STRUCTURE, GROWTH, DEVELOPMENT AND REPRODUCTION OF FOREST TREES

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Summary

It is very difficult to define a tree and clearly distinguish it from a shrub or other woody plant. Their size and form are extremely variable and this variation may extend to species within a genus, varieties within a species and even the same species in different environments. Despite the great variation, development of the tree from the embryonic stage follows very similar patterns. Shoots develop from shoot apical meristems and roots from root apical meristems. The form of shoots and roots depends on the number and amount of growth of lateral structures that result from an interaction of the genetics of the tree and the environment.

Understanding how the different structures making up the tree develop gives insight into how the many variations arise. The stem is of most interest in forest trees because of wood formation for many forest products. It has been the exploitation of forests for lumber, fuel, paper and cellulose products in recent times that has drawn attention to forest tree growth and development. However, leaves, roots, fruits and seeds have also been an integral part of the lives of people for thousands of years. Leaves are the primary photosynthetic tissue, essential in carbon sequestration and tree growth. They are extremely responsive to environmental changes.

Roots are the least understood part of trees, hidden from view, but important in soil-tree interactions, absorption of water and minerals, in symbiotic relationships with fungi, and for nitrogen fixation. Reproduction can be by both sexual (fruits and seeds) and asexual means (coppicing, sprouting, etc.). Hundreds of our important fruit and seed crops used for food have come from forest species, in addition to products for medicinal use. Fruit and seed production for food, and more recently genetic tree improvement of trees have driven work on reproductive processes in conifers and hardwoods.

Reproduction in hardwoods is similar to many crop plants while that of conifers is somewhat different, and slower. Problems of floral initiation, pollination and fruit and seed set are common to all forest trees when we they are domesticated, as they are difficult to control or manipulate. But, understanding these processes is essential for reforestation of our exploited forest lands. If forests are to be renewed, we must understand how to propagate and grow trees effectively while preserving many other environmental conditions for forest animals and plants.

1. Introduction

With few exceptions, such as bamboos, forest trees are woody perennials with complex branching of stems and roots and secondary growth. At germination the embryo has a single growing point (apical meristem) at the tip of the stem and another at the tip of the root. The amount of branching determines the form of the stem and root, and depends on the amount and regularity of branching from the apical meristems and the rate of growth of these branches.

This results from a complex interaction of internal genetic control, physiology, and the environment. The same species of tree growing in different environments can have very different morphology or form.

Wood and fiber production are of major economic importance in most regions of the world and issues relating to sustainable forest development usually focus upon these. However, in addition to wood produced in the stem tissues, many other structures are important to different societies, especially in developing countries. Indigenous peoples around the world have for centuries relied on forest trees for shelter, fuel, food, medicines, and forage for animals.

These products may come from wood and bark of stems and roots, leaves, buds, fruits and seeds. This article will describe basic tree form and structure, and the growth and development from seedlings through juvenile to mature forms. Reproduction by sexual and vegetative means will be briefly described and related to reforestation, biodiversity and sustainable development of forests.

2. Crown form

Crown form refers to size, shape and number of branches in the aerial portion of the plant. There is a great variety of crown forms in forest trees, giving aesthetic value and utility as forest products. A single species can have scores of recognized varieties and cultivars that have been selected and propagated vegetatively, sometimes for centuries. The Asian *Cryptomeria japonica* and new world *Chamaecyparis lawsonia* are classic examples, yet both species also have forms highly suited for timber production.

The horticulturalist finds value in complex branching, unusual crown forms and leaf colors that are of no value to the forester who often considers them undesirable. The forester wants trees with single straight trunks, few and small branches.

Most temperate region trees can be described as either excurrent or decurrent with regard to branching and crown form. An excurrent tree, such as pines and most other gymnosperms, has a leader shoot that grows more than the subtending lateral branches. This produces a dominant central stem and often a cylindrical crown. Such species are highly valued in the timber industry because of their long trunks that may be free of branches throughout much of their length.

