

Knowing how forest trees grow can help woodland owners predict yields. It can help them understand how different trees might be affected by environmental stresses, and how thinning and pruning affect wood production. Understanding the growing cycles of different trees will help the owner decide when and how to plant, thin and prune trees to increase wood production.

Forest trees grow in both height and diameter. Trees grow taller-and branches longer-because of the division of cells at the tips of branches. Roots also grow at their tips. By contrast, the diameter of trees' woody parts increases as a result of cell division in a layer located between the bark and wood. This layer is called the cambium (see Fig. 1).
Trees vary widely in their growth patterns. They vary in crown form; ultimate size; longevity and branching habits; and in the growth rates of roots, stems and leaves. Growth patterns differ between temperate-zone trees and tropical trees, evergreen

Figure 1. Annual layers of wood in a tree's stem and branches.
and deciduous trees, and in different parts of the same tree. In many temperate-zone trees, roots begin to grow earlier in the year before shoots elongate, and diameter growth begins even later (Fig. 2).


Variations in height, dianeter, and roatgrowth of a white pine tree.
Figure 2. Seasonal differences in height growth, diameter growth and root elongation of an eastern white pine tree.


## HEIGHT GROWTH AND ELONGATION OF BRANCHES

Species vary in the duration of their seasonal height growth. Some complete their growth in height within 2-6 weeks during the early part of the growing season. Others may increase in height for several months. Duration of height growth and branch elongation are controlled genetically.

## Species with Fixed Growth

In some species, such as red pine, white pine and beech, the winter bud contains an unexpanded shoot (a branch tip with its leaves and appendages). The shoots form late in the growing season of one year and then expand during the following year. Height growth and branch elongation occur relatively rapidly in species with fixed growth. Wisconsin red pines, for example, complete their height growth by the end of June, although the needles continue to elongate until much later in the summer. Thus, a drought in August will not affect their height that year, but may affect growth in the following year.

## Species with Free Growth

In other species, such as poplars and birches, some of the winter buds contain some shoots that are only partially formed (others are fully formed). In such species, leaves preformed in the bud one year expand the next year, but new leaves also form and expand as a stem or branch elongates. Height growth and elongation of branches usually take much longer in species with free growth than in species with fixed growth. Species with free growth will respond to stresses such as drought differently than species with fixed growth. A drought in August would be likely to decrease that year's growth.

## Species with Recurrently Flushing Growth

In still other species, annual height and branch growth involve elongation of more than one terminal bud per shoot. This is the case for some temperate zone pines (such as loblolly and slash pines of the southern states), most tropical pines and many broad-leaved tropical trees. There are no trees with recurrently flushing growth which grow in Wisconsin. Pines with this kind of growth, for example, increase in height by extending a succession of buds formed at the tip of the stem. After a period of bud extension, height growth stops briefly while a new terminal bud cluster forms. Shortly thereafter this recently formed bud expands to "increase the height of the tree further. At the same time, a whorl of lateral branches grows from lateral buds at the base of the main bud. Typically, there are two to four such periods of elongation growth every year. The annual increase in height represents the cumulative growth of several growth flushes. Trees with recurrently flushing growth can be very productive because they continue to grow over many months. They are more affected by late season environmental stresses than are fixed growth species.

## Abnormal Late-Summer Shoots

Some species with fixed growth have a tendency to produce abnormal late-summer shoots from buds that normally do not open until the following year. Hickory from some seed sources, pines, spruce, and oak are especially well-known for such shoots. Abnormal late-summer shoots are subject to winter injury because they may not harden adequately.

## Tree Form

Shoots on a tree do not all grow to the same length. Differences in the elongation of shoots in different parts of a tree help determine the tree's shape. In many trees, upper shoots interfere with the elongation of lower shoots. In most conifers, for example, the terminal leader (main stem) elongates more each year than the branches below it. Furthermore, whorls of lateral branches elongate more at the top of the tree than at the bottom, and branches growing from the main stem elongate more than branches growing from other branches. This orderly pattern of growth produces a tree with a conical shape.

Many Christmas tree growers routinely "shear" trees to shape them. Removing the tips of lateral shoots stimulates expansion of subordinate shoots and the formation and expansion of new buds into additional shoots. The result is a well-shaped, bushy Christmas tree.

Shoot growth does not vary in such an orderly manner in many broad-leaved trees. Rather, many shoots elongate at about the same rate, and the trees branch and rebranch until sometimes the main stem becomes difficult to identify. Such trees often have characteristic crown shapes. Beech and oak, for example, tend to have oval or elongated crowns, whereas American elm has a vase- or umbrella-shaped crown.

