

forms laminate colonies. Dendroceratid sponges occur chiefly in tidal and shallow coastal regions of all seas.

The genus *Darwinella* possesses diactinal or polyactinal spicules of spongin in addition to dendritic fibers. *Hexadella*, lacking a fibrous skeleton, has a derma layer of spongin. *Ianthella*, a genus of uncertain relationships, bears spongioblasts isolated in cavities in the fibers. See DEMOSPONGIAE

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Dendrochronology

The science that uses annual tree rings dated to their exact year of formation for dating historical and environmental events and processes. Trees are intimately bound to the environment, making them one of the most consistent and dependable recorders of processes and events that occur in nature. Trees, like most plants, are sensitive to both natural (precipitation and temperature patterns) and human-related

(air and water pollution) events that trigger certain responses in the vigor of the tree as seen in its growth rate. In most geographic regions, climate patterns in any year cause a response by trees in the volume of wood the tree produces, and often leave indelible "fingerprints" in certain physical and chemical properties of the wood. These fingerprints can be seen in the varying widths of tree rings. In some years, environmental conditions may be favorable for tree growth, allowing trees to produce greater volumes of wood. In other years, climate conditions may be generally unfavorable for tree growth, causing a reduction in the volume of wood produced. See DENDROLOGY; TREE; TREE GROWTH.

History. In the early 1900s, Andrew E. Douglass, an astronomer at the University of Arizona, was analyzing the relationship between sunspots and climate. He speculated that any change in solar energy caused by sunspot activity would cause changes in the amount of energy received by the Earth, and therefore would affect Earth's climate. Because climate affects the growth of plants, Douglass reasoned that sunspot cycles should be reflected in the growth of trees. His subsequent studies established a link between tree-ring widths and climate, and he soon confirmed the cross-matching of tree-ring widths among different trees, a technique known as crossdating. In 1914, Clark Wissler of the American Museum of Natural History noted Douglass's successful attempts at dating tree rings, and asked him if he could use tree-ring techniques to date the Puebloan ruins of the American Southwest. Fifteen years later, dendrochronology matured into an accepted science when Douglass overlapped his chronology developed from living trees with chronologies developed from trees used in many southwestern archeological sites. This accomplishment, published in *National Geographic Magazine* in 1929, provided archeologists with dates to the exact year when many southwestern pueblos were built. The importance of dendrochronology eventually led to the establishment of numerous tree-ring laboratories throughout the United States and Canada, Europe, South America, Asia, and Australia. See CLIMATOLOGY; DATING METHODS.

Annual ring formation. A tree grows by forming a new sheath or layer of woody tissue each year, much like a stack of cones one on top of the other. This growth occurs in a thin layer of cells that completely shrouds the tree just inside the bark, and is called the vascular cambium. Here, cambial cells divide, with outer cells contributing to the formation of phloem, and inner cells contributing to the formation of woody tissue. In temperate and subpolar regions, most trees break from winter dormancy and begin growth by forming new cells of wood using nutrient reserves stored from the previous growing season. In conifer trees, these cells are large and less dense, and have thin walls, producing light-colored wood called earlywood. Toward the end of the growing season, before the tree begins its dormancy period, smaller, denser, thick-walled cells are formed

