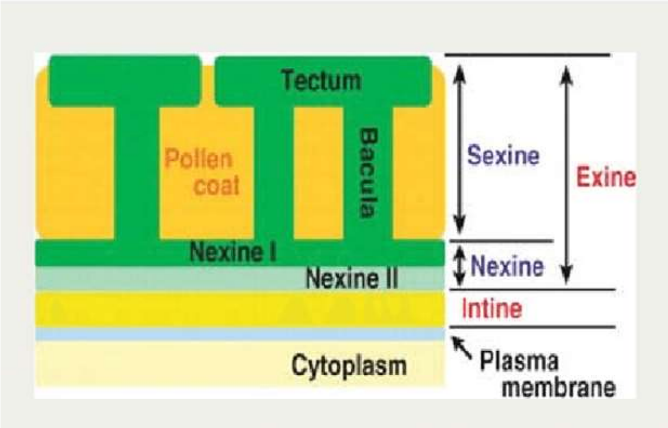

Fig. 12.12 (A) Diagram Showing the Pollen Wall Layers

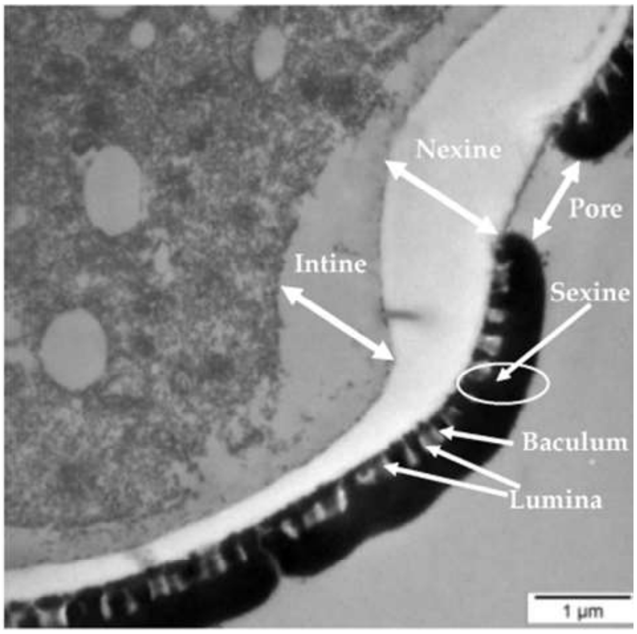

Fig. 12.12 (B) SEM of Pollen Grain Showing the Wall Layers

Check Your Progress

1. What is androecium?
2. Define anther.
3. Define connective.
4. How do primary sporogenous tissue behaves?
5. What is epidermis?
6. What is tapetum?

12.3 POLLEN MORPHOLOGY

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Pollen is a fine to coarse powdery substance comprising pollen grains which are male microgametophytes of seed plants, which produce male gametes (sperm cells). Pollen grains have a hard coat made of sporopollenin that protects the gametophytes during the process of their movement from the stamens to the pistil of flowering plants, or from the male cone to the female cone of coniferous plants. If pollen lands on a compatible pistil or female cone, it germinates, producing a pollen tube that transfers the sperm to the ovule containing the female gametophyte. Individual pollen grains are small enough to require magnification to see detail. The study of pollen is called palynology and is highly useful in paleoecology, paleontology, archaeology, and forensics. Pollen in plants is used for transferring haploid male genetic material from the anther of a single flower to the stigma of another in cross-pollination. In a case of self-pollination, this process takes place from the anther of a flower to the stigma of the same flower. Pollen is commonly used as food and food supplement. However, because of agricultural practices, it is often contaminated by agricultural pesticides

The study of morphology of pollen grains is known as **Palynology**. After the meiotic division of microspore mother cell, a group of four pollen grains are formed (tetrad). Each pollen grain has two poles at opposite end of the polar axis. The proximal pole is towards the centre of the tetrad whereas distal pole is away from the centre of the tetrad.

An aperture is a thin area on the pollen surface which is associated with its germination (Refer Figure 12.13). Long apertures are called colpi whereas short are known as pores (Refer Figure 12.14). Pollen grains having colpi are known as colpate whereas pollen grains having pore are known as porate. A pollen grain having colpus and pore is known as colporate.

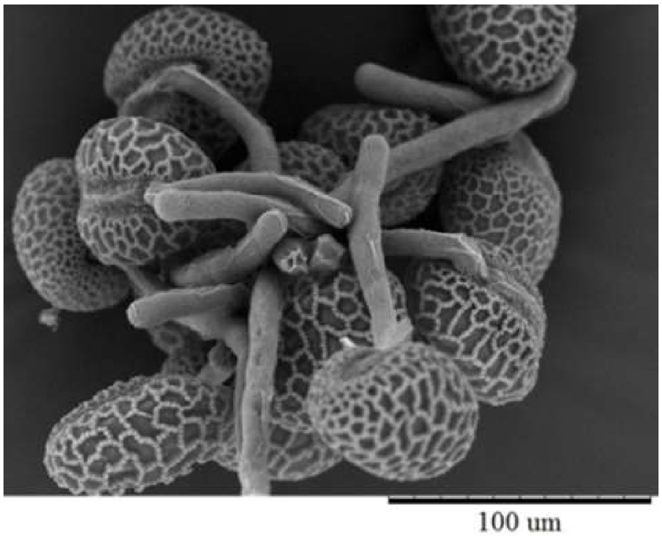

Fig. 12.13 *SEM of Pollen Grains Showing the Germination from Aperture*

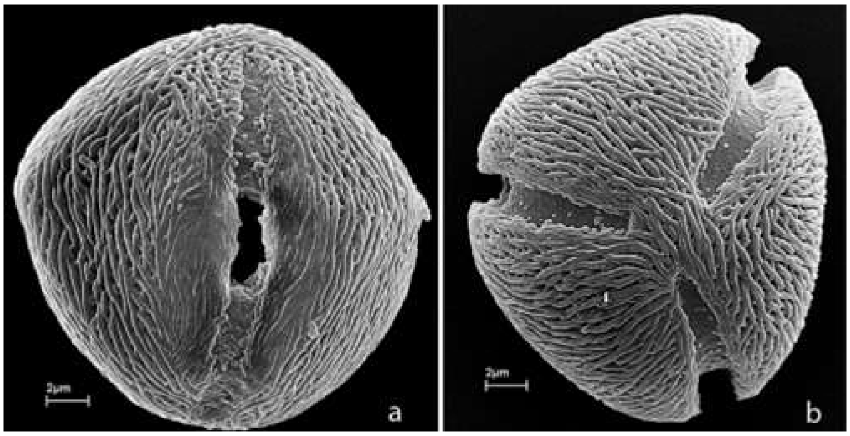

Fig. 12.14 *SEM of Pollen Grains Showing the (a) Single Pore and (b) Three Colpi*

Morphological Characteristics of Pollen Grains

Morphological characteristics of pollen grains have been categorised into different groups:

- Pollen Units
- Polarity
- Symmetry
- Shape
- Size
- Apertures
- Sub-Divisions of the Pollen Surface
- Sporoderm Stratification
- Exine Ornamentation
- 'Lo' Analysis

Pollen Units

The pollen grains are produced within the anther of the flower. Pollen mother cells originate from the sporogenous tissue of the anther which later divide meiotically to form four pollen grains called tetrad.

The pollen grains do not remain united at maturity, and are dissociated into single pollen grain called monad. Sometimes rarer types like dyads (two pollen grains), Octads (eight pollen grains) and Polyads (many pollen grains) are also observed (Refer Figure 12.15).

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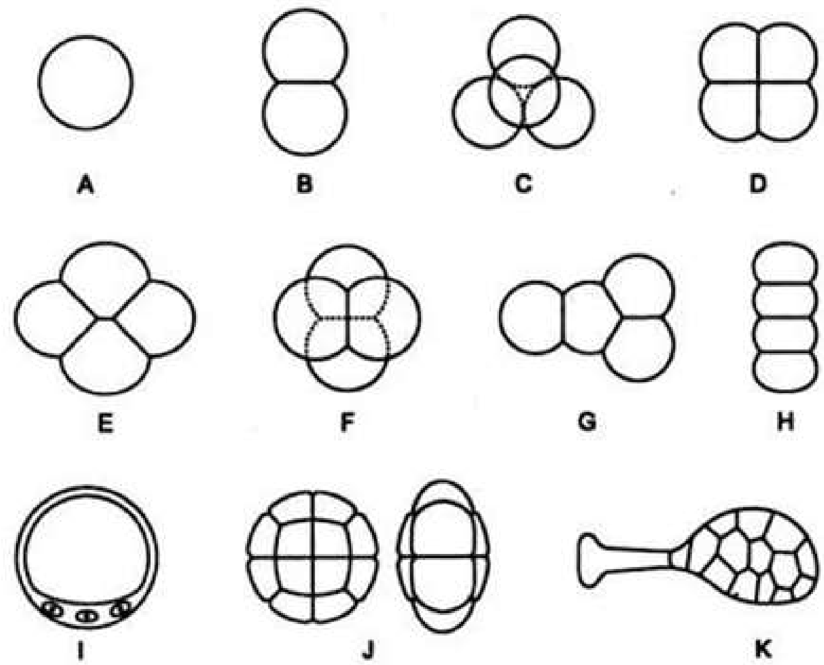

Fig. 12.15 Pollen Units (A = Monad, B = Dyads, C = Tetrahedral Tetrad, D = Teragonal Tetrad, E = Rhomboidal Tetrad, F = Decussate Tetrad, G = T-Shaped Tetrad, H = Linear Tetrad, I = Cryptotetrad, J = Polyads, K = Pollinia)

- **Dyads:** Pollen grains which are united in pairs and shed from the anthers as doubles are called dyads. Dyads are present in *Scheuchzeria palustris* and other members of *Podostemonaceae*. The dyads are formed due to the incomplete break up of individual grain or monad.
- **Tetrads:** Four pollen grains are united to form tetrad. Tetrads are the unseparated product of meiosis. Tetrads maybe categorized into different types based on their arrangement.
- **Tetrahedral Tetrad:** Pollen grains are arranged in two different planes. Three grains are in one plane and one lies centrally over the other three. In some cases, the pollen grains are released from the anther in the tetrad condition. These types of tetrads are called obligate or permanent tetrads, viz., *Drymis* (Winteraceae), *Drosera* (Droseraceae), *Rhododendron* (Ericaceae).
- **Tetragonal Tetrad:** All the four pollen grains are arranged in one plane, for example *Typha latifolia* (Typhaceae), *Hedycaria arborea (*Monimiaceae).
- **Rhomboidal Tetrad:** All pollen grains are arranged in one plane forming rhomboidal shape, for example *Annona muricata* (Annonaceae).
- **Decussate Tetrad**: Pair-wise the pollen grains are at right angle to each other, for example *Magnolia grandiflora* (Magnoliaceae).

- **T-Shaped Tetrad:** The first division of pollen mother cell is transverse to form a dyad. The upper or lower cell of dyad undergoes a vertical or longitudinal division instead of transverse, yielding either straight or inverted T-shaped configuration, for example *Aristolochia* sp. (Aristolochiaceae), *Polyanthes* sp; (Amaryllidaceae).
- **Linear Tetrad:** The first division of pollen mother cell is transverse and a dyad is formed. Each cell of the dyad again divides transversely to form a linear tetrad, for example *Mimosa pudica*.
- **Cryptotetrad or Pseudomonad:** Here tetrads are formed without partition walls between the four compartments. One out of the four nuclei develops normally and the rest three obliterate. Thus an apparent monad but homologous to the tetrad is formed, for example *Cyperaceae*.
- **Polyads:** In most of the Mimosaceae members each of the tetrad cells divides once or twice or more, yielding a group of 8 to 64 cells which remain together after maturity. These compound grains are usually held together in small units and are called polyads, for example *Acacia auriculiformis, Adenanthera pavonina, Calliandra hematocephalla, Samania saman* and *Albizzia lebbeck.*
- **Pollinia:** In Orchidaceae and Asclepiadaceae the whole contents of an anther or anther locule which shed as one united mass of pollen are called Pollinia. The pollinium (singular) apparatus is the functional unit of a 'corpusculum' with its two attached arms (translator) and Pollinia, for example *Calotropis* sp., *Daemia* sp., etc., of the *Asclepiadaceae* and majority of the family Orchidaceae.

Polarity

The orientation of polarity is an important criterion in identification and description of pollen grains, as apertural position is of primary phylogenetic and functional significance. All pollen grains are in tetrad stage during development and the polarity is determined in this stage, prior to their separation.

The part of the pollen grains which is nearest to the centre of the tetrad is the proximal pole and that towards the opposite side is the distal pole. The imaginary line between the proximal and distal pole of the grain is called the Polar Axis (PA) which passes through the centre of the spore to the centre of the tetrad.

The plane perpendicular to the polar axis through the middle of the grain is the equatorial plane (equatorial diameter). Positions on the surface of the grain maybe determined by their latitude, comparing to the latitude on a regular sphere. Similarly, surface features in a pole to pole direction at right angles to the equatorial plane are called meridional.

The pollen grains maybe either apolar or polar.

In **apolar** spores, poles or polar regions cannot be distinguished in individual spore (monad) after separation from tetrad. Among the polar types the pollen

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grains are either isopolar or heteropolar depending upon the demarcation between two equal or unequal polar faces, respectively.

In **isopolar** grains the distal and proximal faces (above and below the equatorial plane) look alike.

In heteropolar grains the two faces are distinctly different, either in shape, ornamen-tation or apertural system. Thus one face may have an opening (aperture) and the other not.

The pollen grains showing slight differences between the distal and proximal faces are also called paraisopolar or subisopolar ,for example one face (distal) is convex and the other face (proximal) is plane or concave or vice versa. Their equatorial plane is usually more or less curved. Sometimes there are small differences in the surface details of the two poles viz. Carya, Ulmus, etc.

In some bryophyte spores like Calobryum dentatum, Haplomitrium hookeri, the distal and proximal faces have dissimilar sculpturing and lack tetrad mark. This type of spores is called **Cryptopolar**.

Symmetry

Pollen grains or spores are symmetric or asymmetric. The asymmetric grains are either non- fixiform (without fixed shape) or fixiform (with fixed shape). Asymmetrical grains have no plane of symmetry. They are rare in occurrence. The Symmetric grains are either radiosymmetric (radially symmetrical) or bilateral (having a single plane of symmetry).

In radiosymmetric grain the shape is such that any plane including the polar axis that passes through will produce identical halves. So the radiosymmetric grains have more than two vertical planes of symmetry. Radially symmetrical isopolar grains have one horizontal and two or more vertical planes of symmetry. Radially symmetrical heteropolar grains have no horizontal plane of symmetry.