Most temperate hardwood species, angiosperms or flowering trees, are decurrent, with the lateral branches elongating as much or more than the leader and forming broad crowns. In many, the terminal bud on the leader is lost early in development and many lateral branches grow upward to form a complex broad crown. Although many hardwoods have extremely valuable wood, their form often results in a short usable trunk.

Tropical forest trees are mostly hardwoods and at least 23 different architectural types have been described based on crown form. Variations in crown form can be traced to features of shoot elongation, phyllotaxy, lateral bud formation and apical dominance. It has been generalized that narrow pyramidal or columnar crown forms are characteristic of trees grown in high latitudes and dry habitats, whereas broad spherical crowns are characteristic of trees grown in humid and moist environments. The development of crown form has a strong genetic basis, but is affected by habitat. Tree breeders treat crown form as an important trait for selection because in most species it is highly heritable (see *Techniques for Tree Breeding*).

Tropical trees show the greatest plasticity in architecture and crown form. These vary with tree age and with the position of the tree within the canopy. The tallest trees have the widest and flattest crowns, those in the next layer of the canopy have crowns that are about as wide as high, and those in the lower strata tend to have narrow tapering crowns.

These crown forms may reflect the efficiency of trees in intercepting the greatest amount of irradiant energy for photosynthesis. Crown form may vary with tree age, as well as with site and competing vegetation. Most young trees have excurrent branching, which may be a means of outgrowing competing vegetation.

3. The Stem

The stem or trunk of the tree is the structure of most interest to forestry. This is the primary source of timber for lumber, pulp and paper. The stem is present in rudimentary form in the embryo contained within the seed. It is a short axis with an apical meristem (apex) at one end that may be covered by tiny leaves and is joined through a short stem to the root apex at the other end.

Most tree species have two or sometimes many cotyledons (embryonic leaves) that serve as storage organs for the germanent. In some species, cotyledons photosynthesize but they are short-lived and usually wither during the first weeks or months, or remain underground providing nutrients for a short time.

As the stem grows upward, the apex undergoes rapid cell divisions producing cells below that in turn divide and elongate. The apex will also form new leaf primordia that rapidly expand and assume most of the photosynthesis as the storage products in the cotyledons are depleted. The arrangement (phyllotaxy) and shape of leaves may change as the seedling grows into a young tree. In the axils of most young leaves, at the juncture of the stem and the upper surface of the leaf, lateral or axillary shoots are initiated.

These consist of an apex, like that of the main stem. Lateral apices, like the terminal apex, may initiate leaves and/or bud scales that enclose and protect the apex. They form lateral branch or axillary buds (Figure 1). The branch bud may remain dormant for a time, then elongate and grow in a manner similar to the main shoot. This is called proleptic growth. Or, the branch apex may form leaves and stem tissues that simultaneously elongate without an intervening dormant period.

This is called sylleptic growth. At first, the stem consists mostly of soft parenchymatous tissues with longitudinal strands of vascular or conducting tissues arranged in a cylinder. These vascular strands or bundles consist of several tissues.

Xylem is most abundant on the inner surface of the bundle. It consists mostly of hollow, dead tube-like cells that conduct water and minerals up from the root to the leaves and upper stem tissues.

On the outer surface of each vascular bundle is the phloem tissue, consisting of living cells that store food and conduct dissolved sugars and other substances down from the photosynthetic leaves and up from the storage tissues in the lower portion of the stem or in the root. A layer of cells, the vascular cambium, between the xylem and the phloem remains meristematic, forming additional xylem and phloem. In herbaceous plants, stem tissues may not develop further and woody tissues may not form.