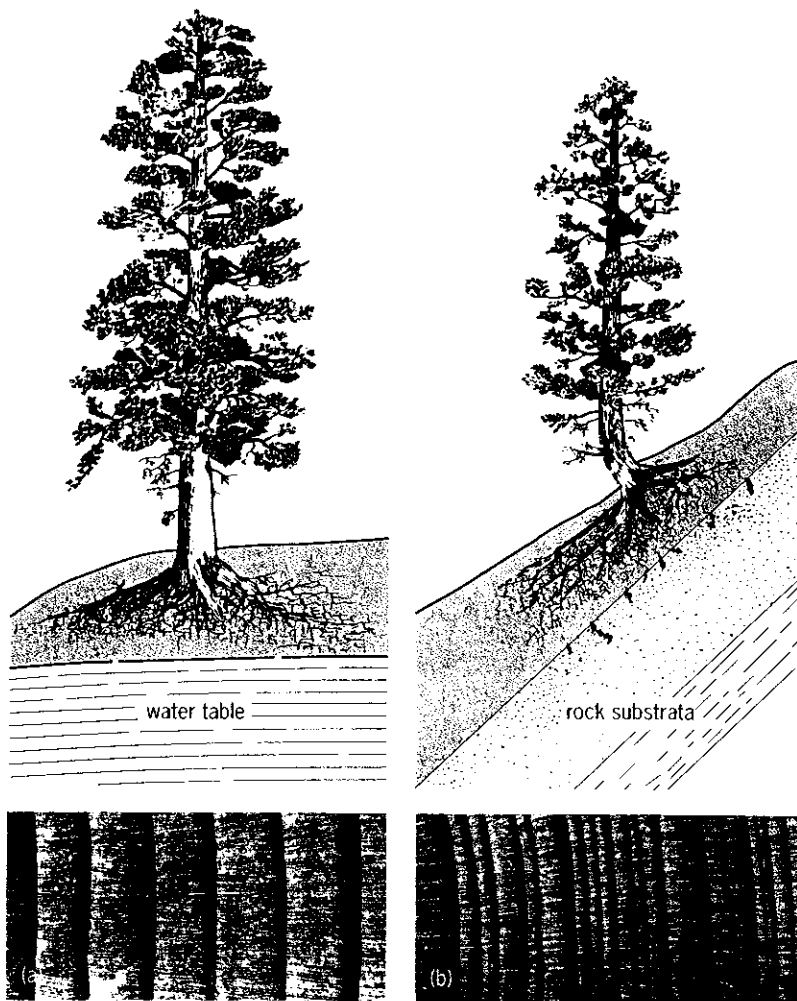


Fig. 1. Ring patterns showing complacent and sensitive ring series. (a) Climate has minimal effect on ring widths when trees have ample moisture. (b) Maximum variations occur on sites where factors favorable to growth are limited. (Laboratory of Tree-Ring Research, University of Arizona)

that are darker in color and called latewood. Taken together, these two bands of wood form an annual tree ring. In certain hardwoods, such as oaks, large cells called vessels are formed in the earlywood, while the latewood often lacks such vessels. See WOOD ANATOMY.

The formation of annual rings holds true for most trees in temperate and subpolar latitudes, but recent studies have shown some tropical and subtropical tree species also may produce annual rings. Occasionally, a tree may form latewood toward the end of the growing season, but a new flush of growth due to favorable environmental conditions may again form earlywood cells. This intraannual band of latewood between earlywood bands is a false ring, but often is anatomically different from a true tree ring when magnified. In contrast, environmental conditions during some years may be so unfavorable that some trees may not form new wood, resulting in a missing ring, or a locally absent ring in the trunk of the tree. In most cases, the locations of false and locally absent rings are identified by dendrochronologists using the process of crossdating.

Principles. To search for and collect tree-ring data, dendrochronologists are guided by the following principles.

Limiting factors. Rates of plant processes are constrained by the primary environmental variable that is most limiting. For example, precipitation is often the most limiting factor to plant growth in arid and semiarid areas. In these regions, tree growth cannot proceed faster than that allowed by the amount of precipitation, causing the width of the rings (that is, the volume of wood produced) to be a function of precipitation.

Ecological amplitude. Plant processes function at their optimum within a defined geographic range constrained by one or more interacting limiting factors. Species are more sensitive to changes in environmental factors along the periphery of this geographic range. Tree species useful for dendrochronology are often found near the margins of their natural range.

Site selection. Sites useful to dendrochronology can be identified based on criteria that will produce tree-ring series sensitive to the environmental variable being examined. For example, trees especially responsive to drought conditions are usually found where the water supply is limiting, such as rocky outcrops and cliffs, mountain slopes, and arid and semiarid regions (Fig. 1). See PLANT-WATER RELATIONS.

Replication. The strength of the environmental signal being investigated can be maximized by collecting more than one sample per tree and more than one tree per site. Obtaining numerous trees from one site, and perhaps several sites in a region, ensures that the amount of noise (environmental or physiological factors not being studied) in a tree-ring series is minimized.

Collecting tree rings. After appropriate sites and trees have been located, dendrochronologists collect tree-ring data using an increment borer, a threaded hollow metal tube that is screwed into the trunk of a



Fig. 2. Small core being taken from a tree with an increment borer. (Laboratory of Tree-Ring Research, University of Arizona)

tree (Fig. 2). An extractor is inserted under the tree core that now resides inside the borer shaft, and is gently pulled from the tree. The hole left by the increment borer rarely does harm in conifer trees, but may cause internal wood discoloration and the formation of fungi that decay wood in hardwood tree species. Usually, at least two cores are extracted from opposite sides of the tree, and are placed in paper straws or plastic tubes to prevent breakage. In the laboratory, the pencil-thin cores are glued to grooved wooden mounts and sanded with progressively finer sandpaper (usually with a belt or orbital sander), until a high polish is obtained and the cell structure of the wood is easily discernible under a microscope. Occasionally, certain projects require complete cross sections from the trunks of dead trees, and a chainsaw is most often used.