## Height Growth and Tree Age

A tree's annual increase in height varies with its age. Height growth of a young seedling increases a little each year, usually until the tree reaches the pole stage. The annual growth in height then remains relatively constant for a number of years and then declines fairly rapidly. Of course, the amount of height growth differs appreciably from year to year as environmental conditions, particularly water supply, vary.

## Maximum Height

Trees also vary greatly in the ultimate heights they reach. A tree's maximum height is more related to its longevity than to its annual growth rate when young or to the type of shoots it produces. Trembling aspen grows fast when young, but never becomes very tall because it ages rapidly and is relatively short-lived. By contrast, the long-lived white oak, a slow grower when young, often becomes a tall tree. Tables 2 and 3 show variations in size, growth rate and longevity. Note: Both tables list species in addition to those which grow in Wisconsin.

## GROWTH IN DIAMETER

The diameter of a tree determines how it can be used, and its value. In general, and particularly with hardwood species, the larger the diameter the greater the value (and age) of the tree. Trees grow in diameter because each year new layers of wood and inner bark are inserted between the previous year's layer of wood and bark. The new layers are produced by the division of cells in the cambium, a thin layer just under the bark (see Fig. 1). These cells divide to produce wood (xylem) cells toward the inside of the tree and living bark cells (phloem) toward the outside. The cambium produces more wood than bark. Bark cells eventually collapse and die and some of the old outer bark is shed.

Because of this mode of growth, a tree's stem consists of annual increments of wood, one added on top of another. If you cut the tree in half from top to bottom you would see a series of overlapping cones (see Fig. 3).

Figure 3. Cross-section of an oak stem.


People often use annual rings as a way to determine the age of a tree. But a tree may appear to be different ages depending on where in the stem the rings are counted. There will be fewer rings higher on the tree than at its base. Trees sometimes grow more on one side than another. The annual rings of wood in a stem cross section result from variations in growth rate and differences in the kind of wood produced early and late in the growing season. Wood formed early, called springwood or earlywood, has cells of large diameter and is much less dense than wood formed late in the season, which is called summerwood or latewood. Annual rings are visible in stem cross sections because of the differences in density of the earlywood of one year and the adjacent latewood of the previous year.
Temperate zone trees usually produce one ring of wood each year. However, they may produce more than one in some years. Foresters can recognize "false" or "multiple" rings as well as "missing" ones. There also may be "discontinuous" rings, formed when the cambium is dormant on one side of a tree, as sometimes happens in trees with injured crowns and in very old trees. Frosts that occur after annual growth starts may injure a tree's cambium and cause "frost" rings, which are sometimes mistaken for annual rings. So ring counts do not always indicate a tree's true age.

## Seasonal Duration of Diameter Growth

A tree's growth in diameter usually continues later into the summer than its growth in height does. However, the duration of diameter growth varies among species and crown classes and with weather and site. Diameter growth is very responsive to water supply and often slows during a drought and speeds up after a rain. Seasonal diameter growth in one year usually continues for a longer time in conifers than in deciduous trees because conifers retain their needles and continue to produce carbohydrates and growth regulating hormones later in the fall.

Dominant trees, whose crowns extend above the general level of the crown canopy, not only grow faster, but they continue to produce wood much later into the summer than suppressed trees do. Dominant trees may continue to grow in diameter throughout most of the growing season, whereas suppressed trees (whose crowns are completely below the general crown canopy) may increase in diameter during only a small part of the growing season. Dry weather can shorten the duration of diameter growth substantially, especially in suppressed trees.

## Vertical Distribution of Diameter Growth

A tree does not grow in diameter at the same rate all along the stem. In fact, the rate of diameter growth varies consistently. The annual sheath of wood laid down by the cambium is quite thin near the top of the tree. It is thicker further down the stem, becoming thickest in deciduous trees at about the stem height where the number of leaves is greatest. In pines, the annual sheath is thickest somewhere between the middle and base of the crown.

How the thickness of the annual sheath varies with stem height depends on the tree's crown class (Fig 4). In dominant trees, the sheath becomes thinner below the crown and thickens again near the stem base. In suppressed trees, maximum sheath thickness occurs at a greater stem height and,

below the height of maximum thickness, the sheath becomes thinner and does not thicken near the base of the tree. The annual layer of new wood in suppressed trees is also thinner overall than in dominant trees. Stems of very suppressed trees which often lay down very little wood near the base are much less tapered than those of dominant trees. However, even though there is more diameter growth in the upper stem than in the lower stem of suppressed trees, the trees are still thicker toward the base where there are more annual rings of wood (see Fig. 3). Unlike dominant and suppressed trees, opengrown trees usually show a progressive increase in thickness of the annual sheath from the height of maximum crown width to the base of the stem.