Bilateral heteropolar pollen grains have two vertical planes of symmetry. Bilateral isopolar grains have three planes of symmetry, one horizontal and two vertical. In some bean- shaped or boat-shaped spore/pollen there is only one vertical plane of symmetry with an opening towards the end of the grain.

Shape

The shape of the pollen grains varies from species to species. Shape of the grains is found to be useful in spore/pollen identification. However, the shape may vary considerably within one grain type or even within one species.

Pollen grains and spores are often described by the shape (non-angular and angular) of their outline both in polar and equatorial views. The shape of the pollen/ spores may be circular, elliptical, triangular, rectangular, quadrangular or in other geometrical shapes

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Size

Pollen grains show a great variety in their sizes. Smallest pollen grains of about 5 x 2.4 μm is noted in Myosotis palustris and some members of Boraginaceae, while the largest pollen grains (> 200 μm in diameter) are observed in Curcurbitaceae, Nyctaginaceae and Orectanthe ptaritepuiane (Abolbodaceae).

In taking measurements of size the length of Polar Axis (PA), equatorial diameter (ED) and sometimes Equatorial Breadth (EB) are considered in bilateral grains.

In radially symmetrical pollen grains the PA and the greatest ED can be measured in equatorial view, while the EB can be measured in polar view only. It is also necessary to measure exine elements, taking into consideration the thickness of exine, sexine/nexine thickness ratio and the thickness of the exine projections greater than 0.5 μm if any.

Apertures

Morphologically aperture is an opening or thinning of the exine where the in tine is usually thick; physiologically it is a germination zone or a harmomegathus (A mechanism accommodating changes in volume of the semirigid pollen exine) or both.

With regard to their position the apertures are polar, global or equatorial. The polar apertures are either monopolar (either in proximal or in distal pole) or bipolar (both in proximal and distal face). Global apertures are uniformly distributed over the pollen/spore surface. Equatorial apertures are meridionally arranged.

Some taxa have ‘atreme’ (trema, a Greek word means aperture) pollen/spore, i.e., they seem to have no special aperture, are termed as ‘inaperturate’ or non-aperturate.

Majority of the pollen grains described as ‘inaperturate’ seem to be ‘omniaperturate’, that is, the entire pollen wall is made up of a thin exine and a thick intine or at least thick as the exine, for example Canna sp. of Cannaceae. There are two types of apertures known as Pores (Porus, p1. Pori) and furrows (Colpus, p1. Colpi. or Sulcus, p1. Sulci). In most cases the furrows act as harmomegathi.

1. NPC System

NPC refers to number, position and character of apertures. Depending upon the number of apertures, pollen grains have been classified as atreme ($N_{0,}$ having no aperture), monotreme ($N_{1,}$ having single aperture), ditreme ($N_{2,}$ having two apertures), tritreme ($N_{3,}$ having three apertures), tetratreme ($N_{4,}$ having four apertures), pentatreme ($N_{5,}$ having five apertures), hexatreme ($N_{6,}$ having six apertures). Pollen grains having more than 6 apertures are known as polytreme and represented by N_7. If the apertures are irregularly placed, they are known as anomotreme N_8.

On the basis of the position of apertures, they have been classified into seven groups. When the aperture is present on the proximal face it is known as catatreme (P_1), if present on both proximal as well as on distal end known as anacatatreme (P_2), and if present on the distal face only known as anatreme (P_3). When the apertures are on the equator in a single row, pollen grains are called as zonotreme (P_4), and when present in two rows known as Dizonotreme (P_5). When the apertures are uniformly distributed over the pollen surface, this is known as pantotreme (P_6).

The character groups are also classified in seven groups. When pollen has an aperture like thin area known as leptoma (C_1), the aperture either may be on the proximal face or on the distal face. If aperture is present on the proximal face it is known as catalept and if present on the distal face it is known as analept. The pollen grain having a 3-slit colpus are called trichotomocolpate (C_2). Pollen grains having colpate, porate, colporate and pororate are termed as C_3, C_4, C_5 and C_6 respectively (Refer Figure 2.15).

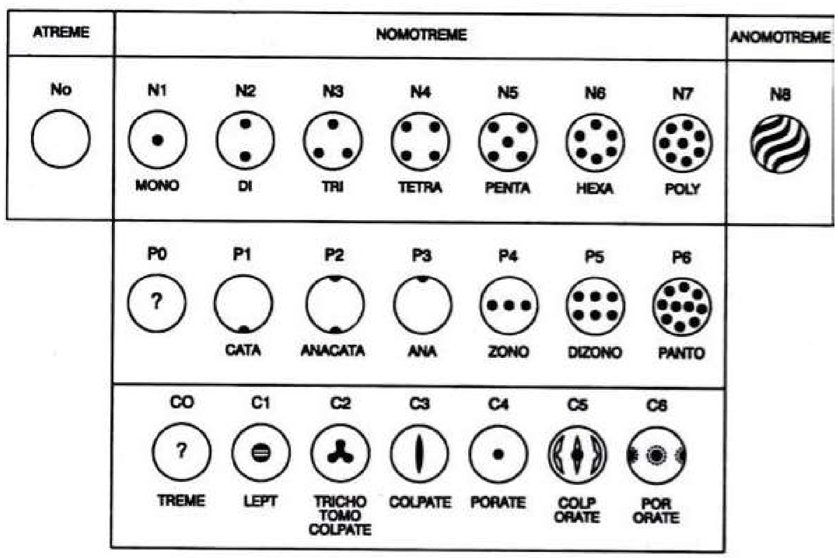

Fig. 12.16 *Diagram Showing Number (N), Position (P), and Character (C) of Apertures (NPC System).*

2. Apertural Types

Apertures are of two basic types namely, Simple aperture, i.e., with one type of aperture and Compound aperture, i.e., with two different types of apertures.

- **Simple Aperture:** Simple opening or thinning overlaying a thick intine. Say for example, lete, porus, orus, ulcus, sulcus, colpus, etc.
- **Lete:** Slit like aperture situated at the proximal end viz. pteridophytes spores. Spore with one slit is called monolete, for example Psilotum, Polypodium, etc., and spore with triradiate slit is called trilete, for example Lycopodium, Dryopteris, etc.

- **Porus:** Equatorial simple circular aperture with length/breadth ratio <2. The pollen grains with porus apertures are referred to Porate, for example *Urticaceae, Ulmaceae,* etc.
- **Periporus:** Global simple circular aperture with length/breadth ratio <2. The pollen grains of this apertural type are called Pantoporate or Periporate, for example *Amaranthaceae, Chenopo- diaceae, Malvaceae*, etc.
- **Ulcus:** Distal simple circular aperture with length/breadth ratio <2 and restricted to less than half the distal surface. The pollen grains with this aperture are referred to Ulcerate, for example *Poaceae*.
- **Sulcus:** Distal simple elongated boat-shaped aperture, generally with tapering ends showing length/breadth ratio>2. The aperture is parallel with the equatorial breadth. Pollen grains with sulcus aperture are called Sulcate, for example *Arecaceae, Magnoliaceae*, etc.
- **Sulculi:** Sulculi are sulcoid apertures, parallel to equator and usually situated between the equator and the distal pole. If united apically, the sulculi form a zone, or ring parallel to the equator, for example Eupomatia, Cephalostemon, Atherosperma, etc.
- **Colpus:** Meridional simple long furrow-like aperture with length/breadth ratio >2. Aperture is facing pole to pole direction. The pollen grains of this apertural type are referred to Colpate, for example *Lamiaceae, Brassicaceae.*
- **Pericolpus:** Global simple, long furrow-like aperture with length/breadth ratio >2. The pollen grains with pericolpus apertures are aperture and the branches are more than twice referred to Pantocolpate/Pericolpate, for example Portulacaceae, Martyniaceae.

Sub-Divisions of the Pollen Surface

The areas on a pollen grain that are not occupied by apertures are given names depending on whether they are adjacent to colpi or pori.

According to Erdtman, (1952) Apocolpium is a region at the pole of a zonocolpate pollen grain delimited by lines connecting the apices of the colpi. Similarly Apoporium is an area at the pole of a zonoporate pollen grain that is delimited by a line connecting the borders of the pores.

Iversen and Troels -Smith (1950) used the term Polar area as synonym of apocolpium. Punt (1974) proposed a term Apocolpial field for a region at the pole of a parasyncolpate pollen grain, delimited by the margins of the anastomosing colpi.

Mesocolpium is the area of a pollen grain surface delimited by lines between the apices of adjacent colpi. Similarly Mesoporium is the area of a pollen grain surface delimited by lines between the margins of adjacent pores.

Apocolpium index (Synonym, Polar area index) is used to determine the ratio of the distance between the apices of two ectocolpi of a zonocolpate pollen grain to its equatorial diameter.

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Sporoderm Stratification

The pollen wall, the sporoderm is generally stratified, i.e., layered. The walls of the mature pollen, at least in angiosperms, consists of two fundamentally different layers, intine and an outer acetolysis resistant layer exine composed of sporopollenin.

The exine covers the entire pollen surface except germinal apertures where it is absent or greatly reduced. The exine of pollen grains can be divided into an outer sculptured sexine and an inner unsculptured nexine.

Sexine again consists of two layers: the outer, ectosexine and inner, endosexine. The sexine is generally constituted of a set of radially-directed rods supporting a roof-like structure (tectum or tegillum), which may be partially perforated or completely absent.

Exine Ornamentation

There are two different types of exine ornamentation, the structure or texture and the sculpturing. The structure comprises of all the internal (infratectal) baculae of various form and arrangements. All the ektexine characters belong to the structural features, while the sculpturing comprises external (supratectal) geometric features without reference to their internal construction.

'LO' Analysis

An optical section does not always make the fine structure of the sexine as clear as one might expect. A careful focusing through the sculpturing and patterning presented in a surface view of the grain provide a good deal of information.

Erdtman (1952) proposed the term LO-Analysis (derived from two Latin words: lux means light and obscuritas means darkness) which is a method for analysing patterns of sexine organisation by means of light microscopy. This method is valuable for elucidating exine patterns. The surface types show the holes or lower areas to be dark and any raised areas or projecting elements to be light.

On focusing carefully down through the exine their appearance would change due to a changing that diffraction images produced. For example, when focused at high level, raised sexine elements appear bright, whereas holes in the tectum are relatively dark.

At lower focus holes become lighter and the sexine elements become darken. If a reverse sequence occurred, i.e., a pattern of ornamentation that appears to show dark islands at high focus and that become bright at low focus, it is given the term OL- pattern. This system works very well as long as the pollen grains are embedded in such a medium having lower refractive index.

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Check Your Progress

7. Define pollen.
8. What is sporopollenin?
9. Where is pollen used?
10. What is palynology?

12.4 POLLEN STIGMA COMPATIBILITY

The phase of pollen biology, from pollination until the pollen tube reaches the embryo sac, is generally referred to as pollen-pistil interaction. It involves a series of reactions between the male gametophyte and sporophytic tissue of the stigma and style. These interactions result in generation of appropriate physical and chemical signals which elicit the required responses in the pollen or pistil. The major events that take place during pollen-pistil interaction are:

Pollen Adhesion

↓

Pollen Hydration

↓

Pollen Germination

↓

Pollen Tube Entry Into the Stigma

↓

Pollen Tube Growth Through the Style

↓

Pollen Tube Entry Into the Ovule

Stigma receives the pollen grains and provides all the conditions which are necessary for pollen germination. Before pollen germination, pollen adhesion and pollen hydration are the two important steps which also take place on the stigmatic surface. There are two types of stigma:

- Wet Stigma
- Dry Stigma

Wet Stigma: The stigma that secretes exudates on their stigmatic surface are called wet stigma. The stigmatic exudate is basically rich in lipid and phenols. Besides this, it also contains sugar, amino acids and proteins. The viscosity of the exudates is due to the presence of mucopolysaccharides. This exudate shows the non-specific esterase activity. In the wet stigma, the exudate begins to accumulate in the subcuticular region. During the releasing of exudate, both cuticle and pellicle become distended and get ruptured. The wet stigma consists of a secretory zone and storage zone. Many of the epidermal cells divide to form stigmatic papillae. Wet stigma is a characteristic feature of families such as Solanaceae, Liliaceae, Rosaceae and Malvaceae.

This stigmatic exudate helps in pollen adhesion, hydration and pollen germination. It protects the stigma from dehydration as well as from any microbial infection or insect attack. It also provides the nutrition for the developing pollen tubes.

Dry stigma: This stigma does not secrete any exudates but it consists of a hydrated layer known as pellicle over the cuticle. The proteins present in pellicle shows the non-specific esterase activity but pellicle does not show any kind of enzymatic property. As soon as the pollen grains land on this dry stigmatic surface, it becomes moist due to the presence of pellicle. The pellicle is considered to be the receptor sight for exine proteins on the stigma and the interaction between these two proteins help in the recognition of the pollen grains. Dry stigma is a characteristic feature of families such as *Brassicaceae, Asteraceae* and *Caryophyllaceae*.

The style traversed by the pollen tube to reach the ovule, may be hollow or solid. The solid style is characterized by the presence of conducting tissue or transmitting tissue. The cells of the transmitting tissue are ususllay uninucleate and densely cytoplasmic. In hollow style, a stylar canal is lined by a single layer of glandular canal cells.

Pollen adhesion on the stigmatic surface is the first step after the pollination. Pollen wall surface and extracellular matrix of stigma play an important role in pollen adhesion. In the plants having dry stigma adhesion is mediated by pollen coat whereas in wet stigma, stigmatic exudate is responsible for pollen adhesion as it consists of various proteins and enzymes. Due to pollen adhesion

Hydration of pollen grains is necessary for pollen germination. In wet stigma, exudate is responsible whereas in dry stigma it is pellicle layer which helps in pollen adhesion. It is because of the presence of lipids in pollen coat (dry stigma), and in exudates (wet stigma), which help pollen tubes to penetrate the stigma. Some mutants that lack lipid rich pollen coat is unable to hydrate or germinate on the stigmatic surface. Hydration stimulates physiological activation in the cytoplasm of pollen grains, also causes swelling of pollen grains leading to pollen germination. Exine ruptures and intine comes in the form of a pollen tube through aperture. Pollen tube consists the entire cytoplasm of pollen grains. In monosiphonous, only one pollen tube emerges but in polysiphonous more than one pollen tube emerges from the pollen grain but only one of them reaches into the ovule. In compound pollen grains such as pollinia (Asclepiadaceae), many pollen tubes emerge simultaneously and all of them continue to grow. The most distinct response of the stigma to incompatible pollen is the development of callose plug which appears at the tip of the pollen tube, thereby preventing its further growth.