Crossdating. Crossdating is the primary guiding principle in dendrochronology, and concerns the matching of patterns of ring widths from one tree with corresponding patterns for the same years from another tree (Fig. 3). Crossdating allows scientists to accurately assign calendar dates to tree rings by matching the sequence of tree-ring widths against a known reference chronology. Crossdating is possible because climate is largely a regional phenomenon, affecting trees in a like manner, so that similar patterns of ring widths are produced among many trees. A unique pattern of wide and narrow rings formed during a 50-year period is unlikely to be formed during any other 50-year period, because climate varies from year to year. Furthermore, crossdating helps identify false and locally absent rings that may otherwise be recorded as true rings.

In many laboratories, crossdating is accomplished with graphical comparisons called skeleton plots (Fig. 4) that accentuate the importance of narrow

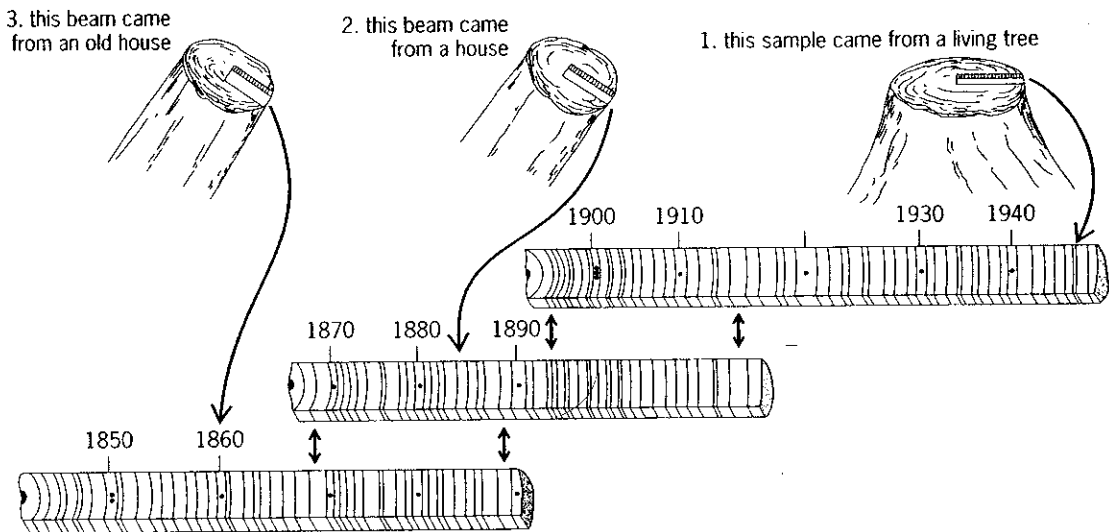


Fig. 3. Chronology building. Chronologies are extended backward in time by matching patterns of wood samples whose ages overlap.

rings. The pattern of narrow rings is matched, or crossdated, against a reference chronology until a firm match is found. The tree-ring widths are then measured, and the crossdating accuracy is statistically confirmed using computer software. To ensure a high level of confidence in the dates assigned to tree rings, dendrochronologists look for high levels of statistical significance, higher than those normally used in statistics to identify a probable match. Only after a tree-ring series has been crossdated precisely, both graphically and statistically, can dates for a wood sample be used.

Measuring tree rings. The widths of individual tree rings are measured using a measuring stage accurate to a hundredth of a millimeter. This stage is interfaced to a microscope, screen display, and a computer running software that records the measurement of each ring. Other physical properties of tree rings can be measured and used, including the average density of

the tree ring, the minimum density of the earlywood, or the maximum density of the latewood, as well as the widths of the earlywood or latewood themselves. Density measurements are obtained using x-ray images made of tree cores that have been thin-sectioned with a microtome. In recent years, scanning techniques, image analysis, and sophisticated software have provided new techniques to easily capture tree-ring data. The information from scanned images of tree rings produces data similar to the changing density of the individual cells that constitute the tree rings.

Chronology building. The measurements for individual years create a continuous time series for the full length of the individual cores. However, the raw measurements are rarely suitable for developing a site chronology because (1) trends are apparent simply due to physiological aging, (2) individual trees experience differences in growth rates, and (3) possible localized ecological disturbances (for example, the death of an individual tree) may impact growth of a subset of the sampled trees. Dendrochronologists are interested in average growth rates of trees at a site and must control for variation not due to climate. To accomplish this, all measurement series are separately standardized using complex mathematical expressions (for example, negative exponential curves) that provide predicted values of tree growth in any given year. The actual measurement is then divided by the predicted value (or sometimes the predicted value is subtracted from the actual measurement) to create an index of tree growth. The indices from all series for any given year are then averaged together to develop an average index. The final tree-ring index chronology represents the collective information from numerous trees within a site, and captures the majority of variability in tree-ring widths for a particular year.