In managed plantations, the annual increment of new wood changes in rather predictable ways. When the trees are young, the annual layer is progressively thicker from the top of the tree downward. As the trees grow older and the crowns grow together or "close," competition for light, water, and minerals intensifies among the trees, and the zone where the layer is thickest moves upward. Below this height, the thickness of the layer decreases toward the stem base. Removing some trees by thinning a stand stimulates cambial growth near the stem base of the remaining trees. As the trees subsequently become more crowded, the position of greatest layer thickness again moves upward. Therefore, to obtain optimum volume growth (and value) it is important to keep forest stands in an uncrowded condition.

## Effects of Thinning and Pruning on Diameter Growth and Stem Form

There is much interest in cultural practices which stimulate diameter growth of trees. Although an increase in diameter growth by such practices increases stem taper, normal crown closure tends to keep these effects from becoming serious.

Generally, thinning accelerates diameter growth and the greater wood volume combined with an increase in log grade more than compensate for change in stem form.

Thinning a stand of trees increases the growing space for the remaining trees and accelerates physiological activity in their crowns. As a result, the remaining trees grow faster in diameter, and the form of their stems changes. Thinning usually stimulates wood production most near the stem base, resulting in a more tapered stem. How much a tree responds to thinning of a stand depends among other things on its crown class. Dominant trees with large crowns often do not show much response to thinning. More suppressed trees show much greater response.
Pruning branches has just the opposite effect from thinning. Removing lower branches tends to slow diameter growth at the stem base, so more wood is produced in the upper stem after pruning. Pruning, in other words, tends to reduce stem taper. The extent to which tapering is reduced depends on the severity of the pruning and the crown class of the tree. Pruning affects diameter growth of open-grown trees more than stand-grown trees. Both the amount of wood formed and its distribution along the stem of a large-crowned tree vary with the intensity of pruning and the tree's age. Many pruning trials have not changed stem form appreciably because too few branches were removed or the trees were pruned too late.
Extreme taper is normally not a problem in forest-grown trees because they can be bucked into shorter logs, minimizing the impact of volume lost to taper. Nevertheless, using pruning and thinning to manage stem form can pay off in higher stumpage prices.

## ROOT GROWTH

The most common types of roots are tap roots (found in oaks and hickories), and fibrous root systems, such as those in pines. However, for many species, rooting characteristics are not fixed because site conditions alter the pattern of root growth. Red maple, for example, has a very plastic root system. It develops many shallow laterals in swamps and a deep taproot in dry upland soils.

The root system of a tree consists of large perennial roots and many small ones that are short-lived. In many tree species, root hairs on the surface of these small roots increase their absorbing surface. Most of these hairs live only days or weeks. As old hairs die, new ones form behind the growing root tips. Many of the small roots normally die, mostly during winter, but also at other times from unfavorable environmental conditions or attacks by pests. Complete defoliation of a tree may induce death of most of these small "feeder" roots.
Roots usually begin to elongate earlier in the spring, and to continue longer, than shoot growth (Fig. 2). The rate of root growth varies during the growing season and in many species occurs in cycles regulated by environmental changes. Root growth rate varies at different soil depths because of differences in water and mineral supply, aeration, temperature and other factors. In woody roots, seasonal cambial growth begins near the soil surface, then the zone of growth moves downward like a wave. Cambial growth in roots is much more irregular than in stems. False and double rings are common in roots, as are roots that are eccentric in cross section.

Closely related species of trees often become joined by root grafts. When growing roots of related trees come into contact, their tissues often fuse in such a way that carbohydrates, growth hormones, water, minerals and disease agents such as fungus spores may pass from one tree to another. Sometimes stumps stay alive for many years because they receive carbohydrates and growth hormones through root grafts with another tree. Herbicides injected into one tree can move through grafted roots and kill other trees by "backlash."

## REPRODUCTIVE GROWTH

To produce a large seed crop, a tree must go through several sequential stages. It must form flower buds and then flower. The flowers must be pollinated and female and male reproductive cells must unite (fertilization). The fruits and seeds must grow and ripen, and then the seeds must be shed. Poor seed years often result from a breakdown in one of these essential stages of reproductive growth.