After pollen germination, pollen tube traverses through the style. In hollow style, pollen tube grows through the stylar canal whereas in solid style it traverses through the intercellular spaces. After reaching into the ovary, pollen tube enters into the ovule. It may be through micropyle (porogamy), through chalazal end (chalazogamy) or through integument (mesogamy) (Refer Figure 12.17). Irrespective of the place of entry of pollen tube into the ovule, pollen tube enters into embryo sac through micropyle. It enters through filiform apparatus and one synergid forms the seat for pollen tube discharge in the embryo sac. One of the two synergids degenerates before or after the entry of pollen tube, whereas the other one degenerates shortly after the embryo sac has received the pollen tube discharge.

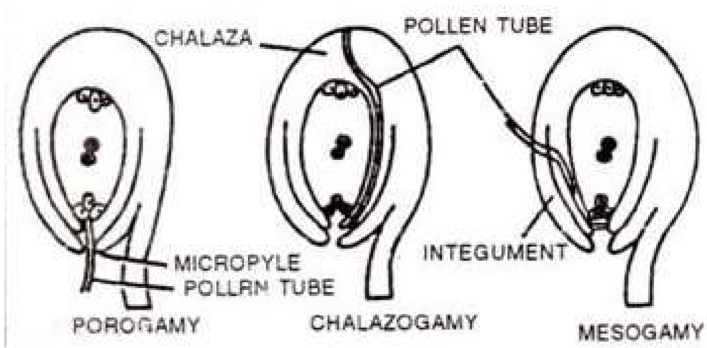

Fig. 12.17 *Modes of Entry of Pollen Tubes into the Ovule*

Check Your Progress

11. What is pollen-pistil interaction?
12. How many types of stigma are there?
13. What is dry stigma?

12.5 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. The male reproductive part of a flower is known as stamen, collectively known as androecium.
2. Each stamen has a lower sterile thread like structure filament and upper fertile two pollen sacs known as anther.
3. The median sterile portion of anther is called connective.
4. Primary sporogenous tissue either directly behaves as microspore mother cell or after few mitotic divisions it behaves as micropsore mother cells.
5. Epidermis is the outermost layer of anther and protective in nature. In *Alangium* stomata may occur in the epidermis.
6. Tapetum is the innermost layer of anther which provides the nourishment to the developing pollen grains and therefore also known as the nutritive layer.

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7. Pollen is a fine to coarse powdery substance comprising pollen grains which are male microgametophytes of seed plants, which produce male gametes (sperm cells).
8. Pollen grains have a hard coat made of sporopollenin that protects the gametophytes during the process of their movement from the stamens to the pistil of flowering plants, or from the male cone to the female cone of coniferous plants.
9. Pollen in plants is used for transferring haploid male genetic material from the anther of a single flower to the stigma of another in cross-pollination. In a case of self-pollination, this process takes place from the anther of a flower to the stigma of the same flower. Pollen is commonly used as food and food supplement. However, because of agricultural practices, it is often contaminated by agricultural pesticides.
10. The study of morphology of pollen grains is known as Palynology.
11. The phase of pollen biology, from pollination until the pollen tube reaches the embryo sac, is generally referred to as pollen-pistil interaction.
12. There are two types of stigma:
    - Wet Stigma
    - Dry Stigma
13. Dry stigma stigma does not secrete any exudates but it consists of a hydrated layer known as pellicle over the cuticle.

12.6 SUMMARY

- The male reproductive part of a flower is known as stamen, collectively known as androecium.
- Each stamen has a lower sterile thread like structure filament and upper fertile two pollen sacs known as anther. The median sterile portion of anther is called connective.
- Each anther is a bilobed and tetrasporangiate structure. In young anther, a single layer of epidermis is surrounded by meristematic cells.
- In each lobe, some cells below the epidermis (hypodermal cells), become more evident because of their larger size than neighbouring cells and prominent nuclei. These cells are known as archesporial cells, which are arranged in a plate like or crescent shaped manner.
- Primary sporogenous tissue either directly behaves as microspore mother cell or after few mitotic divisions it behaves as micropsore mother cells.
- Epidermis is the outermost layer of anther and protective in nature. In *Alangium* stomata may occur in the epidermis.

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- Endothecium is the subepidermal layer of the anther. Usually it is single layered but in some plants it becomes multilayered. In *Coccinia indica*, it is two layered.
- The cells are radially elongated and develop thickenings at maturity. These thickenings are made up of á-cellulose and slightly lignified. Thickenings help in the dehiscence of anther because of its hygroscopic nature.
- The cells of middle layer are short-lived and degenerate before the anther dehiscence. In *Momordica charantia*, soon after the meiosis middle layer degenerates.
- Tapetum is the innermost layer of anther which provides the nourishment to the developing pollen grains and therefore also known as the nutritive layer.
- Tapetum is composed of single layer of cells characterized by the presence of dense cytoplasm and prominent nuclei. Sporogenous tissue is completely surrounded by tapetum.
- Amoeboid tapetum is also known as invasive or periplasmodial tapetum. This tapetum is characterized by the early degeneration of inner and radial walls of its cells.
- Secretory tapetum is also known as parietal or glandular tapetum. Secretory tapetum is present in most of the angiosperms.
- At the pre-meiotic stage of microspore mother cell, tapetal cells are thin and all cell organelles such as mitochondria, ribosomes, plastids and dictyosomes are present.
- The cell walls are also thin composed of middle lamella with a small amount of cellulosic primary wall. Some special kind of spherical cells are also present known as pro-ubisch bodies.
- The number of plastids and microtubules are reduced. At this stage pro-ubisch bodies pass into anther locule from tapetal cells and now they are known as ubisch bodies.
- Endomitosis type is the replication of chromosomes and separation of chromatids within the intact nuclear membrane without spindle formation.
- Tapetum plays an important role in pollen wall formation. Exine chiefly composed of sporopollenin is mainly contributed by tapetum.
- Tapetum is also concerned with the synthesis of callase enzyme which is responsible for the dissolution of callose wall around the microspore tetrad.
- Pollen grains or micropsores represent the first cell of male gameophyte. Pollen grains are formed due to the meiotic division in the Microspore Mother cell. This division is completed in two steps.
- Microspore or pollen grains represent the first generation of male gametophyte. After releasing from the tetrads, each microspore is a uninucleate structure.

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- In entomophilous plants, an oily layer is formed on the outer surface of pollen grains known as pollen kitt.
- Sticky nature, colour and odour of pollen grains are due to its presence in insect-pollinated species. Pollen kitt is made up of carotenoid or flavonoid pigments and therefore imparts yellow or orange colour to the pollen grains.
- Pollen is a fine to coarse powdery substance comprising pollen grains which are male microgametophytes of seed plants, which produce male gametes (sperm cells).
- Pollen grains have a hard coat made of sporopollenin that protects the gametophytes during the process of their movement from the stamens to the pistil of flowering plants, or from the male cone to the female cone of coniferous plants.
- Pollen in plants is used for transferring haploid male genetic material from the anther of a single flower to the stigma of another in cross-pollination. In a case of self-pollination, this process takes place from the anther of a flower to the stigma of the same flower.
- The study of morphology of pollen grains is known as Palynology.
- After the meiotic division of microspore mother cell, a group of four pollen grains are formed (tetrad).
- Each pollen grain has two poles at opposite end of the polar axis. The proximal pole is towards the centre of the tetrad whereas distal pole is away from the centre of the tetrad.
- The pollen grains are produced within the anther of the flower. Pollen mother cells originate from the sporogenous tissue of the anther which later divide meiotically to form four pollen grains called tetrad.
- The orientation of polarity is an important criterion in identification and description of pollen grains, as apertural position is of primary phylogenetic and functional significance.
- The part of the pollen grains which is nearest to the centre of the tetrad is the proximal pole and that towards the opposite side is the distal pole. The imaginary line between the proximal and distal pole of the grain is called the Polar Axis (PA) which passes through the centre of the spore to the centre of the tetrad.
- In apolar spores, poles or polar regions cannot be distinguished in individual spore (monad) after separation from tetrad.
- In isopolar grains the distal and proximal faces (above and below the equatorial plane) look alike.
- In heteropolar grains the two faces are distinctly different, either in shape, ornamen-tation or apertural system.

12.7 KEY WORDS

NOTES

- **Androecium:** The male reproductive part of a flower is known as stamen, collectively known as androecium.
- **Anther:** Each stamen has a lower sterile thread like structure filament and upper fertile two pollen sacs known as anther.
- **Connective:** The median sterile portion of anther is called connective.
- **Pollen**: Pollen is a fine to coarse powdery substance comprising pollen grains which are male microgametophytes of seed plants, which produce male gametes.
- **Palynology**: The study of morphology of pollen grains is known as palynology.
- **Pollen-pistil interaction:** The phase of pollen biology, from pollination until the pollen tube reaches the embryo sac, is generally referred to as pollen-pistil interaction.
- **Wet stigma**: The stigma that secretes exudates on their stigmatic surface are called wet stigma.

12.8 SELF ASSESSMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. What is anther?
2. Draw a well-labelled diagram to show the structure of stigma.
3. What is endothecium?
4. Define amoeboid tapetum,
5. List the functions of tapetum.
6. Draw a well-labelled diagram of development of male gametophyte.
7. What is polarity?

Long Answer Questions

1. What is anther? Explain with the help of examples.
2. Explain anther development Stages.
3. Write a note on tapetum.
4. Discuss about nuclear divisions in tapetal cells.
5. Elaborate a note on sporogenous tissue.

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6. Briefly discuss about the development of male gametophyte.
7. Discuss in detail about pollen morphology.
8. Write a note on NPC system.
9. Discuss in detail about pollen stigma compatibility.

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UNIT 13 MEGASPOROGENESIS AND NUTRITION OF EMBRYO SAC

NOTES

Structure

13.0 INTRODUCTION

Megasporogenesis is the process of formation of megaspores from the megaspore mother cell. In the hypodermal region of nucellus towards the micropylar end develops a primary archesporial cell. It is distinguished from the other cells by its dense cytoplasm and a prominent nucleus. The archesporial initial either acts directly as a megaspore mother cell or divides periclinally into an outer primary parietal cell and the inner primary sporogenous cell which later functions as megaspore mother cell. In the former case, there is no nucellar tissue between the megaspore mother cell and nucellar epidermis. Such ovules are called tenuinucellate and are characteristics of gamopetalous and dicotyledons with unitegmic ovules.

In the latter case where a primary parietal cell and a primary sporogenous cell is formed by archesporial initial, the parietal cell divides repeatedly as a result of which sporogenous cell becomes deep seated in the nucellar tissue. Such ovules are known as crassinucellate and are formed in polypetalous dicotyledons with bitegmic ovules. The megaspore mother cell divides meiotically to form four haploid megaspores. These are arranged in a longitudinal row (linear tetrads). Occasionally, megaspore cells arrange themselves in T-shaped or inverted T-shaped tetrads. Megaspore is the first cell of the female gametophyte. Among the linear tetrads, three megaspores towards the micropylar end degenerate. The lower most, i.e., the chalazal megaspore enlarges and remains functional. Its nucleus undergoes three divisions to produce eight nuclei. The chalazal megaspore later produces an embryo sac.

The ovule develops as multicellular placen-tal outgrowth including the epidermal and a number of hypodermal cells. With further deve-lopment, this gives

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rise to nucellus and one or two integuments from its basal region. In ovules, with two integuments, usually the inner one is formed first than the outer one. The inner one is more delicate and inconspicuously developed than the outer one. One hypodermal cell of the nucellus becomes differentiated from the other by its bigger size, dense cytoplasm and conspicuous nucleus, called archesporial cell. The archesporial cell divides transversely and forms an inner primary sporogenous cell and an outer primary parietal cell. During their early growth, the embryos of all vascular plants exist as virtual parasites depending for nutrition on either the gametophyte or the previous sporophyte generation through the agency of the gametophyte or, in the special case of the angiosperms, upon an initially triploid tissue, the endosperm, which is itself nourished by the parent sporophyte. The early nutrition of the sporophyte in ferns, horsetails, and club mosses such as Lycopodium is clearly provided by the gametophyte. In these groups the young sporophyte produces a multicellular structure, the foot, which remains embedded in the tissues of the gametophyte throughout early development withdrawing nutrients.

The endosperm is a tissue produced inside the seeds of most of the flowering plants following fertilization. It is triploid in most species. It surrounds the embryo and provides nutrition in the form of starch, though it can also contain oils and protein. This can make endosperm a source of nutrition in animal diet. For example, wheat endosperm is ground into flour for bread (the rest of the grain is included as well in whole wheat flour), while barley endosperm is the main source of sugars for beer production. Other examples of endosperm that forms the bulk of the edible portion are coconut meat and coconut water, and corn. Some plants, such as orchids, lack endosperm in their seeds.

In this unit, you will study about megasporogenesis o female gametophyte, nutrition of embryo sac and endosperm types in detail.

13.1 OBJECTIVES

After going through this unit, you will be able to:

- Discuss about megasporogenesis of female gametophyte
- Explain nutrition of embryo sac
- Analyse endosperm types

13.2 MEGASPOROGENESIS: FEMALE GAMETOPHYTE

Female reproductive structure is known as gynoecium, which is made up of one to many carpels. Each carpel consists of a basal swollen portion ovary, middle portion style and the upper most portion stigma for receiving pollen grains (Refer Figure 13.1). Ovary bears ovules which develop into seeds after fertilization.

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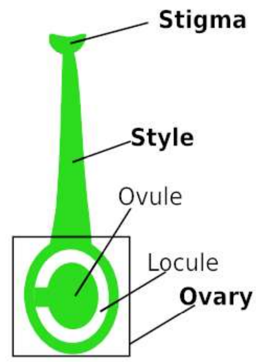

Fig.13.1 *Structure of a Carpel*

Each ovule consists of a stalk through which it is attached to the placenta known as funicle. The cells of ovule are parenchymatous known as nucellus. Nucellus is surrounded by one or two integuments, except a pore at the apex, This pore is known as micropyle which allows the entry of pollen tube into ovule. The basal region of the ovule, where funiculus is attached is known as chalaza. Inside the ovule, there is embryo sac also known as female gametophyte. An embryo sac is a 7 celled and 8 nucleate structure. Of these 8 nuclei, three cells present at micropylar end form egg apparatus (one egg cell and 2 synergids), three cells present at chalazal end form antipodal cells and 2 nuclei present in the centre form polar nuclei or secondary nucleus (Refer Figure 13.2).