Applications. Dendrochronology has become a useful tool in many areas of research.

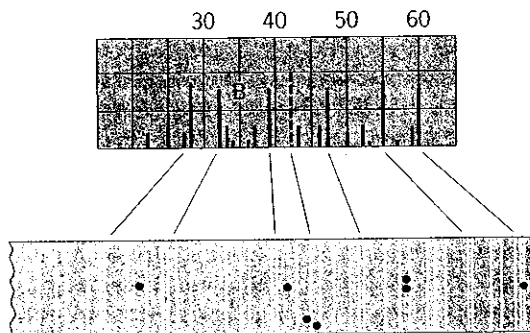


Fig. 4. Skeleton plot from an idealized tree-ring sequence. Ring widths are represented by vertical lines in an inverse proportion; that is, tall lines represent narrow rings. An exceptionally wide ring is designated by a B (big). The location of a missing ring, marked on the specimen by offset pinholes, is identified by a broken line. The number scale indicates years. (After R. Berger, ed., *Scientific Methods in Medieval Archeology*, UCLA Center for Medieval and Renaissance Studies Contribution, IV, University of California Press, 1970)

Dendroarcheology. This science uses tree rings to date wood material from archeological sites or artifacts, and is most often applied in the southwestern United States and Europe. Dendroarcheology has established the exact year of construction for individual rooms in many ancient Native American ruins throughout the Southwest, providing important clues on changes in human populations hundreds of years before Euro-American settlement. In Europe, dendrochronologists often date the period of construction for barns, manors, cathedrals and churches, Roman bridges, wells and fountains, pile dwellings in lakes, and Neolithic settlements. Recently, dendrochronologists announced the development of a multimillennial tree-ring chronology that helped clarify Mediterranean archeological history. See ARCHEOLOGY.

Dendroclimatology. This science was first developed by Edmund Schulman, who was a student of Douglas and reconstructed climate for the American Southwest. Because temperature, precipitation, and other climatic variables affect tree growth, the climatic information can be mathematically extracted from the tree-ring record and reconstructed back in time for the length of the tree-ring record. For example, bristlecone pines growing in the White Mountains of eastern California have provided information on both temperature and precipitation fluctuations for the past 8000 years (Fig. 5). Reconstructions of annual rainfall for the American Southwest over the past 2000 years have provided new clues concerning century-scale climate change and its probable impact on ancient Native American cultures. Dendroclima-

tologists also use tree-ring records to quantify the rising levels of atmospheric carbon dioxide to better understand global warming.

Dendroecology. This science analyzes changes in ecological processes over time using tree-ring information. Forest trees are subject to a variety of ecological processes and disturbances that may alter forest structure and composition. For example, periodic insect outbreaks (such as the eastern spruce budworm) can defoliate or kill large stands of trees. Defoliation can be recognized in the tree-ring record as a group of continuous and progressively narrower tree rings. Other applications that fall under dendroecology include analyzing (1) the effects of air, water, and soil pollution on tree growth and forest health, (2) the age, maturity, and successional status of forest stands, and (3) the effects of human disturbances and management on forest vitality. See ECOLOGY.

Dendropyrochronology. This science reconstructs the history of wildfires from tree rings. Humans have greatly affected the natural course of wildfires, largely by fire suppression, often not realizing the beneficial nature of wildfires to forest ecosystems. In recent years, many land management agencies have sought to restore fire. This field takes advantage of the fact that a low-intensity surface fire will kill a part of the living cambium on the lower portion of the tree trunk which subsequent growth will preserve, thus leaving a fire scar in the tree-ring record. Dendrochronologists date tree rings that contain these fire scars to learn the frequency of past fires before widespread and pervasive human disturbances (such as fire suppression) occurred.

Dendrogeomorphology. This science studies earth surface processes using tree-ring data. Mass movements, such as landslides and snow avalanches, can kill or bend the trees in the movement path or along the edges of the movement. Tree-ring scientists can date when these trees were killed (by dating the outer ring of the tree) or when they were bent (by analyzing when dramatic changes in tree growth occurred). Therefore, a chronology of past landslide or avalanche events can be developed back in time to help assess the hazard potential for the low-lying areas at the base of these slopes. Tree rings are also used to learn about glacier movements and past climate by dating the moraines created along the sides and at the terminus of these glaciers. See GEOMORPHOLOGY.