## Flowering

Flowers of most forest trees are small and inconspicuous. Some trees, such as birches and alders, have female and male flowers on the same plant. Poplars and willows have female and male flowers on separate plants. Only female trees of these species produce seeds.

Many broad-leaved trees form flower parts between late May and early June in the season preceding the spring in which the flowers open. Weather and site conditions influence the timing.

Flowers of most broad-leaved trees open sometime between March and mid-June, with the order of bloom varying among species. The usual order of flowering is as follows: silver maple, willows, red maple, American elm, birches, sugar maple, oaks, black cherry, and black locust. Unlike these early-flowering species, witch hazel does not flower until autumn. The actual date of flowering of a given species varies from year to year because of differences in weather, especially temperature (Table 1). Over a 48-year period the dates of first flowering of silver maple and black locust trees in southern Wisconsin varied by 43 and 26 days, respectively.

Table 1. Variation in dates of flowering of silver maple and black locust trees in Dane County, Wisconsin.

| Year | Silver Maple | Black Locust |
| :--- | :--- | :--- |
| 1945 | March 7 | May 31 |
| 1950 | April 4 | June 6 |
| 1955 | March 15 | May 20 |
| 1960 | April 8 | June 1 |
| 1965 | April 11 | May 25 |
| 1970 | April 5 | May 24 |
| 1975 | April 11 | May 24 |

## Growth of Fruits and Cones

The time required for fruits and cones to grow and mature varies a lot. The fruits of elms, poplars, red maple and green ash ripen within $4-6$ weeks after pollination. Fruits of most other broad-leaved species develop throughout the entire growing season. Acorns are exceptions and require two years to mature.

On most conifers-including firs, larch and spruce-cones ripen and shed their seeds during one season. Pines, however, require a much longer time to mature seeds. Red pines growing in central Wisconsin, for example, require three growing seasons to produce mature seeds. Cones begin to form in August of one year, but do not become visible until late May or early June of the next year. They grow little during this year, but grow rapidly in the third year, and the seeds ripen by early September.

## Periodicity of Seed Production

It is important to know seed production intervals for seed collecting. If you expect to collect and sell seed or use it for your own tree regeneration you will need to know which species are likely to produce heavy seed crops. If you plan to depend on natural seed production for forest regeneration, knowing seed production cycles will help you develop forest management plans.

Forest trees go through a juvenile stage during which they do not produce any seeds. Once they reach adulthood, however, they may produce seeds for as long as they live, providing that environmental conditions are suitable. The length of the juvenile, non-flowering stage varies from 5-10 years for shadeintolerant species to 30-40 years for shade-tolerant species. Jack pine may produce cones by the third year. Slash pine usually takes about 10 years and does not produce many cones until about 20 years of age. The juvenile period may last 20-25 years in Norway spruce and 30-40 years in beech.

As trees age and lose vigor, both the size and quality of their seed crops decrease. Even after reaching adulthood, forest trees do not produce seeds every year because environmental conditions influence flowering. Open-grown trees and those on the edge of a stand usually produce more seeds-and at an earlier age-than do trees growing in a dense stand.
Irregular and unpredictable seed production by many forest trees is one of the most serious problems in forestry. The amount of seed produced by forest trees varies greatly among species and among trees of the same species. It also varies from year to year in the same tree. Some species produce good crops almost every year, while others have good crops irregularly and still others at regular intervals of several years.
Even closely related tree species show considerable variation in seed production. Red maple and silver maple have good seed crops almost every year, whereas sugar maple produces a good seed crop every 2-5 years. Black oak and bur oak tend to have good seed crops every 2-3 years; white oak has irregular heavy seed crops, at roughly 4 - to 10-year intervals. Poplars also vary widely in seed production. Black poplar and cottonwood typically have good annual seed crops, but trembling aspen and big-tooth aspen have good crops at 4- to 5 -year intervals. Poor seed crops seem to be due to blocking of one or more of the sequential reproductive phases. Each phase is necessary for a good seed crop.

## Tree Vigor and Seed Production

Dominance and vigor are important factors in a tree's capacity to produce large seed crops. In the same forest stand, dominant trees of a given species produce much larger seed
crops than trees of intermediate or suppressed crown classes do. In very dense stands, suppressed trees may not produce any seeds at all. Within a tree, variations in the vigor of branches also affect seed production. Red pines, for example, typically produce larger cones on the vigorous branches in the upper and middle part of the crown than on the less vigorous lower branches. Furthermore, the large cones contain more and higher-quality seeds than the small cones.