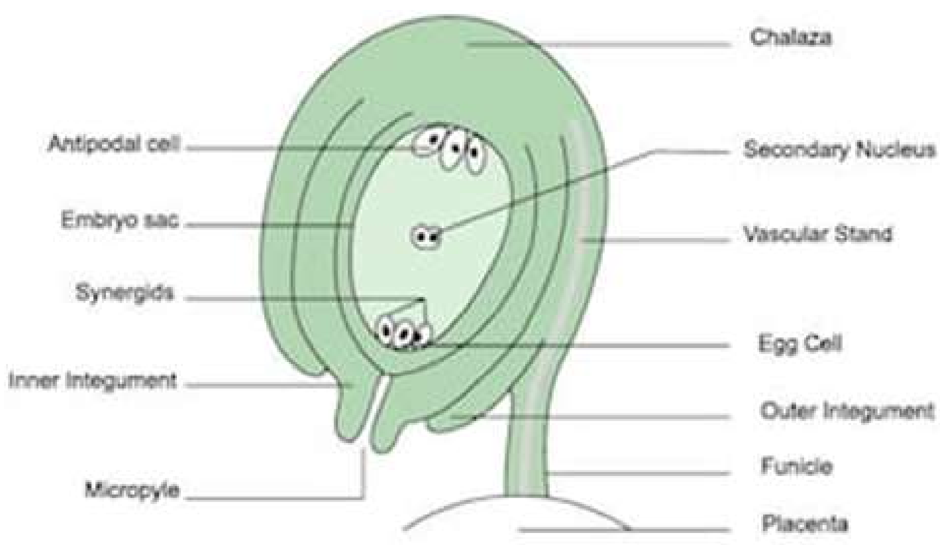

Fig. 13.2 *Structure of An Ovule*

Types of Ovules

Following are the types of ovules (Refer Figure 13.3):

- **Atropous or Orthotropous:** The ovule is straight, so that the micropyle, chalaza and funicle lie in a straight line. For example, *Polygonum*, *Piper*.

- **Anatropous:** In this type, the body of the ovule is inverted through 180^0, because of this micropyle come close to the chalazal end. The micropyle and chalaza lie on the same line but funicle lies parallel to it. It is the most common type of ovule present in angiosperms. For example, *Helianthus*, *Castor.*
- **Amphitropous:** When the curvature of the ovule is so much prominent that the embryo sac also bends and becomes a horse-shoe shaped structure. For example, *Poppy.*
- **Campylotropous:** In this type the curvature of the ovule is less than that of the anatropous ovule. Here, micropyle and chalaza do not lie at the straight line and funicle lies at the right angle to the chalaza. For example, *Pea*, *Mustard.*
- **Hemitropous:** In this type, ovule is curved at 90^0, i.e., horizontally placed on the funicle. The nucellus and integuments lie at the right angles to the funicle. For example, *Ranunculus.*
- **Circinotropous:** In this type, nucellar protuberance is at first in the same line as the axis, but the rapid growth on one side makes it anatropous. The curvature continues till the ovule has turned over, completely with the micropylar end again pointing upward. For example, *Opuntia.*

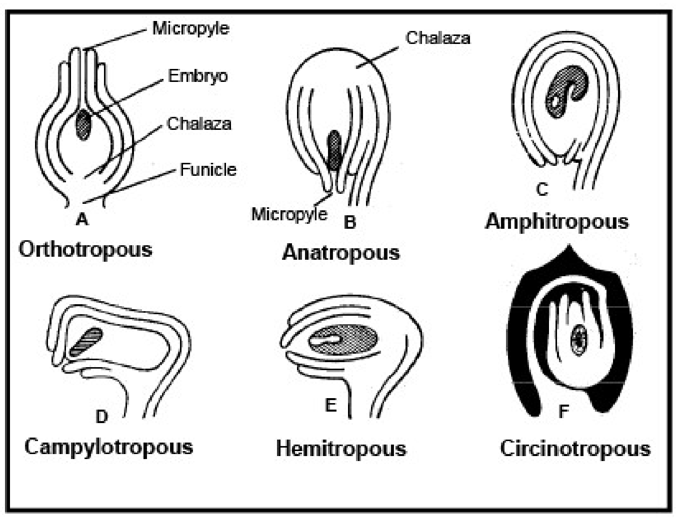

Fig. 13.3 *Different Types of Ovules*

Development of Ovule

The development of ovule initiates as a small hemispherical protrusion on the placenta. First division is periclinal which takes place in the epidermis of the placenta. It is soon followed by various anticlinal divisions and therefore the protrusion gets enlarged. After the differentiation of archesporium, integuments start developing. In bitegmic ovules, inner integument develops earlier and it develops from the epidermis whereas outer integument develops from the sub-epidermal layer (Refer

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Figure 13.4). Integuments cover the nucellus except at the pore which is known as micropyle.

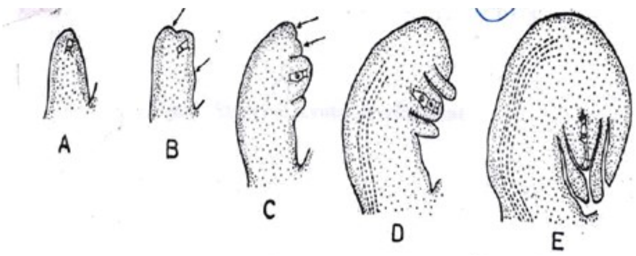

Fig. 13.4 *Stages in the Development of Ovule*

Parts of Ovule

The various parts of the ovule are as follows:

Integuments: Ovule having one integument is called unitegmic and those having two integuments are called bitegmic. Integuments are absent in the ovules of some plants such as, *Olax imbricata*, *Crinum*, etc. These ovules are known as ategmic. Bitegmic ovules usually occur in Polypetalae and monocotyledons, whereas unitegmic ovules are present in Sympetalae. It is considered that unitegmic condition of the ovule has been developed from the bitegmic ovule either by the fusion of two integuments or due to the suppression of one of the integument. In bitegmic ovules, both the integuments arise independently, but the inner integument differentiates earlier but the growth of outer integument is faster than inner integument. In Betulaceae and Ranunculaceae unitegmic condition of the ovule is due to the fusion of both the integuments whereas in Salicaceae it is due to the abortion of inner integument. In some members of Cactaceae, a prominent air-space has been observed between the outer and inner integuments at chalazal end (Refer Figure 13.5). It has been reported in *Bassia*, *Tetragonia tetragonioides*.

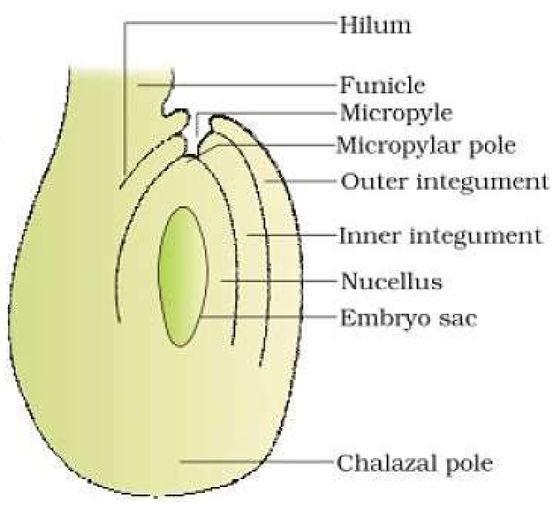

Fig. 13.5 *L.S. of an Ovule of Brassica at Mature Embryo Sac Stage to Show the Prominent Air Space Between the Two Integuments*

In Euphorbiaceae, due to the proliferation of cells of the outer integument at the tip, a fleshy whitish structure is present in mature seed which is known as caruncle (Refer Figure 13.6). Caruncle is sugary in nature and therefore eaten by ants and thus helps in seed dispersal.

Fig. 13.6. Caruncle in the Seed of Castor

In some plants, a colourful appendage develops in seed from the funiculus or testa to attract the animals. It is known as aril which partially or wholly covers the ovule after fertilization. Aril is also considered as third integument. In nutmeg, aril surrounds the seed which is used as a spice called mace (Refer Figure 13.7a). In litchi, the edible part is also aril (Refer Figure 13.7b).

Fig. 13.7 *(a) Aril Surrounding the Nutmeg Seed in Myristica*
(b) Edible White Part of Litchi

In Sympetalae, with unitegmic and tenuinucellate ovules, nucellus is degenerated or reduced in the early stage of ovule development. It is represented by a single layer of cells. The innermost layer of the integument develops special kind of cells which provide the nourishment for the developing embryo sac. This tissue is known as endothelium or integumentary tapetum. The cells are radially elongated, rich in cytoplasmic content and store starch and fats (Refer Figure 13.8). Sometimes these cells also show polyploidy. The endothelial cells also show the meristematic and secretory activity at ultrastructural level as these cells possess high concentration of proteins, RNA, carbohydrates and other enzymes. Adventive embryony has also been observed by these cells. The presence of endothelium has been observed in 65 families of dicotyledons.

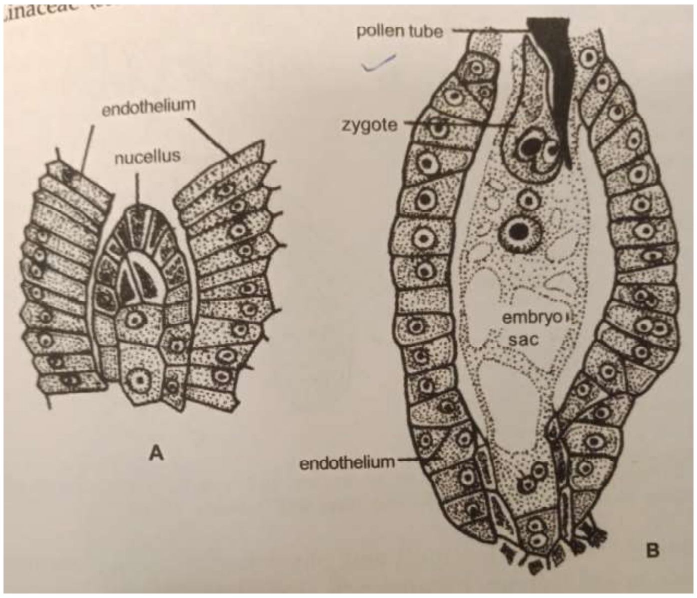

Fig. 13.8 *Endothelium or Integumentary Tapetum*

Micropyle: It is a small pore present towards the apex of the ovule, which helps in the entry of pollen tube into the embryo sac. In bitegmic ovules, either it is formed by both the integuments or only by the inner integument. In Euphorbiaceae and Podostemaceae this pore is formed by the outer integument. When both the integuments are involved in the formation of micropyle, the passage formed by outer integument is known as exostome and by the inner integument is known as endostome. In some plants where exostome and endostome is not in a straight line, then a zig-zag path is formed. In leguminosae the exostome and endostome are at the right angles to each other.

Nucellus: Nucellus is thin walled parenchymatous cells, surrounded by integuments. Each ovule has a single nucellus but as abnormality twin nucelli has also been observed in some plants such as *Aegle marmelos*, *Hydrocleis nymphoides*, and *Herminium angustifolium*.

In Sympetalae the archesporial cell differentiated below the nucellar epidermis, does not undergo any division and directly behaves as megaspore mother cell. Such ovules are called tenuinucellate ovules where sporogenous cell is hypodermal and nucellar tissue around sporogenous cell is single layered. In most of the plants belonging to Polypetalae, archesporial cells divides by a transverse

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division, resulting into the formation of outer parietal cell and inner sporogenous cell. The parietal cell again divides by periclinal and anticlinal divisions forming a massive nucellar tissue in which sporogenous cell is deeply embedded. Such ovules are called crassinucellate ovules (Refer Figure 13.9). Tenuinucellate ovule is considered to be phylogenetically more advanvced as compared to crassinucellate ovule. In some plants nucellar epidermis also divides to form the massive nucellar tissue where the sporogenous cell becomes sub-hypodermal, this condition is known as pseudo-crassinucellate.

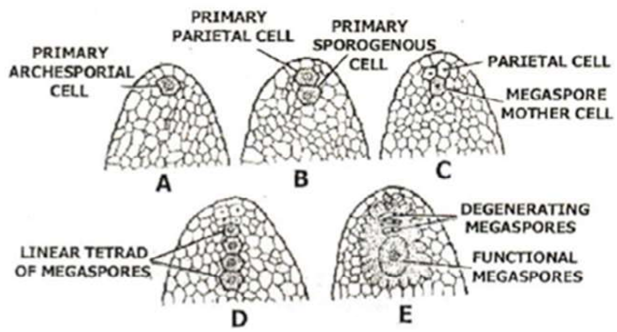

Fig. 13.9 *Various Stages of Megasporogenesis*

Usually the nucellus is consumed by embryo sac and endosperm during their development. Therefore in mature ovule nucellus is either degenerated or very much reduced but in some families such as *Piperaceae, Amaranthaceae, Cannaceae* and *Zingiberaceae* nucellar tissue is persistent in seed. Persistent nucellus is known as perisperm and it functions as nutritive tissue (Refer Figure 13.10).

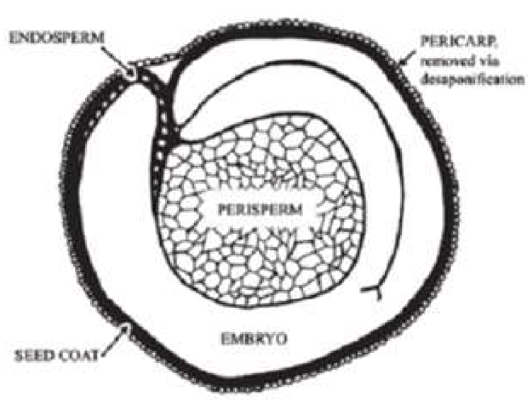

Fig. 13.10 *Perisperm in Black Pepper*

Hypostase: A group of cells with lignified cell walls present below the embryo sac and above the vascular supply is known as hypostase. These cells have poor cytoplasmic content. Sometimes the cells of the hypostase, surround a portion of female gametophyte and sometimes even extend into the micropylar half of the ovule. Hypostase has been observed in many families such as *Liliaceae, Zingiberaceae, Euphorbiaceae, Theaceae, Apiaceae* and *Crossosomataceae*.

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Van Tieghem was the first person to coin this term. Some scientists consider that this tissue help in maintaining the water balance during the dormancy of seeds while some consider its role in protection in mature seeds by producing enzymes and hormones.

Hypostase is derived from the nucellar cells below the embryo sac while epistase originates from the nucellar epidermis above the embryo sac.