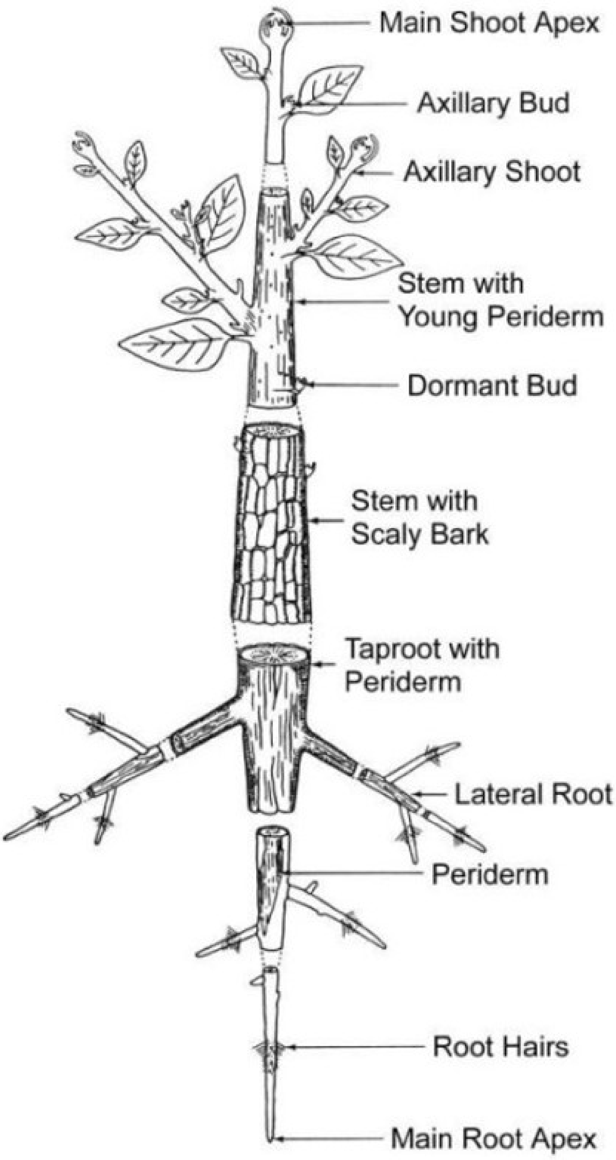

Figure 1. Diagram of a young hardwood tree illustrating the positions of the apices and the branching and secondary growth of shoots and roots. (From Esau, K. (1965), Plant Anatomy, 2nd ed. John Wiley and Sons, New York).

The center or pith of the stem may become hollow or be filled with storage cells. Cells between the vascular bundles and the epidermis covering the stem form the cortex. It consists of several layers of parenchyma cells that may photosynthesize and store nutrients.

Woody plant stems start to develop in a manner similar to herbaceous plants, but as the vascular bundles enlarge, the separate bundles fuse and the vascular cambium forms a continuous cylinder between the xylem (wood) and the phloem (inner bark) for the life of the tree (see *History, Nature and Products of Wood*).

3.1. Vascular Cambium Structure and Function

The vascular cambium is an unusual meristem, in that it consists of two types of cells that divide in a very orderly fashion producing daughter cells that are similar in size and shape to the initials. It is in theory a sheet of cells one cell wide that encircles the stem (and root) between the xylem and phloem (Figure 2).

In reality, it is often several cells thick with maturing but still meristematic cells on the outer and inner surfaces. Cells of the vascular cambium divide to form secondary xylem cells to the inside, and secondary phloem cells to the outside.

The long tapering cells in the vascular cambium, the fusiform initials, form in the axial system of the secondary xylem and phloem. Smaller rectangular cells in the vascular cambium are arranged as uniseriate (one cell wide) or multiseriate groups often many cells in height.

These are the ray initials that form the radial system, the vascular rays, that extend inward into the secondary xylem and outward into the secondary phloem. The vascular cambium commonly forms by cell divisions, eight to ten cells toward the inside (xylem) for every one cell to the outside (phloem).

The vascular cambium in temperate trees undergoes rapid cell division in the spring forming many cells, has fewer cell divisions during summer, then stops dividing in the fall and winter. In many tropical trees, the vascular cambium may divide at about the same rate throughout the year or slow in division during the dry or cooler season.