In conifers, pollen cones and seed cones form at different locations and at different times of the year. In pines, pollen cones form at the base of the current year's growth in the lower crown. The seed cones develop in the upper crown, sometimes forming clusters near the end of the current year's growth. In balsam fir, seed cones form mostly in the upper 4-5 feet of the crown, pollen cones much lower. In tamarack, pollen cones develop on 1-or 2-year-old branches; seed cones on older branches (usually 2-4 years old). Pollen cones usually form before seed cones.

## Effect of Seed Production on Vegetative Growth

Trees do not grow as much in heavy seed years as they do in other years. Branches of flowering balsam firs elongate only about half as much as those of non-flowering trees. Furthermore, the shoots of flowering balsam firs have poorly developed needles.

Both conifers and broad-leaved trees grow less in diameter in years of abundant seed production. In beech, for example, the width of annual rings that form in good seed years may be only half as wide as those formed in years of low seed production. In fact, ring width may be reduced for two years after a good seed year. Apparently, the reproductive phase in trees monopolizes substances needed for growth. Reproductive growth and vegetative growth seem to compete for carbohydrates, and vegetative growth often loses out.

## For More Reading

Physiology of Woody Plants by P. J. Kramer and T.T. Kozlowski. Academic Press, New York, 1979.

Table 2. Variations in Size, Growth Rate, and Longevity of North American Conifers

| Common Name | Scientific Name | Maximum height | Maximum diameter | Growth Rate | Longevity |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | (feet) | (feet) |  | (years) |
| Arbovitae (see Whitecedar) |  |  |  |  |  |
| Douglas fir | Pseudotsuga menziesii | 270 | 15 | Rapid | - |
| Balsam fir | Abies balsamea | 85 | 3 | Rapid | 100-150 |
| Fraser fir | A. fraseri | 65 | 2.5 | Moderate | 200-300 |
| Grand fir | A. grandis | 250 | 6 | Moderate | 200-400 |
| White fir | A. concolor | 200 | 6 | Moderate | 100-400 |
| Hemlock (eastern) | Tsuga canadensis | 160 | 6 | Slow | 300-600 |
| Juniper (see Redcedar) |  |  |  |  |  |
| Larch (see Tamarack) |  |  |  |  |  |
| Jack pine | Pinus banksiana | 90 | 2 | Rapid | 80-150 |
| Jeffrey pine | P. jeffreyii | 130 | 9 | Moderate | 300-500 |
| Loblolly pine | P. taeda | 190 | 5 | Rapid | 150-250 |
| Lodgepole pine | P. contorts | 150 | 3 | Slow | 120-300 |
| Longleaf pine | P. palustris | 150 | 4 | Rapid | 300-400 |
| Pinon pine | P. edulis | 50 | 3 | Very slow | 150-400 |
| Pitch pine | P. rigida | 100 | 3 | Rapid | 100-200 |
| Ponderosa pine | P. ponderosa | 235 | 9 | Moderate | 300-500 |
| Shortleaf pine | P. echinata | 150 | 4 | Rapid | 200-300 |
| Slash pine | P. elliottii | 130 | 3 | Rapid | 150-250 |
| Sugar pine | P. lambertiana | 250 | 10 | Rapid | 300-600 |
| Virginia pine | P. virginiana | 100 | 3 | Moderate | 100-200 |
| White pine (eastern) | P. strobus | 220 | 6 | Rapid | 300-500 |
| White pine (western) | P. monticola | 120 | 8 | Rapid | 200-500 |
| Redcedar (eastern) | Juniperus virginiana | 100 | 4 | Slow | 150-300 |
| Redwood | Sequoia sempervirens | 365 | 20 | Rapid | 800-1500 |
| Giant Sequoia | S. gigantea | 350 | 38 | Rapid | 2000-3000 |
| Black spruce | Picea mariana | 100 | 3 | Slow | 150-250 |
| Red spruce | P. rubens | 120 | 4 | Slow | 200-300 |
| Sitka spruce | P. sitchensis | 300 | 16 | Rapid | 400-750 |
| White spruce | P. glauca | 120 | 4 | Slow | 150-350 |
| Tamarack | Larix laricina | 100 | 3 | Moderate | 100-200 |
| Whitecedar (northern) | Thuja occidentals | 125 | 6 | Slow | 300-400 |

Table 3. Variations in Size, Growth Rate, and Longevity of North American Broadleaved Trees

|  |  | Maximum | Maximum |  | (fiameter |
| :--- | :--- | :---: | :--- | :--- | :---: |

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