Obturator: In some families like *Lamiaceae, Acanthaceae, Anacardiaceae, Magnoliaceae* some uni or multicellular hairs originating from placenta or funiculus present at the basal part of the ovule known as obturator (Refer Figure 13.11). It helps in directing the growth of pollen tube towards the micropyle. There may be variation in their origin, morphology, anatomy and development.

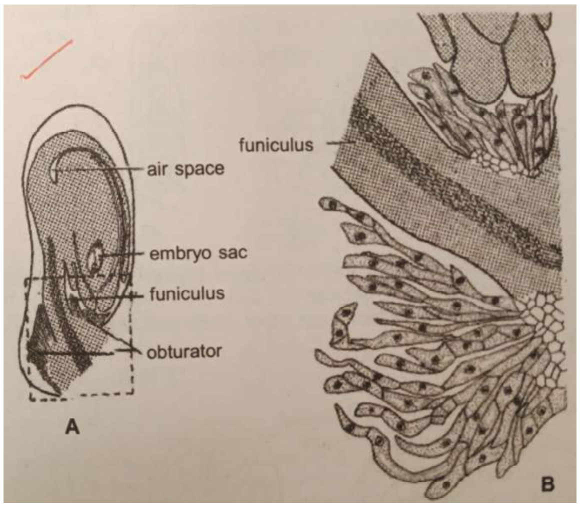

Fig. 13.11 *L.S. of an Ovule at the Mature Embryo Sac Stage*

Megasporogenesis

During the development of ovule, a single hypodermal cell in the nucellus differentiates as the archesporial initial (Refer Figure 13.12). It becomes more prominent than its other neighbouring cells because of its large size, dense cytoplasm and large nucleus. Usually archesporium is single celled in ovule but in *Paeoniaceae* and *Crossomataceae* multicellular archesporium is formed but all the cells are not functional. Multicellular archesporium is a characteristic feature of family *Loranthaceae*. In crassinucellate ovule, the archesporial cell divides periclinally forming outer primary parietal layer and inner primary sporogenous cell. Sporogenous cell now behaves as megaspore mother cell. Whereas in tenuinucellate ovule, archesporial cell directly functions as megaspore mother cell.

Megaspore mother cell represents the last cell of sporophytic generation. It undergoes a reductional division to form linear tetrad of haploid megaspores. Of the four megaspores of a tetrad, it is usually the chalazal megaspore is functional and other three degenerates by providing nutrition to the functional megaspore (Refer Figure 13.12). The functional megaspore is the first cell of female

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gametophyte. As the functional megaspore grows, many small vacuoles appear in its cytoplasm which later join together to form a large vacuole. The nucleus undergoes three mitotic divisions to form eight nuclei. Nuclear division is not followed by wall formation.

The first mitotic division is oriented along the vertical axis of the ovule as a result two daughter nuclei are formed. These two daughter nuclei are separated by a large central vacuole. As the vacuole enlarges, one nucleus is moved towards the chalazal end and other to the micropylar end. These two nuclei divide twice through mitotic division and therefore four nuclei are formed at each pole. At this stage, all eight nuclei are present in the common cytoplasm. Of the four nuclei, three nuclei at the micropylar end form egg apparatus (one egg and two synergids) and fourth one is moved towards the centre of the embryo sac to form the upper polar nucleus. The two synergids are in direct contact with the wall of embryo sac. Out of four nuclei present at chalazal end, three nuclei form antipodal cells and the fourth one form the lower polar nucleus. Both of the polar nuclei lie in the centre of the embryo sac and also known as secondary nuclei. This type of embryo sac development is known as monosporic 8-nucleate embryo sac or Polygonum type because the embryo sac develops from a single megaspore of the tetrad, which is present at the chalazal end. It is the most common type of embryo sac found in flowering plants.

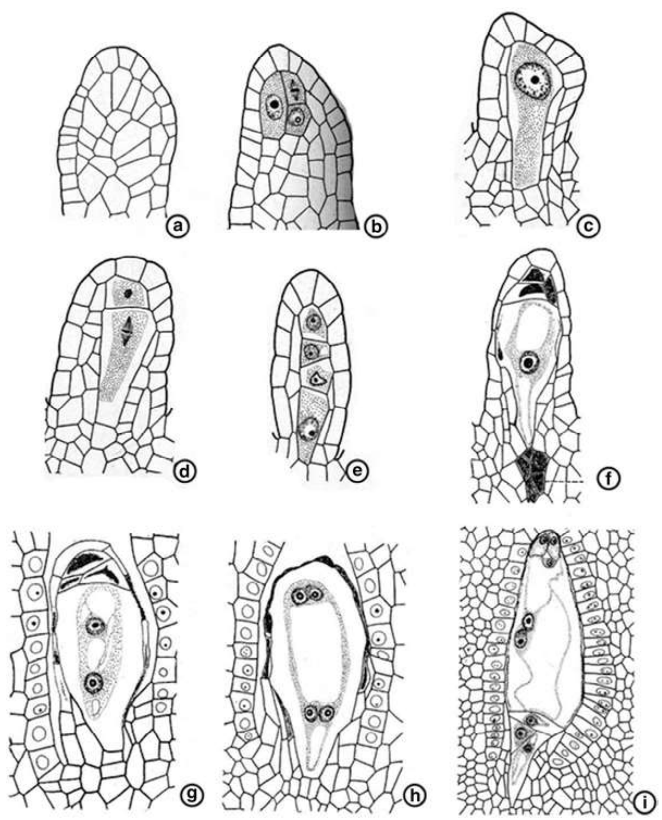

Fig. 13.12 *L.S. of an Ovule Showing the Stages of Megasporogeneis and Megagametogenesis*

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The above Figure 13.12 shows the L.S. of an ovule showing the stages of megasporogeneis and megagametogenesis in which, a). Ovule showing No Differentiation; b). Archesporial Cell has been Differentiated; c). Megaspore Mother Cell; d). Dyad Stage; e). Tetrad Stage; f). Functional Megaspore and other 3 Megaspores Degenerating; i). L.S. of Ovule Showing Different Stages of Megagametogenesis.

13.2.1 Types of Embryo Sacs

In addition to monosporic embryo sac (female gametophyte), in some plants embryo sac can also develop from two or all the four megaspores. On the basis of the number of megaspores involving in the formation of embryo sac, it has been classified into three categories:

- Monosporic
- Bisporic
- Tetrasporic

Monosporic: Megaspore mother cell divides by a single meiotic division and four megaspores are formed, arranged in a linear tetrad, out of which only a single megaspore is functional which gives rise to the embryo sac. A monosporic embryo sac develops from a single megaspore and therefore, all nuclei of the embryo sac are genetically similar. Monosporic embryo sacs are of two types (Refer Figure 13.13):

- **Polygonum Type**: Here the embryo sac develops from the chalazal megaspore and this megaspore nucleus divides by three mitotic divisions to form 8-nucleate embryo sac (3 antipodals, 1 egg, 2 synergids and 2 polar nuclei). It is the most common type of embryo sac.
- **Oenothera Type**: This type of embryo sac develops from the micropylar megaspore but this functional megaspore divides only twice and therefore four nuclei are formed. Out of these four, three form egg apparatus (1 egg and 2 synergids) and fourth one functions as polar nucleus (n) and therefore, the endosperm is diploid (2n). This type of embryo sac is a characteristic feature of family Onagraceae.

Bisporic: Megaspore mother cell divides by first meiotic division which is accompanied by wall formation, so that a dyad is formed. Only one of the dyad cells undergoes the second meiotic division, whereas the other one degenerates. In the functional dyad, after the second division, cell wall formation does not take place. Both the megaspore nuclei of a dyad involve in the formation of embryo sac. Each nucleus undergoes two mitotic divisions to form eight nuclei. Bisporic embryo sacs are of two types:

- **Allium Type**: Here the embryo sac develops from the chalazal dyad cell.
- **Endymion Type**: Here the embryo sac develops from the micropylar dyad cell.

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Tetrasporic Embryo Sacs: Megaspore mother cell divides by a meiotic division and it is not followed by cytokinesis. Therefore, all the four megaspores are present in a common cytoplasm forming a coenomegaspore. Because all the four nuclei are involved in the development of embryo sac, therefore tetrasporic embryo sac is more heterogenous than bisporic embryo sac. On the basis of nuclear fusion and number of the mitotic divisions tetrasporic embryo sacs are of the following types:

- **Adoxa Type**: All the nuclei divide by a single mitotic division and therefore 8 nuclei are formed. The arrangement of 8 nuclei is similar to that of Polygonum type**.**
- **Plumbago Type**: In this type also, all the nuclei divide by a single mitotic division and therefore 8 nuclei are formed. The arrangement of 8 nuclei is very much different to that of Polygonum type, the mature embryo sac consists of an egg cell and a four nucleate central cell. The other three nuclei are cut-off as peripheral cells. Synergids and antipodals are absent in this type of embryo sac.
- **Penaea Type**: In this type of embryo sac, all the nuclei divide by two mitotic divisions resulting into the formation of 16 nuclei. These 16 nuclei are arranged themselves in 4 groups of three cells each, one group present at micropylar end, one at chalazal end and other two groups arranged at the lateral side. The rest 4 nuclei behave as polar nuclei. Triad present at the micropylar end functions as egg apparatus. This type of embryo sac is characterized by the presence of an egg apparatus and four polar nuclei. No antipodal cells are present in the embryo sac.
- **Peperomia Type**: Here also, nuclei present in coenomegaspore divide by two mitotic divisions resulting into the formation of 16 nuclei. The mature embryo sac at the micropylar consists of an egg and one synergid, six peripheral cells which can be compared as antipodal cell, and a central cell with eight polar nuclei. This type of embryo sac is characterized by the presence of an egg with a single synegid.
- **Drusa Type**: This type of embryo sac consists of 16 nuclei. The mature embryo sac at micropylar end consists of an egg apparatus, two nuclei functions as polar nuclei and remaining 11nuclei act as antipodal cells. This type of embryo sac is characterized by the presence of large number of antipodal cells.
- **Fritillaria Type**: In some plants, after the second meiotic division three megaspore nuclei fuse to form a triploid nucleus at the chalazal end of the coenomegaspore and the fourth one remain haploid at the micropylar end. Each of these nuclei divides by a two mitotic division and therefore, four triploid nuclei at the chalazal end and four haploid nuclei at the micropylar end are formed. The mature embryo sac consists of an egg apparatus (an egg and 2 synergids) with all the cells haploid at micropylar end, three

triploid nuclei at chalazal end as antipodal cell and a central cell with two polar nuclei (one haploid and one triploid).

- **Plumbagella Type**: Here the early development of embryo sac is similar to that of Fritillaria type and thus a triploid nucleus at chalazal end and a haploid nucleus at micropylar end are formed. Each of these nuclei divides by a single mitotic division and therefore two groups of two nuclei are formed. One haploid nucleus forms the egg at micropylar end with no synergids, one triploid nucleus at chalazal end form antipodal cell. One haploid nucleus from micropylar end and one triploid nucleus from chalazal end move towards the centre and form tetraploid polar nucleus. This type of embryo sac is characterized by the presence of a single egg with no synergids.

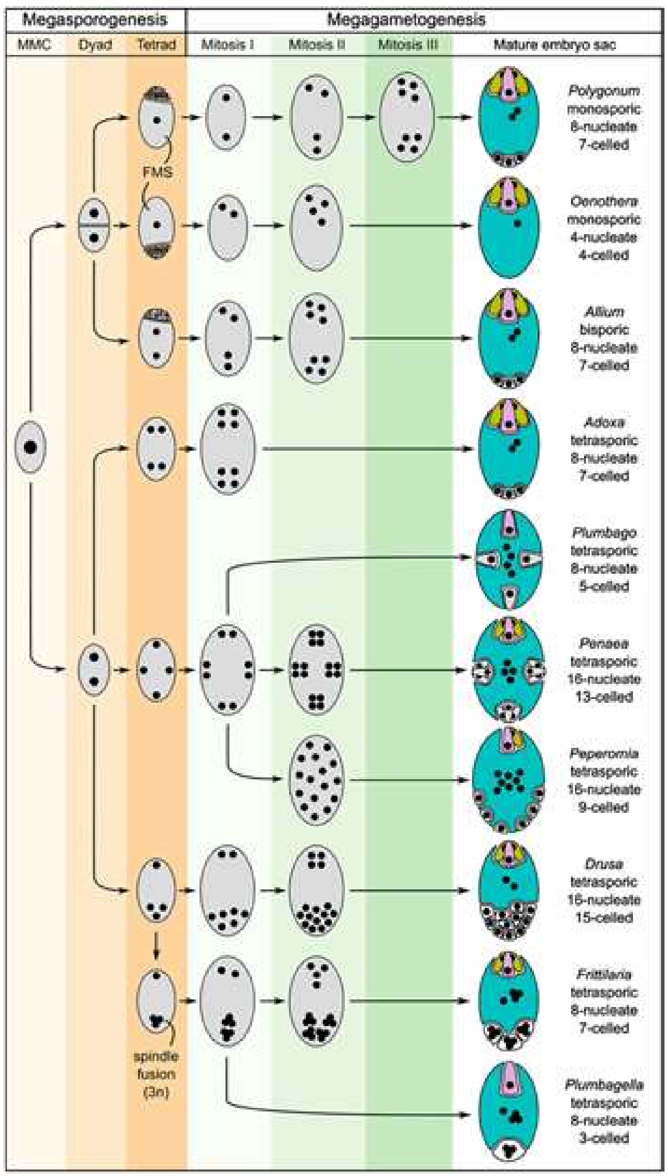

***Fig. 13.13** Different Types of Embryo Sac Development*

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Placentation and Their Types

The arrangement of ovules in the ovary is called placentation. Depending on the number of locules and the position of ovules in the ovary, placentation is of the following types (Refer Figure 13.14):

- **Marginal Placentation**: Gynoecium is monocarpellary and unilocular and the placenta is borne on the fused margins of the same carpel. The ovules are present along the ventral sutures of the carpel. For example, *Leguminoseae*.
- **Axile Placentation**: Gynoecium is multicarpellary, syncarpous and multilocular. The placenta developes from the central axis of a compound ovary and locules are borne on the fused margins of the same carpel. For example, *Solanaceae*.
- **Parietal Placentation**: Gynoecium is multicarpellary, syncarpous and unilocular and the placenta is born on the fused margins of the two adjacent carpels. For example, *Cucurbitaceae*.
- **Free-central Placentation**: Gynoecium is multicarpellary, syncarpous and unilocular. The placentae are born on fused margins of the same carpel but margins detach from the ovary wall during development of gynoecium. Therefore, ovules appear to arise from the central column. For example, *Carypohyllaceae*.
- **Basal Placentation**: Gynoecium is unilocular and a single ovule arises from the base of the ovary. For example, *Asteraceae*.
- **Superficial Placentation**: Here the ovules develop over the entire inner surface of the carpels. This type of placentation is present in multicarpellary ovary. For example, *Nymphaeaceae*.