The rate of cell division is regulated by plant growth substances (hormones) and food reserves, which in turn are affected by environmental factors (day length, temperature, soil nutrients and water) and the physiology (photosynthesis and respiration) within the tree.

For a discussion and illustrations of softwood and hardwood structure, see *History, Nature and Products of Wood.*

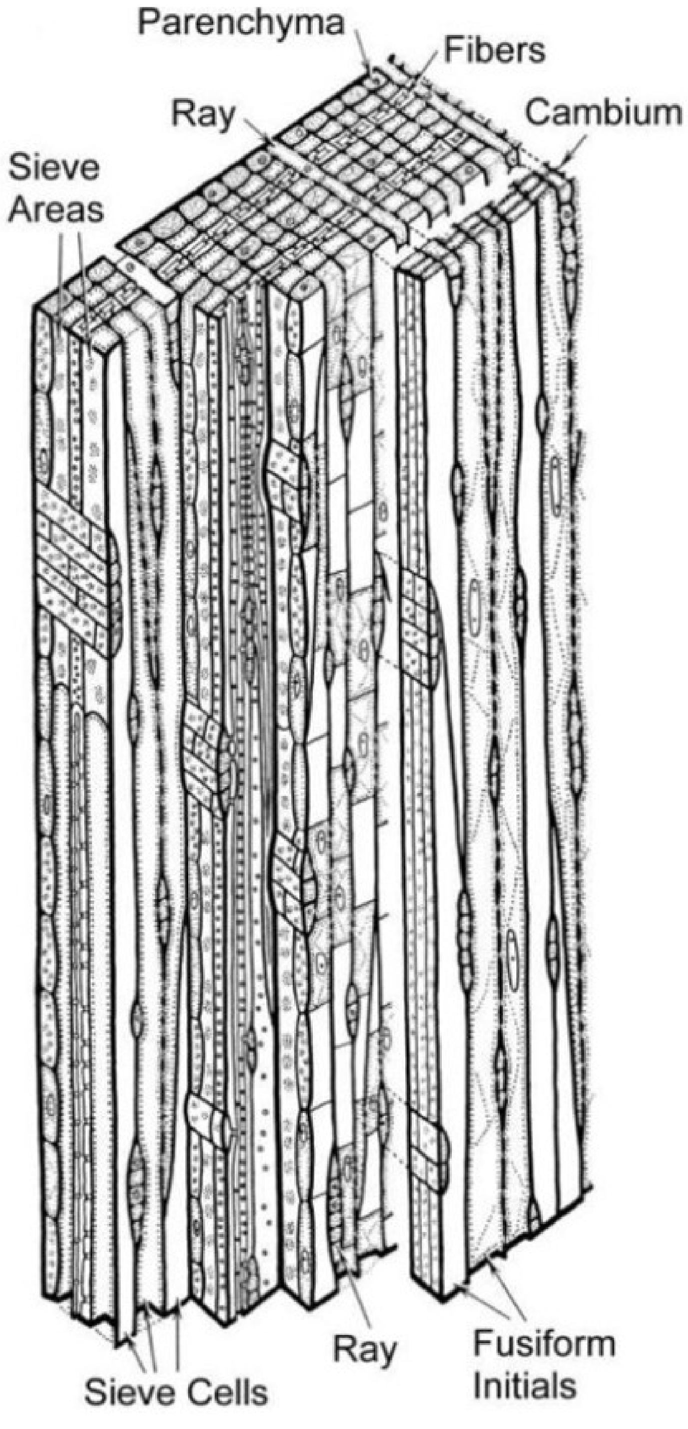

Figure 2. Block diagram of the vascular cambium and secondary phloem of a conifer (Thuja occidentalis, white cedar). (From Esau, K. (1965), Plant Anatomy, 2nd ed. John Wiley and Sons, New York).

