PUBLICATION 8235

FOREST STEWARDSHIP SERIES 5

Tree Growth and Competition

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Understanding how trees grow is the key to assessing the condition of the trees on your property and the potential of your site to grow the kind of forest you want. The trees on your property are engaged in a constant competitive struggle with each other and with other plants for water, sunlight, and nutrients. The plants that are winning this struggle are best adapted to the site's environmental conditions; these are the most healthy and vigorous plants on the site. The most successful plants may not always be trees. Getting to know the species, their tolerances, and the health of the trees on your site is a critical first step in understanding how best to manage your property.

Objective

Understand how trees grow as individuals and as part of a forest in order to facilitate evaluation of the effects of management alternatives.

Competencies

- Learn tree requirements for growth and survival, basic tree physiology and functions, and how competition for sunlight, moisture, and nutrients affects trees of different species.
- Understand that forests are shaped by competition between trees and develop predictable patterns and structures over time, with important implications for wildlife and biodiversity.
- Understand that management practices such as thinning can promote tree health and growth and enhance forest productivity.

Related Forest Stewardship Series Publications

- Vegetation Management (ANR Publication 8236)
- Forest Ecology (ANR Publication 8233)
- Forest Regeneration (ANR Publication 8237)

TREE PHYSIOLOGY

Each part of a tree plays an important role in maintaining the tree's health and vigor (fig. 1). The tree crown is comprised of its branches and leaves. Photosynthesis occurs in the leaves and produces all the sugar (energy and building material) that the tree uses to grow and perform other functions necessary for survival. The tree's crown is essentially its food-producing factory, but the crown also casts shade that can stifle the growth of other plants competing with the tree for light, water, and nutrients. The roots anchor the tree and absorb water and nutrients necessary for tree survival and growth. The trunk, or stem, supports the crown and houses the circulation system that conducts water up from the roots to the leaves and distributes sugar (sap) produced by the leaves or needles. This circulation system has two components: the sapwood, or xylem, and the phloem (fig. 2).

The sapwood carries water and nutrients up from the roots of a tree to its leaves or needles. Sapwood is created by the cambium, the tree's stem cell tissue that produces all the trunk's growth. The cambium produces a new layer of sapwood (a tree ring) and a new layer of bark each year. Heartwood forms when inactive sapwood is replaced by newer sapwood. Heartwood is not living tissue. It gives the tree's trunk its strength and stiffness. The inner bark, or phloem, carries the sugars made in the leaves or needles to the branches, trunk, and roots. The outer bark, or cork layer, reduces moisture loss and protects the tree from mechanical damage, disease, heat, cold, and fire.

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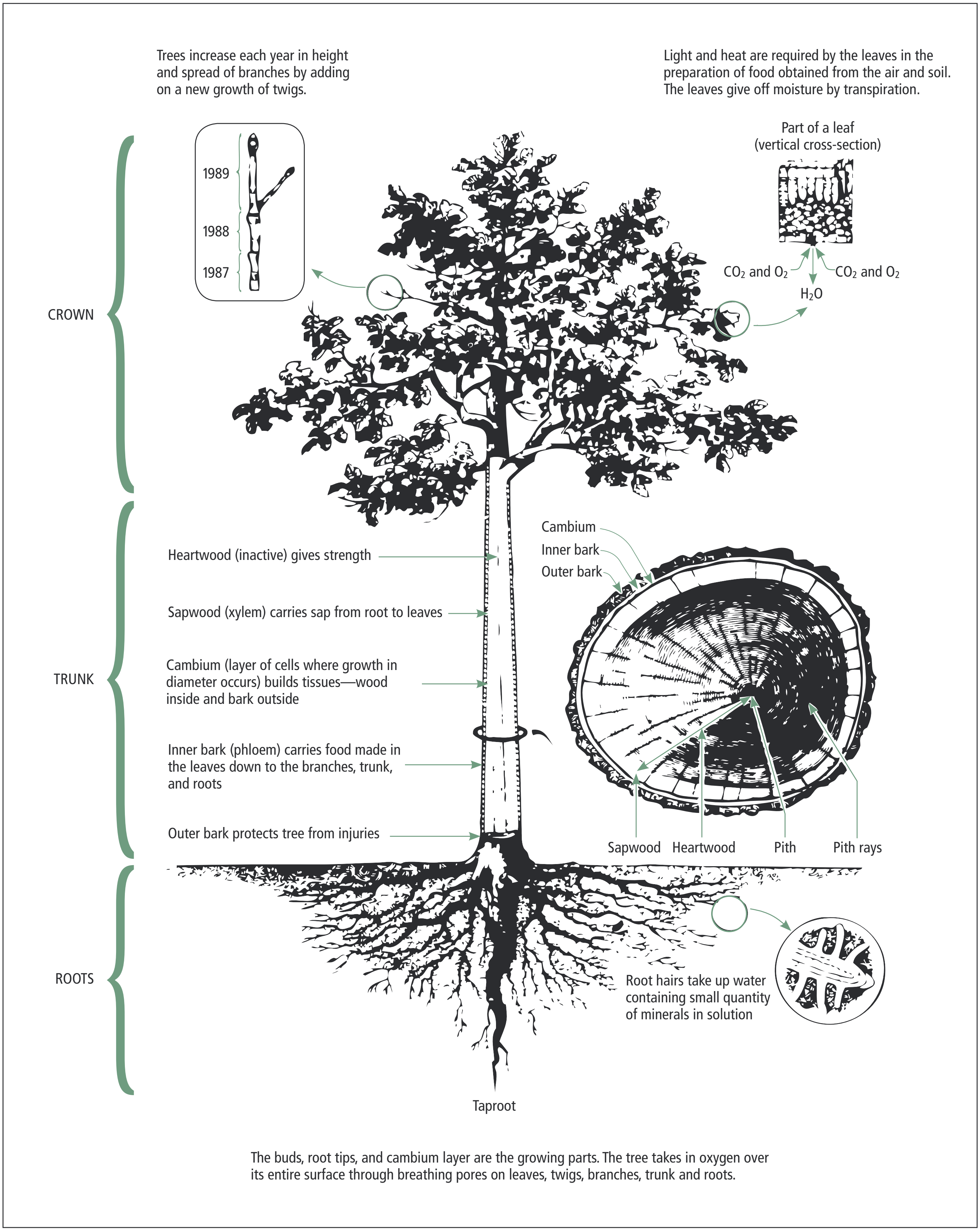
Figure 1. How a tree grows. *Source:* U.S. Forest Service.