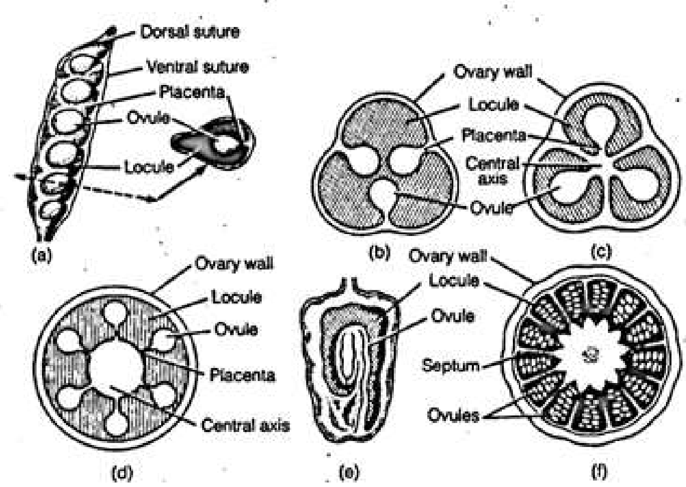

Fig. 13.14 *Different types of Placentation*

Structure of Mature Embryo Sac

A mature embryo sac is a 7-celled and 8 nucleate structure. It consists of an egg apparatus (one egg and two synergids) at micropylar end, three antipodal cells at chalazal end and two polar nuclei in the centre (Refer Figure 13.15). However, the number of synergids, antipodals and polar nuclei vary in different types of embryo sacs. All the cells of embryo sac are associated with each other through plasmodesmata but the wall of embryo sac lacks plasmodesmata. Sometimes wall is covered by a thin layer of cutin.

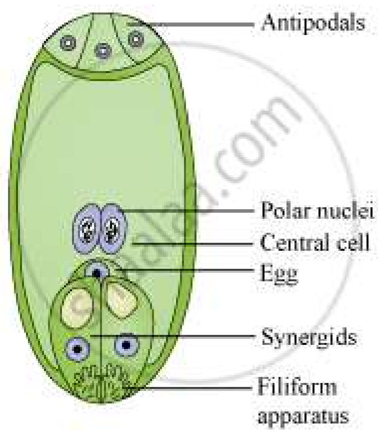

Fig. 13.15 *Structure of a Mature Embryo Sac*

Egg Cell

Egg cell is present at micropylar end with two synergids. Egg cell is connected through synergids and polar nucleus through plasmodesmata. The wall of the egg cell is thicker towards the micropylar end where it is associated with synergids and consists of cellulosic cell wall, whereas at the chalazal end, it is covered by a thin plasma membrane. In *Gossypium*, *Maize* and *Torenia* cell wall is completely absent towards the chalazal end. The egg cell shows polarity during its development. At the micropylar end a large vacuole appears, whereas chalazal end shows the dense cytoplasmic content. It is just reverse to that of the synergids. The egg cell also shows the presence of plastids and ribosomes. Young egg cell is physiologically more active than mature ones because of the presence of more cell organelles in young stage. Ultrastructure studies showed that towards the maturity mitochondria have less or few cristae, dictyosomes are either less in number or nonfunctional. The egg cell also contains the starch which is consumed during fertilization. In some embryo sacs where synergids are absent, finger like projections have been observed at the micropylar end of the egg cell such as *Plumbago capensis*. These projections also show the presence of insoluble polysaccharide like synergids. These features suggest that in the absence of synergids egg cell takes over the function of synergids.

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Synergids

Synergids attached to the micropylar end of the embryo sac which partially embraces the egg cell. The synergids have a distinct cell wall towards the micropylar end whereas at the chalazal end it is thin. Synergids also show the polarity but it is opposite to that of egg cell. In the synergids, chalazal end is vacuolated whereas micropylar end shows the presence of well developed mitochondria, endoplasmic reticulum and dictyosomes especially towards the micropylar end. This region is also rich in lipids, RNA and proteins.

Some finger like projections are present at the micropylar end of the synergids called filiform apparatus. These projections arise from the cell wall of the synergids and penetrate into the cytoplasm of the central cell. These projections show the presence of hemicellulose, pectin, callose, proteins and rich in insoluble polysaccharide. Starch is absent in *Maize* and *Petunia*. The shape of filiform apparatus is variable. It may be spherical as in *Torenia*, wedge shaped between the tips of synergids as in *Petunia* and *Helianthus*. In some cases, synergids may persist till the fertilization.

Synergids are ephemeral in nature. One of the two synergids of embryo sac degenerates before the entry of pollen tube whereas the other one degenerates after the entry of pollen tube into the embryo sac. Synergid haustoria has also been reported in some species such, as *Sedum sempervivoides* and *Qunichamalium chilense.*

Functions of Synergids

- Filiform apparatus plays an important role in guiding the growth of pollen tube to the synergids.
- Filiform apparatus increase the surface area of the plasma membrane and therefore facilitates the transport of substances into and out of the synergid.
- Filiform apparatus also help in the absorption and transportation of substances into the embryo sac from nucellus.
- Degenerated synergid forms the seat for the pollen tube discharge into the embryo sac.

Antipodal Cells

Antipodal cells are present at chalazal end of the embryo sac. There is so much variation in the number of antipodal cells. Antipodal cells are usually ephemeral, which degenerate before or soon after fertilization. In *Caltha palustris*, these antipodal cells persist up to the octant stage of the proembryo. In grasses these cell divide by several mitotic division, results into the formation of large number of antipodal cells. The highest number of antipodal cells has been reported in *Sasa paniculata.* Multinucleate condition has also been observed in some pants such, as *Tagetes*. Sometimes antipodal cells show polyploidy condition as in

Chrysanthemum. In some plants such as *Haplopappus* and *Quinchamalium* antipodal cells develop haustoria. In *Argemone*, antipodal cells are larger than any other cell of the embryo sac. Antipodal cells are rich in mitochondria, plastids and dictyosomes. The vesicles present in cytoplasm originate from the endoplasmic reticulum.

In some plants, such as maize and rice antipodal cells show the presence of transfer cells, confirming that they provide the nourishment to the embryo sac. In some plants where these cells persist, they also show their nutritive nature. Antipodal cell are also rich in starch, lipids and proteins which are consumed by developing embryo or endosperm.

13.2.2 Nutrition of Embryo Sac

It is usually the chalaza and nucellus which provide the nourishment to the embryo sac. Morphologically it is the chalazal end of the embryo sac through which the nutrition traverses into embryo sac. In some plants where nucellus degenerates in early stages integumentary tepetum or endothelium provides nourishment. In some plants, a tissue develops below the embryo sac known as hypostase, also provides the nourishment to the embryo sac.

The presence of transfer cells in the antipodal cells also confirms the role of chalazal end in the nourishment of embryo sac. The nutritional pattern of the embryo sac changes after fertilization. Before fertilization, nourishment is provided to the egg cell by synergids and to polar nuclei through antipodal cells. But as the fertilization occurs, antipodal cells and synergids start degenerating then chalazal and micropylar endosperm haustoria takes over the function of nourishment.

Endosperm

Endosperm is the nutritive tissue which provides the nourishment to the developing embryo. It is formed due to the fusion between polar nuclei and a male gamete, therefore it is triploid (3n) in nature and fusion is known as triple fusion. In some families, there is a variation in the number of polar nuclei in embryo sac, therefore, in such plants the ploidy level of endosperm also varies. In Oenotherea type of embryo sac, there is only one polar nucleus, so the ploidy level of endosperm is diploid (2n), whereas in Peperomia, ploidy level of endosperm is 9n because embryo sac has eight polar nuclei. There are three families in which endosperm are not present. These families are Orchidaceae, Podostemaceae and Trapaceae. In some plants, endosperm is consumed during the embryo development and food is stored in the mature cotyledons. These seeds are known as non-endospermic or ex-albuminous seeds such as bean, pea, etc. On the other hand in some plants endosperm persists in mature seeds and they are known as endospermic or albuminous seeds, such as wheat, corn, etc.

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Types of Endosperm

The following three types of endosperm have been classified:

- Nuclear Endosperm
- Cellular Endosperm
- Helobial Endosperm

Nuclear Endosperm

The first few divisions of primary endosperm nucleus are not accompanied by wall formation and therefore all the nuclei scattered in the cytoplasm of the embryo sac. This condition remains for a longer duration until it is consumed by developing embryo (*Limnanthes*). In some plants wall formation takes place in the later stages and it is usually centripetal, i.e., from periphery towards centre (Refer Figure 13.16). In *Mangifera*, *Citrus* and *Primula* wall formation takes place at a very late stage where hundreds of free nuclei are present along the periphery in the cytoplasm whereas in *Crotolaria*, *Rafflesia* wall formation takes place only at 8 or 16 nucleate stage. In *Cardiospermum* and *Tropaeolum* wall formation does not take place. The number of divisions of endosperm nuclei depends upon the size of the embryo sac, smaller the embryo sac less the divisions.

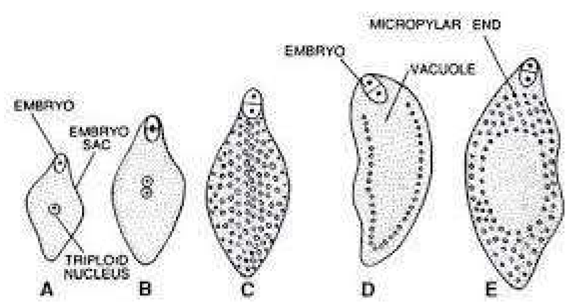

Fig. 13.16 *Stages in the Development of Nuclear Endosperm*

The degree of cellularization varies in different species. In *Phaseolus* cellularization occurs only around the embryo, whereas in *Crotolaria* wall formation is confined only to the upper region of embryo sac, the chalazal region remains free nuclear and it behaves as a haustorium. Usually the nuclei present at the micropylar end are smaller than those present at the chalazal end.

A good example of a nuclear endosperm is endosperm of coconut. The primary endosperm nucleus divides by free nuclear divisions and embryo sac is filled with white fluid in which several free nuclei are suspended it is also known as liquid syncytium. Later on, these free nuclei start settling along the periphery towards the centre. This is known as coconut meat. In mature coconut, liquid endosperm does not contain free nuclei.

In *Areca catechu* the development of endosperm is similar to that of coconut. The endosperm occupies the entire cavity of the embryo sac and it is very hard.

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Cellular Endosperm

The first and subsequent divisions of primary endosperm nucleus are accompanied by cell wall formation. The first division of PEN is usually transverse dividing the embryo sac into a micropylar and chalazal region (Refer Figure 13.17). In some embryo sacs it may be vertical or oblique.

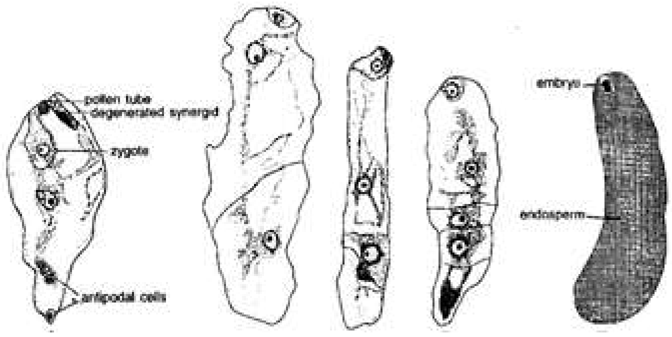

Fig. 13.17 *Stages in the Development of Cellular Endosperm*

The presence of haustoria is a common feature of cellular endosperm. The haustoria may be present at micropylar end, chalazal end or at both the ends. The haustoria penetrate the nucellar tissue to absorb nutrition. Micropylar haustoria is present in *Impatiens roylei*. A prominent chalazal haustorium is present in *Magnolia obovata* where first division is transverse forming the two chambers of equal size in embryo sac. In micropylar chamber, nuclear divisions are followed by wall formation and therefore cellular endosperm is formed at micropylar region. At the chalazal end, divisions are comparatively slow and not followed by wall formation. In a mature endosperm, the multinucleate chalazal chamber appears to be attached like a tail to the micropylar tissue. The chalazal tail acts as a haustorium and penetrates the chalazal nucellus (Refer Figure 13.18).

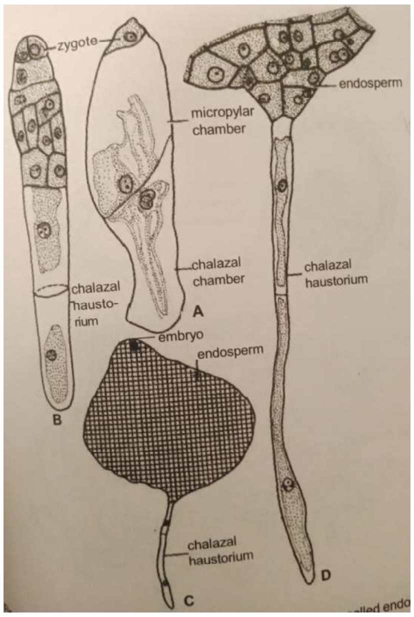

Fig. 13.18 *Endosperm Development in Magnolia obovata*

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The above Figure 13.18 shows the endosperm development in *Magnolia obovata* in which, A). 2-celled endosperm; B). 13-celled endosperm; C). globular embryo at the 2-celled chalazal haustorium; D). a portion from C enlarged to show the chalazal haustorium with a few cells of the endosperm proper

In *Loranthaceae*, being no true ovule, all the embryo sacs in an ovary lie close to each other. After fertilization, PEN moves towards the basal part of the embryo sac. All the endosperms of the embryo sacs in an ovary fuse to form a composite endosperm (Refer Figure 13.19).