3.2. Annual rings

In most temperate trees the annual growth rings are prominent in stems and branches. In conifers, the early wood consists of tracheids with large diameters and thinner walls than in late wood, thus early wood is less dense than late wood (see *History, Nature and Products of Wood*). The transition from early to late wood may be abrupt or gradual.

There is a high correlation between wood density and the amount of late wood present. In temperate hardwoods there is less change in cell size and wall thickness between early and late wood and the types and proportions of different cell types figure more prominently in wood density. In tropical trees, especially those growing in aseasonal regions where weather varies little throughout the year, growth rings may be impossible or difficult to delineate. In other tropical trees growing where there are distinct wet and dry seasons, growth rings may be distinct, but there may be more than one per year.

3.3. Sapwood and heartwood

Sapwood refers to the younger outer wood in which water conduction is most active. This may contain up to 10% living cells and is active in storage, conduction and support. As the xylem ages, tyloses fill and plug the vessels and tracheids, parenchyma cells die and the wood turns dark in color forming the heartwood (see *History, Nature and Products of Wood*). Heartwood ceases to function in conduction and active storage, but is very important in mechanical support. Many extractive substances accumulate in heartwood including tannins, oils, gums, resins, polyphenols and aromatic compounds. Many of these are of commercial value ranging from terpentine to amber (see *Products of Resin Production*). Moisture content is higher in conifer sapwood than in heartwood, but this feature is extremely variable in hardwoods. The outline of the heartwood core is irregular and does not follow a specific annual ring. Heartwood usually begins to form at a stem height of 1 to 3 m and tapers from base to tip as the tree grows taller.

3.4. Phloem structure and function in conifers

Phloem or inner bark in conifers has both axial and radial systems that have cells that are homologous with those in the xylem. Cells that differentiate from the cells produced by division of the fusiform initials may be conducting cells, supporting cells or storage cells (Figure 2). Sieve cells are the long tapering conducting cells that at maturity are living and have many modified pits (sieve areas) in the sidewalls. These aggregations of small pores allow for movement of soluble stored reserves from cell to cell. When concentrations of soluble sugars are high in the upper stem and leaves, where photosynthesis occurs, the net movement of solutes is usually downward in the phloem. In contrast, in the early spring, stored materials in the lower stem and roots may be converted to a soluble form and move upward where the concentration is lower. Some conifers have long fibers in the phloem that function in support and are similar in structure to fibers in the xylem. They may also have several types of thick walled sclerenchyma cells that function as structural elements, rather than for storage. Several types of parenchyma cells are usually found in long strands. Some function for storage and may eventually give rise to part of the outer bark, whereas others have a little understood function in regulating the conduction of the sieve elements.

The radial system in conifer phloem consists of uniseriate to multiseriate vascular rays consisting of brick-shaped parenchyma cells. They are continuous with xylem vascular rays and function in lateral conduction of soluble materials and for storage. They may also dedifferentiate in older phloem, as do axial parenchyma, and produce part of the outer bark.

3.5. Phloem structure and function in hardwoods.

The axial and radial systems have similar structure and most of the same cell types as in conifers. The axial conducting cells, sieve tube members, are tubular in shape and the sieve areas are primarily restricted to the end walls with only small and few sieve areas in the sidewalls. These sieve tube members join end to end to form long sieve tubes that conduct soluble materials axially. Each sieve tube member has one or more closely associated small parenchyma cells that have the function of loading and regulating the metabolism and function of that sieve tube member. When a sieve element dies, so does the associated companion cell. There may also be phloem fibers, sclerenchyma and parenchyma cells of various types but having functions similar to that found in conifer phloem.

Phloem produces many substances used for medicinal purposes as well as spices, flavoring, food, and structural products (see *Food, Forage and Medicinal Resources of Forests*). Many, such as the latex for natural rubber production, are harvested from plantations and natural stands.