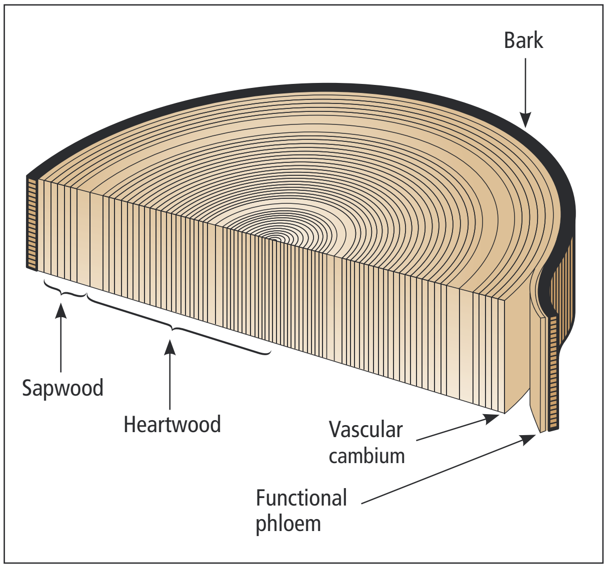


Figure 2. Cross-section of a hardwood dicot tree trunk. The outer bark, or cork, protects the tree from losing moisture, insulates against cold and heat, and wards off insects. The inner bark, or functional phloem, is conductive tissue that moves photosynthate sugars (sap) from the leaves to the rest of the tree. As the phloem ages and dies it becomes cork and part of the outer bark. The vascular cambium is a thin tissue of stem cells that eventually become the phloem and sapwood. The sapwood, or xylem, conducts water and nutrients from the roots to the leaves and branches. As the inner rings of the sapwood age they fill with chemical compounds, lose their conductive properties, and become heartwood. Heartwood provides structural support for the tree and can produce rot resistant lumber like redwood.

TREE NEEDS

Trees must obtain adequate amounts of sunlight, water, air, and nutrients in order to survive and grow.

Sunlight

Like all plants, trees convert sunlight energy into sugars (chemical energy) through the process of photosynthesis. The tree burns, or respires, the sugar to produce the energy necessary for all its growth and physiological processes.

Trees compete with each other and with other plants for the sunlight available on a site. When trees get overtopped and shaded by others, their access to sunlight is reduced or eliminated. As a result, the growth of overtopped trees slows or halts. Depending on the species, trees may eventually die after being overtopped.

The leaves on branches that are shaded conduct only a limited amount of photosynthesis but still cost the plant energy, nutrients, and water to maintain. These branches generally die and get knocked off by wind or snow in a process called self-pruning after they can no longer maintain themselves. Some trees (e.g., white fir) are better able to photosynthesize at lower light levels than others (e.g., ponderosa pine), and may retain their lower, shaded branches. Eucalyptus is an example of a widely planted tree that self-prunes, and dense stands of eucalyptus often have high fuel loads as a result.