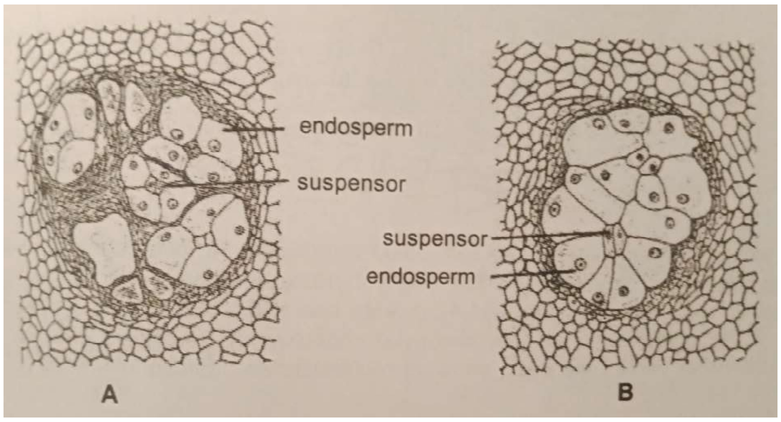

Fig. 13.19 *Composite Endosperm in Tolypanthus*

The above Figure 13.19 shows the composite endosperm in *Tolypanthus*; A. T.S of ovary, showing four embryo sac, each with 4-striate endosperm and a biseriate suspensor; B. Same, at a later stage of development. All the endopserms in the ovary have fused and formed a composite structure.

Helobial Endosperm: This type of endosperm is present in monocotyledons. The primary endosperm nucleus migrates to the chalazal end of the embryo sac where it divides forming a large micropylar chamber and a small chalazal chamber. Nuclear divisions are confined only in micropylar chamber. Earlier these divisions are free nuclear and in later stages wall formation occurs and therefore it becomes multinucleate (Refer Figure 13.20). Nucleus of the chalazal chamber either remains undivided or divides only a few times. If there is a division, it is free nuclear division. In helobial endosperm the haustoria develop from the micropylar tissue.

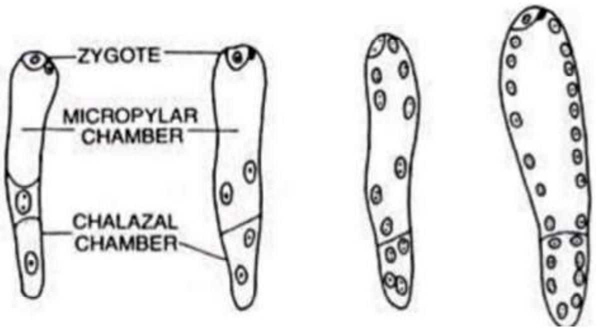

Fig. 13.20 *Development of Helobial Type Endosperm in Eremurus*

Functions of Endosperms

In Angiosperms, the endosperm is formed after fertilization. It is a nutritive tissue which provides the nourishment to the developing embryo. It is rich in carbohydrates, fats and proteins which are utilized during the successful establishment of seedling during seed germination.

- At the time of fertilization very little nutrition is available in the embryo sac but after the development of endosperm enough food material becomes available for the developing embryo.
- In majority of the Angiosperms, division of zygote starts only when the endosperm is sufficiently developed. In some cases where zygote starts its development before the endosperm, the latter surpasses its growth.
- If the endosperm gets abort during its development, the growth of the embryo is also adversely affected which shows that without endosperm, development of embryo cannot be completed.
- In some families where endosperm is absent (Podostemaceae, Orchidaceae and Trapaceae) embryo and endosperm haustoria, pseudoembryo sac such structures are present to ensure the adequate food supply to the developing embryo.
- In some plants endosperm has special kind of cells known as transfer cells which helps in the transport of substances from the maternal tissue into the endosperm.
- Liquid endosperm of coconut from immature fruit is very nutritious and this nutritional quality is used in growing the embryos in artificial medium as it provides the nourishment to developing embryos. Immature endosperm of coconut, corn and walnut are capable for inducing the divisions even in mature cells, whereas the mature ones are devoid of these stimulatory properties. The young endosperm is rich in growth hormones such as auxin, gibberellin and cytokinin. Zeatin, an important cytokinin has been extracted from the young endosperm of maize.

Check Your Progress

1. What happens in amphitropous?
2. How is curvature of the ovule in campylotropous?
3. What is the shape of circinotropous?
4. Give a short note on ovule development.
5. Define endothelium.
6. What is micropyle?
7. Define the term nucellus.
8. Give a short note on monosporic embryo sac.
9. How many types of endosperm are there?

13.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

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1. In amphitropous the curvature of the ovule is so much prominent that the embryo sac also bends and becomes a horse-shoe shaped structure. For example, *Poppy.*
2. In campylotropous the curvature of the ovule is less than that of the anatropous ovule. Here, micropyle and chalaza do not lie at the straight line and funicle lies at the right angle to the chalaza. For example, *Pea*, *Mustard.*
3. In circinotropous nucellar protuberance is at first in the same line as the axis, but the rapid growth on one side makes it anatropous. The curvature continues till the ovule has turned over, completely with the micropylar end again pointing upward. For example, *Opuntia.*
4. The development of ovule initiates as a small hemispherical protrusion on the placenta. First division is periclinal which takes place in the epidermis of the placenta. It is soon followed by various anticlinal divisions and therefore the protrusion gets enlarged. After the differentiation of archesporium, integuments start developing. In bitegmic ovules, inner integument develops earlier and it develops from the epidermis whereas outer integument develops from the sub-epidermal layer. Integuments cover the nucellus except at the pore which is known as micropyle.
5. The innermost layer of the integument develops special kind of cells which provide the nourishment for the developing embryo sac. This tissue is known as endothelium or integumentary tapetum.
6. Micropyle is a small pore present towards the apex of the ovule, which helps in the entry of pollen tube into the embryo sac. In bitegmic ovules, either it is formed by both the integuments or only by the inner integument. In Euphorbiaceae and Podostemaceae this pore is formed by the outer integument. When both the integuments are involved in the formation of micropyle, the passage formed by outer integument is known as exostome and by the inner integument is known as endostome. In some plants where exostome and endostome is not in a straight line, then a zig-zag path is formed. In leguminosae the exostome and endostome are at the right angles to each other.
7. Nucellus is thin walled parenchymatous cells, surrounded by integuments. Each ovule has a single nucellus but as abnormality twin nucelli has also been observed in some plants such as *Aegle marmelos*, *Hydrocleis nymphoides*, and *Herminium angustifolium*.
8. Megaspore mother cell divides by a single meiotic division and four megaspores are formed, arranged in a linear tetrad, out of which only a

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single megaspore is functional which gives rise to the embryo sac. A monosporic embryo sac develops from a single megaspore and therefore, all nuclei of the embryo sac are genetically similar.

9. The following three types of endosperm have been classified:
   - Nuclear Endosperm
   - Cellular Endosperm
   - Helobial Endosperm

13.4 SUMMARY

- Female reproductive structure is known as gynoecium, which is made up of one to many carpels.
- Each carpel consists of a basal swollen portion ovary, middle portion style and the upper most portion stigma for receiving pollen grains.
- Each ovule consists of a stalk through which it is attached to the placenta known as funicle.
- The cells of ovule are parenchymatous known as nucellus.
- Nucellus is surrounded by one or two integuments, except a pore at the apex.
- In Campylotropous the curvature of the ovule is less than that of the anatropous ovule.
- In Hemitropous ovule is curved at 90^0, i.e., horizontally placed on the funicle.
- In Circinotropous nucellar protuberance is at first in the same line as the axis, but the rapid growth on one side makes it anatropous.
- The development of ovule initiates as a small hemispherical protrusion on the placenta.
- Ovule having one integument is called unitegmic and those having two integuments are called bitegmic.
- Integuments are absent in the ovules of some plants, such as, *Olax imbricata*, *Crinum*, etc.
- In some plants, a colourful appendage develops in seed from the funiculus or testa to attract the animals. It is known as aril which partially or wholly covers the ovule after fertilization.
- In Sympetalae, with unitegmic and tenuinucellate ovules, nucellus is degenerated or reduced in the early stage of ovule development. It is represented by a single layer of cells.
- The innermost layer of the integument develops special kind of cells which provide the nourishment for the developing embryo sac. This tissue is known as endothelium or integumentary tapetum.
- Micropyle is a small pore present towards the apex of the ovule, which helps in the entry of pollen tube into the embryo sac.

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- In bitegmic ovules, either it is formed by both the integuments or only by the inner integument.
- In Euphorbiaceae and Podostemaceae this pore is formed by the outer integument.
- Nucellus is thin walled parenchymatous cells, surrounded by integuments. Each ovule has a single nucellus but as abnormality twin nucelli has also been observed in some plants, such as *Aegle marmelos*, *Hydrocleis nymphoides*, and *Herminium angustifolium*.
- Hypostase is derived from the nucellar cells below the embryo sac while epistase originates from the nucellar epidermis above the embryo sac.
- Megaspore mother cell represents the last cell of sporophytic generation. It undergoes a reductional division to form linear tetrad of haploid megaspores.
- The first mitotic division is oriented along the vertical axis of the ovule as a result two daughter nuclei are formed. These two daughter nuclei are separated by a large central vacuole.
- Megaspore mother cell divides by a single meiotic division and four megaspores are formed, arranged in a linear tetrad, out of which only a single megaspore is functional which gives rise to the embryo sac.
- A monosporic embryo sac develops from a single megaspore and therefore, all nuclei of the embryo sac are genetically similar.
- Oenothera type of embryo sac develops from the micropylar megaspore but this functional megaspore divides only twice and therefore four nuclei are formed.
- Megaspore mother cell divides by first meiotic division which is accompanied by wall formation, so that a dyad is formed. Only one of the dyad cells undergoes the second meiotic division, whereas the other one degenerates.
- In peperomia type nuclei present in coenomegaspore divide by two mitotic divisions resulting into the formation of 16 nuclei.
- The mature embryo sac at the micropylar consists of an egg and one synergid, six peripheral cells which can be compared as antipodal cell, and a central cell with eight polar nuclei.
- Gynoecium is monocarpellary and unilocular and the placenta is borne on the fused margins of the same carpel. The ovules are present along the ventral sutures of the carpel. For example, Leguminoseae.
- Gynoecium is multicarpellary, syncarpous and multilocular. The placenta developes from the central axis of a compound ovary and locules are borne on the fused margins of the same carpel. For example, Solanaceae.
- A mature embryo sac is a 7-celled and 8 nucleate structure. It consists of an egg apparatus (one egg and two synergids) at micropylar end, three antipodal cells at chalazal end and two polar nuclei in the centre.
- Egg cell is present at micropylar end with two synergids. Egg cell is connected through synergids and polar nucleus through plasmodesmata.

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- The synergids have a distinct cell wall towards the micropylar end whereas at the chalazal end it is thin.
- Antipodal cells are present at chalazal end of the embryo sac. There is so much variation in the number of antipodal cells. Antipodal cells are usually ephemeral, which degenerate before or soon after fertilization.
- In *Caltha palustris*, these antipodal cells persist up to the octant stage of the proembryo. In grasses these cell divide by several mitotic division, results into the formation of large number of antipodal cells.
- Endosperm is the nutritive tissue which provides the nourishment to the developing embryo.
- The first few divisions of primary endosperm nucleus are not accompanied by wall formation and therefore all the nuclei scattered in the cytoplasm of the embryo sac.
- Helobial Endosperm type of endosperm is present in monocotyledons. The primary endosperm nucleus migrates to the chalazal end of the embryo sac where it divides forming a large micropylar chamber and a small chalazal chamber.

13.5 KEY WORDS

- **Endothelium:** The innermost layer of the integument develops special kind of cells which provide the nourishment for the developing embryo sac. This tissue is known as endothelium or integumentary tapetum.
- **Micropyle**: Micropyle is a small pore present towards the apex of the ovule, which helps in the entry of pollen tube into the embryo sac.
- **Nucellus**: Nucellus is thin walled parenchymatous cells, surrounded by integuments.
- **Hypostase**: A group of cells with lignified cell walls present below the embryo sac and above the vascular supply is known as hypostase.
- **Endosperm**: Endosperm is the nutritive tissue which provides the nourishment to the developing embryo.

13.6 SELF ASSESSMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. What is megasporogenesis?
2. Define ovule.
3. Draw a well-labelled diagram of structure of a carpel.
4. Define integuments.

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5. Give short note on the following:
    - Micropyle
    - Hypostase
6. What are the types of embryo sacs?
7. Explain monosporic and its types.
8. Define bisporic and its types.
9. What is egg cell?
10. What is synergids?
11. What is endosperm?

Long Answer Questions

1. Briefly discuss about megasporogenesis giving examples.
2. Explain the types of ovules along with diagrams.
3. Write a note on development of ovule.
4. Explain various stages of megasporogenesis with the help of diagramms.
5. Discuss about tetrasporic embryo sacs in detail.
6. What are the types of embryo sac developmentphases? Explain with the help of diagramms.
7. Give a detailed note on placentation and their types.
8. Discuss about the structure of mature embryo sac.
9. Explain the nutrition of embryo sac.

13.7 FURTHER READINGS

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UNIT 14 APOMIXIS

NOTES

Structure

14.0 INTRODUCTION

Apomixis refers to a set of reproductive mechanisms that invariably rely on avoiding meiotic reduction and fertilization of the egg cell to generate clonal seeds. After having long been considered a strictly asexual oddity leading to extinction, the integration of more than 100 years of embryological, genetic, molecular, and ecological research has revealed apomixis as a widely spread component of the dynamic processes that shape flowering plant evolution. Apomixis involves several flexible and versatile developmental pathways that can be combined within the ovule to produce offspring. Here we review the large body of classic and contemporaneous contributions that have addressed unreduced gamete formation, haploid induction, and parthenogenesis in flowering plants. We emphasize similarities and differences between sexual and apomictic reproduction, and highlight their implications for the evolutionary emergence of asexual reproduction through seeds. On the basis of these comparisons, we propose a model that associates the developmental origin of apomixis to a dynamic epigenetic landscape, in which environmental fluctuations reversibly influence female reproductive development through mechanisms of hybridization and polyploidization.

Apomixis has tremendous potential for revolutionizing food, feed, and fiber production around the world because it makes possible true-breeding hybrids through seeds. Apomixis not only would fix hybrid vigor but also could make possible commercial hybrids in seed-propagated crops lacking an effective male-sterility system for producing hybrids. The opportunities apomixis offers for developing superior hybrids and simplifying hybrid production have been previously discussed.

Probably more progress has been made in transferring the apomictic mechanism from wild P. squamulatum to cultivated pearl millet than in any other grain crop. The mechanism has been transferred to the BC6 generation where high levels of apomixis have been maintained.

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However, a problem encountered has been the loss of 80–90% of the seed set postanthesis. Efforts are under way to transfer apomixis from Tripsacum dacty³oides (L.) L. to maize and from Elymus rectisetus (Nees in Lehm.) to wheat Carman and Wang, 1992).