Dendrohydrology. This science uses tree-ring data to investigate and reconstruct hydrologic properties, such as streamflow and riverflow, runoff, and past lake levels. This field is closely aligned with dendroclimatology, and requires statistical calibrations of tree-ring data, such as ring width and density, with hydrologic properties recorded during the historical period. For example, estimated flow for the Colorado River using information from gaging stations has been reconstructed from tree-ring data, and has shown that the flow of the river has fluctuated greatly prior to the twentieth century. Riverflow amounts based on twentieth-century



Fig. 5. Bristlecone pines, which attain ages of more than 4000 years, form the basis for the longest chronology yet developed. (Laboratory of Tree-Ring Research, University of Arizona)

observations are therefore not an accurate indicator of potential riverflow in the future. See HYDROLOGY.

Dendrochemistry. This important, emerging field of dendrochronology analyzes the chemical composition of tree rings, especially the mineral elements. Because trees record events in the environment, changes in the amounts of naturally occurring or human-manufactured chemicals are recorded in the tree-ring record. Trees can provide a temporal record of toxic pollutants, such as cadmium, cesium, sulfur, and aluminum, to better understand the impact of pollution in the air, surface-water, or ground-water supply in ecosystems. The record of such trace elements is obtained by a variety of analytical methods that include neutron activation analysis, proton-induced x-ray emission, and atomic absorption spectrometry. See ANALYTICAL CHEMISTRY.

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Dendrology

The division of forestry concerned with taxonomy of trees and other woody plants. Dendrology, called forest botany in some countries, usually is limited to taxonomy of trees but may also include shrubs and woody vines. This basic subject in the training of foresters teaches how trees are named (nomenclature), described (morphology), and grouped (classification); how to find the name of an unknown tree and recognize important forest species (identification); and where trees occur both by geographic ranges of species and by forest types (distribution).

In forestry a tree is defined as a woody plant with a single erect perennial stem or trunk at least 3 in. (7.5 cm) in diameter at breast height (412 ft or 1.4 m above the ground), a more or less definitely formed crown or foliage, and a height of at least 13 ft (4 m). A shrub is a woody plant, generally lower growing than a tree, and frequently having several slender

perennial stems arising at or near the ground.

Common names of trees and lumber in the United States have been standardized by various forest agencies. The scientific name of a tree is in Latin and consists of two parts, a genus and a species; for example, *Pinus ponderosa*, ponderosa pine.

Trees are described and distinguished in botanical terminology largely in terms of their characteristics of form and structure (morphology). The principal parts useful in identification are leaves, flowers, fruits, seeds, buds, twigs, branches, trunk, bark, and wood. See separate articles on trees listed under common names.

Classification. A common but artificial classification groups plants into trees, shrubs, and herbs. However, the 50,000 or more tree species in the world, as well as the numerous other species making up the plant kingdom, are arranged scientifically according to natural relationships as indicated by evolutionary evidence. For example, 10 genera, having a number of characteristics in common, compose the pine family (Pinacea). These and trees of related families make up the gymnosperms (Pinopsida), generally referred to as softwoods by lumber workers. Most tree species, however, are flowering plants, angiosperms (Magnoliophyta), and nearly all of these are dicotyledons (Magnoliopsida), often called hardwoods. Palms and bamboos are monocotyledons (Liliopsida). See PLANT ANATOMY; PLANT KINGDOM.

Native tree species in the continental United States total approximately 679 species in 216 genera and 73 families; 69 species are naturalized. However, only about 175 species in 50 genera are commercially important for lumber. About 100 are subtropical and tropical species of southern Florida. Many others are of limited occurrence, small size, or low-quality wood. Hawaii, with its unique tropical flora, has about 300 native tree species, nearly all not occurring elsewhere.

Identification. The correct scientific name of a recorded species may be determined by means of printed keys or manuals or by comparison with a known tree or with mounted specimens in a herbarium. Even in winter, leafless trees usually can be identified from keys by studying the bud, twig, and bark characteristics. Nearly every state publishes a popular, inexpensive, illustrated pocket guide or bulletin for the identification of the trees of that state. Regional floras are covered in other publications. See PLANT KEYS.

Distribution. Each tree species has its own natural distribution or range. A few tree species of the United States extend across the continent, while others are local and rare in distribution. About two-thirds of the important forest trees are eastern, or southeastern, whereas one-third are western, some in the Rocky Mountains, and others in the Pacific Coast region. Trees also have an altitudinal distribution and zonation in high mountains. See FOREST ECOSYSTEM.

Forest stands of similar composition, appearance, and structure are grouped together into areas characterized by major forest types or formation, and