3.6. Periderm and bark formation

In contrast to the xylem in which the sapwood may function in conduction and active storage for many years, and the heartwood which may function as support for the life of the tree, the secondary phloem usually only lives for a few years. Old phloem is usually sloughed off as the tree ages and increases in girth (see *History, Nature and Products of Wood*). The process is complex and the causes are still poorly understood. Usually, in one to two year-old stems, parenchyma cells in outer regions of the old phloem dedifferentiate and form a band of meristematic cells one to several cells below the surface of the stem. In some species this band may be continuous around the stem, while in others it forms discontinuous lens-shaped zones that join at their margins. This meristematic layer is the phellogen (cork cambium) and it produces files of cells (phellem or cork) to the outside. Cork cells have cell walls that contain the waterproof substance suberin making the cork impervious to water and preventing the entrance of many pathogens. As a result, cells outside the phellogen die but those inside may be protected. These two zones, and the old phloem that was isolated outside the phelogen and thus died, form the rhytidome (scaly bark) (Figure 1). Soon, a new phellogen forms deeper in the old phloem below the older periderm and another deeper rhytidome forms. Many layers may accumulate over several years, or the sequence-shaped pieces of rhytidome or sheets of rhytidome may be shed as scales. In cork-bark oak, the periderm becomes very thick and is harvested for commercial cork.

Bark is a general term used for all the tissues outside the vascular cambium (Figure 1). This includes the functional phloem, the old non-functional phloem and the rhytidome outside these layers. When reference is made to the shedding of bark, what is usually meant is the shedding of the rhytidome. Surface features of bark are useful in tree identification. Bark may become very thick in some species. Bark structure and thickness are important in protection from fire, mechanical damage, many diseases and insect pests.

4. Roots

Roots function in anchorage, absorption of water and minerals, propagating, storage of food and metabolic waste materials and the production of certain plant growth substances. We know less about root structure, development and function than for other parts of the tree because most roots remain underground and their study is more difficult than for aerial portions of the tree. Root weight and above ground weight in trees is a homeostatic feature. It varies among plants in different habitats but is commonly in the ratio of 1:4 (below and above ground) in temperate trees. However, root volume may equal the volume of aerial potions of the tree, and roots may extend laterally beyond the width of the crown. The lateral spread varies with species and soil type. In sandy soil, roots of some hardwoods may extend three times as far as the crown, whereas in loam this may be about twice as far, and in clay only about one and a half times as far. Root depth also varies and may show little relation to the size of the plant above ground. Forest trees, especially in the tropics, tend to develop high concentrations of roots in the surface soil because it is well aerated and watered and contains higher concentrations of organic matter and minerals than deeper layers of soil. Over 90% of the root mass may be in the upper 12 cm of forest soil. But there are many exceptions, where roots penetrate several meters down into the soil.

4.1. Types of roots

Several types of roots are found in forest trees. The first, primary root, that emerges from the seed may persist and branch, forming a tap-root system with many smaller lateral roots (Figure 1), or the primary root may branch then cease to grow and the many lateral roots form a multi-branched fibrous root system. Root systems of many forest trees are heterorhyzic, having both long and short roots. Long roots branch and grow in length and by secondary growth often becoming large and woody. Short roots elongate very little, seldom branch, and have no secondary growth. Adventitious roots arise from older roots, stems, leaves and even floral parts. They may arise from preformed root primordia in the tissue, or from induced root primordia as occurs in air layering. Adventitious aerial roots arising from branches are common in tropical forest trees such as *Ficus* and adventitious stilt roots can arise from the main stem, as in mangroves.

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Biographical Sketch

Dr. John N. Owens is Professor Emeritus and former Director of Forest Biology at the University of Victoria, Victoria, British Columbia, Canada. He has taught and done research in forest tree development and reproductive biology at the University of Victoria since 1963. He has published widely in these areas in both temperate conifers and tropical forest trees. During this time he has served on several federal and provincial forest research committees and as an advisor in forest tree reproduction for the Canadian International Development Agency in Asia. He is a member of the Royal Society of Canada.