The greatest impact of apomixis may be realized by cloning and inserting the gene(s) controlling apomictic reproduction into various sexual species by molecular methods. To be useful, a transferred gene must express itself and be stable in an alien genome. The gene(s) controlling apomixis needs to be mapped before it can be cloned and used in other species. Molecular markers linked to apomixis are being developed in Pennisetum.

In this unit, you will study about apomixis, vegetative reproduction, agamospermy and apospory, exploitation of polyembryony and apomixis in plant improvement programmes.

14.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand about apomixis
- Discuss about vegetative reproduction, agamospermy and apospory
- Explain exploitation of polyembryony and apomixis in plant improvement programmes

14.2 APOMIXIS

To create variations and the successful survival of any species, sexual reproduction is must. The sexual reproduction of any plant influences the amount and structure of genetic variation within a population, which in turn influences the evolutionary potential. In sexual reproduction, there are two important processes:

(1) Meiosis in which micropsore and megaspore mother cell (diploid sporophytic cell) divides by a reductional division and gives rise to the four haploid gametes which represents the gametophytic stage.

(2) Syngamy in which both male and female gametes fuse to form a diploid zygote.

Therefore, in sexual reproduction gametophytic and sporophytic stages show the alternation of generations. In some plants, these two processes cannot be completed or interrupted but still the embryo is formed. Those plants in which sexual process is substituted by asexual means and the progeny is genetically similar to its female parent are called apomictic plants and the process is known as apomixis.

Seed is one of the key factors of crop productivity. Therefore, a comprehension of the mechanisms underlying seed formation in cultivated plants is crucial for the quantitative and qualitative progress of agricultural production. In angiosperms, two pathways of reproduction through seed exist: sexual or amphimictic, and asexual or apomictic; the former is largely exploited by seed companies for breeding new varieties, whereas the latter is receiving continuously increasing attention from both scientific and industrial sectors in basic research projects. If apomixis is engineered into sexual crops in a controlled manner, its impact on agriculture will be broad and profound. In fact, apomixis will allow clonal seed production and thus enable efficient and consistent yields of high-quality seeds, fruits, and vegetables at lower costs. The development of apomixis technology is expected to have a revolutionary impact on agricultural and food production by reducing cost and breeding time, and avoiding the complications that are typical of sexual reproduction, for example incompatibility barriers and vegetative propagation, for example viral transfer. However, the development of apomixis technology in agriculture requires a deeper knowledge of the mechanisms that regulate reproductive development in plants. This knowledge is a necessary prerequisite to understanding the genetic control of the apomictic process and its deviations from the sexual process. Our molecular understanding of apomixis will be greatly advanced when genes that are specifically or differentially expressed during embryo and embryo sac formation are discovered.

In botany, **apomixis** was defined by Hans Winkler as replacement of the normal sexual reproduction by asexual reproduction, without fertilization. Its etymology is Greek for 'away from' + 'mixing'. This definition notably does not mention meiosis. Thus 'normal asexual reproduction' of plants, such as propagation from cuttings or leaves, has never been considered to be apomixis, but replacement of the seed by a plantlet or replacement of the flower by bulbils were categorized as types of apomixis. Apomictically produced offspring are genetically identical to the parent plant.

Some authors included all forms of asexual reproduction within apomixis, but that generalization of the term has since died out.

In flowering plants, the term 'apomixis' is commonly used in a restricted sense to mean **agamospermy**, i.e., clonal reproduction through seeds. Although agamospermy could theoretically occur in gymnosperms, it appears to be absent in that group.

In other words it can be stated that Apomixis is a reproductive mechanism that bypasses the sexual process and allows a plant to clone itself through seed. In Pennisetum, a chromosomally unreduced egg cell develops into an embryo in an embryo sac derived from a vegetative nucellar cell. This type of apomixis is called apospory. In addition to the egg cell developing into an embryo without fertilization by a sperm, pseudogamy or fertilization of the central cell is needed for endosperm and seed development. Apospory is the only type of apomixis confirmed in *Pennisetum.*

Types of Apomixis

- Vegetative Reproduction
- Agamospermy

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Vegetative Reproduction

In this type, plants reproduce though their vegetative parts which are known as propagules. Propagules include bulbs, bulbils, runners and suckers.

Agamospermy

Seeds are formed as an agent of propagation but the two normal processes meiosis and syngamy have been eliminated. There are two types of agamospermy:

- **Adventive Embryony**: When the development of embryo takes place from the sporophytic cell of the ovule, such as integuments and nucellus, this is known as adventive embryony. Citrus and mango are the common examples of adventive embryony. Cells (nucellus and integuments) forming adventives embryos become densely cytoplasmic and divide to form a mersitematic mass of cells. Zygotic and adventives embryos both develop at the same time in embryo sac. Both of these embryos look alike but zygotic embryos have suspensor whereas advntive embryos are without suspensor. Adevntive embryony is common in many families, such as Boxaceae, Euphorbiaceae and Cactaceae.
- **Gametophytic Apomixis:** Here the embryo develops from the cell of the unreduced female gametophyte. If the unreduced embryo sac develops directly from the megaspore mother cell without undergoing the reductional division, it is known as diplospory. If unreduced embryo sac develops directly from any cell of the nucellus it is known as **apospory**.

Diplospory

In this type, in ovule megaspore mother cell differentiates but it does not divide by a meiotic division. This apomictic megasporocyte lacks callose. It divides by mitotic division and develops into the diploid embryo sac and it is of the following types:

Taraxacum Type: Megaspore mother cell undergoes a meiotic division but a restitution nucleus is formed after the first meiotic division. The MMC with restitution nucleus divides mitotically to form a dyad with somatic chromosome number. It is usually the chalazal dyad which develops to form 8-nucleate embryo sac and the micropylar dyad degeneraetes.

Antennaria Type: Megaspore mother cell does not enter meiosis. It increases in size and behaves as diploid embryo sac. The nucleus of the embryo sac divides by a mitotic division and gives rise to form 8-nucletae polygonum type of embryo sac. All the cells of embryo sac are diploid.

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Allium Type: Premeiotic chromosome doubling in megaspore mother cell is the major cause for the formation of unreduced embryo sac. Chromosome doubling may be occur due to the endomitosis and ensuing meiosis results in a dyad of unreduced cells. Two mitosis in the chalazal dyad results into the formation of 8-nucleate embryo sac.

Apospory

Development of diploid embryo sac from the cells of the nucellus or integument is known as apospory. In this type, megaspore mother cell differentiates and undergoes the meiosis but it may or may not be completed to form linear tetrad. At any stage the neighbouring nucellar cell become meristematic and behaves as megaspore mother cell. This cell divides by mitotic division and form diploid embryo sac (Refer Figure 14.1). In those plants where apospory is obligatory, only aposporous embryo sac is developed and the sexual embryo sac degenerates. It is of two types:

- ***Hieracium* Type**: In *Hieracium* the megaspore mother cell divides by meiotic division and forms a linear tetrad. Simultaneously a nucellar cell at the chalazal end of the tetrad becomes functional and develops into the aposporous unreduced embryo sac. All the four megaspores gradually degenerate and only aposporic embryo sac develops. Aposporic embryo sac is 8-nucleate.
- ***Panicum* Type**: It is found in *Panicum* and other grasses. The aposporic embryo sac is 4-nucleate, where 3 celled egg apparatus and a single polar nucleus is present. Antipodal cells are absent.

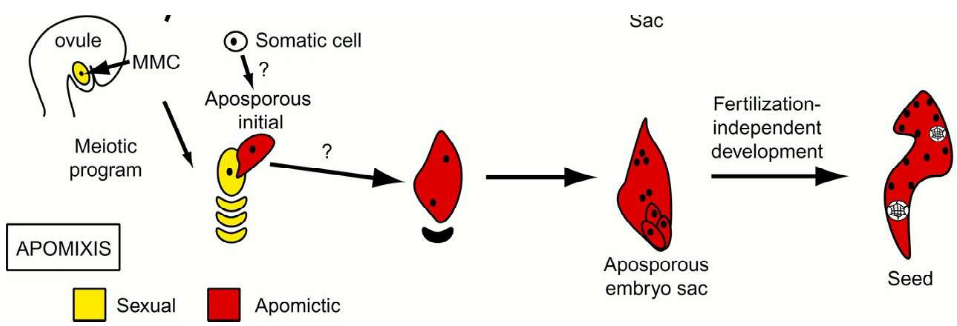

Fig.14.1 *Diagram Depicting the Formation of Apomictic Embryo Sac*

14.2.1 Exploitation of Polyembryony and Apomixis in Plant Improvement Programmes

Adventives polyembryony is of great significance in horticulture and plant breeding. It provides uniform seedlings of the parental type as theses are obtained through vegetative propagation by cuttings. Nucellar polyembryony is the only practical approach to raise virus free clones of polyembryonate *Citrus* varieties. Nucellar embryos are free from any diseases. Besides this, nucellar seedlings have better

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root system than do the cuttings and they also show the restoration of the vigour lost after repeated vegetative propagation.

As meiosis is not involved in Apomictic plants, therefore the possibility of variations and recombinations are completely eliminated. These plants also lack the ability to adapt to changing environmental conditions. Apomictic plants are genetically similar to their mother plant. Therefore, the major advantage of apomixis is to select the individuals with desirable gene combinations and to propagate them as clones. Now a days apomixis is a major goal in applied plant genetic engineering. Because of its major role in crop improvement, apomixis has gained a lot of interest from both scientific and industrial sectors. Scientists are trying to transfer this apomictic trait to other crop plant species through genetic transformation and induced mutagenesis.

Check Your Progress

1. What influences the evolutionary potential?
2. What are the two important processes in sexual reproduction?
3. Define apomixes.
4. What happens in diplospory?
5. What happens in allium?

14.3 ANSWERS TO CHECK YOUR PROGRESS QUESTIONS

1. The sexual reproduction of any plant influences the amount and structure of genetic variation within a population, which in turn influences the evolutionary potential.
2. In sexual reproduction, there are two important processes, as
   (1) Meiosis in which micropsore and megaspore mother cell (diploid sporophytic cell) divides by a reductional division and gives rise to the four haploid gametes which represents the gametophytic stage.
   (2) Syngamy in which both male and female gametes fuse to form a diploid zygote.
3. Apomixis is a reproductive mechanism that bypasses the sexual process and allows a plant to clone itself through seed.
4. In diplospory ovule megaspore mother cell differentiates but it does not divide by a meiotic division.
5. In allium type the premeiotic chromosome doubling in megaspore mother cell is the major cause for the formation of unreduced embryo sac.

14.4 SUMMARY

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- The sexual reproduction of any plant influences the amount and structure of genetic variation within a population, which in turn influences the evolutionary potential.
- In sexual reproduction gametophytic and sporophytic stages show the alternation of generations.
- In some plants, these two processes cannot be completed or interrupted but still the embryo is formed.
- In angiosperms, two pathways of reproduction through seed exist: sexual or amphimictic, and asexual or apomictic; the former is largely exploited by seed companies for breeding new varieties, whereas the latter is receiving continuously increasing attention from both scientific and industrial sectors in basic research projects.
- If apomixis is engineered into sexual crops in a controlled manner, its impact on agriculture will be broad and profound.
- The development of apomixis technology is expected to have a revolutionary impact on agricultural and food production by reducing cost and breeding time, and avoiding the complications that are typical of sexual reproduction.
- In flowering plants, the term 'apomixis' is commonly used in a restricted sense to mean agamospermy, i.e., clonal reproduction through seeds. Although agamospermy could theoretically occur in gymnosperms, it appears to be absent in that group.
- In Pennisetum, a chromosomally unreduced egg cell develops into an embryo in an embryo sac derived from a vegetative nucellar cell. This type of apomixis is called apospory.
- In addition to the egg cell developing into an embryo without fertilization by a sperm, pseudogamy or fertilization of the central cell is needed for endosperm and seed development.
- Apospory is the only type of apomixis confirmed in *Pennisetum.*
- In vegetative reproduction plants reproduce though their vegetative parts which are known as propagules. Propagules include bulbs, bulbils, runners and suckers.
- In agamospermy seeds are formed as an agent of propagation but the two normal processes meiosis and syngamy have been eliminated.

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- In adventive embryony the development of embryo takes place from the sporophytic cell of the ovule such as integuments and nucellus, this is known as adventive embryony.
- Adevntive embryony is common in many families, such as Boxaceae, Euphorbiaceae and Cactaceae.
- In gametophytic apomixes the embryo develops from the cell of the unreduced female gametophyte. If the unreduced embryo sac develops directly from the megaspore mother cell without undergoing the reductional division, it is known as diplospory.
- In diplospory ovule megaspore mother cell differentiates but it does not divide by a meiotic division.
- In taraxacum type the megaspore mother cell undergoes a meiotic division but a restitution nucleus is formed after the first meiotic division.
- In antennaria type, megaspore mother cell does not enter meiosis. It increases in size and behaves as diploid embryo sac. The nucleus of the embryo sac divides by a mitotic division and gives rise to form 8-nucletae polygonum type of embryo sac.
- In apospory megaspore mother cell differentiates and undergoes the meiosis but it may or may not be completed to form linear tetrad.
- In *Hieracium* the megaspore mother cell divides by meiotic division and forms a linear tetrad.
- Adventives polyembryony is of great significance in horticulture and plant breeding. It provides uniform seedlings of the parental type as theses are obtained through vegetative propagation by cuttings.
- Nucellar polyembryony is the only practical approach to raise virus free clones of polyembryonate *Citrus* varieties.
- Apomictic plants are genetically similar to their mother plant. Therefore, the major advantage of apomixis is to select the individuals with desirable gene combinations and to propagate them as clones.

14.5 KEY WORDS

- **Apomixis**: Apomixis is a reproductive mechanism that bypasses the sexual process and allows a plant to clone itself through seed.
- **Apospory:** Development of diploid embryo sac from the cells of the nucellus or integument is known as apospory.

- **Agamospermy:** In agamospermy seeds are formed as an agent of propagation but the two normal processes meiosis and syngamy have been eliminated.

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14.6 SELF ASSESSEMENT QUESTIONS AND EXERCISES

Short Answer Questions

1. Define the term apomixis.
2. What are the two processes in sexual reproduction?
3. Write a short note on adventive embryony.
4. Draw a well-labelled digarm to show the formation of apomictic embryo sac.
5. What is apospory?

Long Answer Questions

1. Write a detailed note on apomixis and its types.
2. Explain vegetative reproduction, agamospermy and apospory with examples.
3. What is diplospory? Explain its types.
4. Write a note on exploitation of polyembryony and apomixis in plant improvement programmes.

14.7 FURTHER READINGS

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