Forests that have closely spaced trees may be unhealthy because too many trees are competing for the available sunlight and moisture. As a result, no individual tree receives enough light or water to grow well and some forests may actually stop growing and stagnate, with photosynthesis just matching the respiration and no surplus sugar available for growth. These forests are very vulnerable to disease, fire, drought, and other threats because the individual trees are weak and unable to resist these stresses. Increasing the spacing between trees by removing some trees (thinning) increases the amount of light and moisture received by the remaining trees and therefore increases their health, growth, and resistance to stresses.

Water

Trees, like other plants, require water. Water is drawn in through the roots and pulled up through the tree to the very top and tips of each branch. In addition to providing metabolic water, this stream also carries minerals and nutrients essential for plant growth. Ninety-five percent of the water used by a tree or plant is evaporated to cool the leaves, while the remainder is used in physiological processes such as photosynthesis and respiration. During photosynthesis, a tree opens small pores in its leaves called stomata to allow carbon dioxide to enter and oxygen to exit. Water vapor is also lost when the stomata are open through a process called transpiration. This loss of water from the stomata pulls water up from the roots to the leaves in the top of the tree through vessels in the xylem. If there is not enough soil moisture to replace water lost through transpiration the tree must close down its stomata and stop photosynthesis and growth.

Inadequate soil moisture can cause yellowed or withered foliage, decreased growth rate, premature shedding of leaves or needles, and dead branches. Moisture stress also makes trees more susceptible to attack by insects or disease. For example, a common syndrome in California forests begins with a period of drought during which trees become vulnerable to attack by bark beetles, followed by extensive tree mortality. This syndrome was evident in Southern California mixed conifer forests in the late

1990s. High-value landscape trees near homes and recreational areas can be irrigated to alleviate moisture stress. To be effective, water must be applied for a sufficient time and in sufficient quantity to penetrate the soil and reach deep roots. This is not practical or economically feasible for a forest. The most practical treatment for forest trees is to ensure that they have adequate water by alleviating overcrowding and competition for limited water through selective thinning.

Nutrients

Trees require the macronutrients nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S) in relatively large amounts (pounds per acre per year) to thrive. Eight other elements are required in such small quantities (ounces or less per acre per year) they are called micronutrients: iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B), molybdenum (Mo), cobalt (Co), and chlorine (Cl).

Nutrients play critical roles in plant physiological processes including photosynthesis, cell growth, nitrogen fixation, protein synthesis, respiration, water absorption, and root growth. Plants grow best when these elements are present in sufficient quantities, and they suffer from deficiencies when these elements are scarce. The quantity of these elements in forest soils is related to their presence in the soil-forming rock and to contributions from decomposition of organic matter (roots, leaves, branches) or atmospheric deposition. Plant-available nitrogen is present in precipitation; in air-polluted areas, unnaturally high levels of nitrogen (NOX, nitrous oxides) in the precipitation may upset the nutrient cycles of ecosystems on which it falls.

Nutrient availability is rarely a problem for California forests, except where soil has been severely disturbed by compaction, erosion, or wildfires, or on serpentine soils (soils that developed from serpentine rock). A few common visual symptoms of nutrient deficiency are stunted tree growth, discolored yellow foliage, premature death of buds and foliage, death of needle tips, and poorly developed root structure. These symptoms may commonly be observed in trees growing on road cuts in the nutrient-poor subsoil. If you observe signs of nutrient deficiency in groups of trees it is reasonable to suspect either unusual soil conditions (e.g., serpentine soils), root disease or root damage, or past land use impacts. Nutrient deficiencies can be treated with fertilizers after diagnosis but this is rarely done in forest stands. If individual specimen trees appear to be suffering nutrient deficiencies, your local UC Cooperative Extension or Natural Resource Conservation Service office can assist you with diagnosis and treatment.

Air

Trees must take in carbon dioxide through their stomata for photosynthesis. They also take in oxygen and water through their roots. About 90 percent of tree roots are found in the upper 3 feet (1 m) of soil. These include specialized feeder roots found in the first foot of soil, where water and air are most available. Depending on soil conditions, roots may extend horizontally 2 to 3 times the width of the tree crown. Think of a tree as a long-stemmed wine glass with a wide base.

The roots of most tree species are colonized by beneficial fungi called mycorrhizae. These fungi increase the roots' ability to absorb water and minerals and offer some protection from root diseases. Soil compaction can restrict root growth, reduce soil water storage capacity, disrupt fungal associations, and cause root death. The soil behaves like a sponge, with water and air stored and transmitted through the pores between the mineral particles. Compaction can reduce the size and number of these pores, thus reducing soil water storage and air transmission. This damage impedes the ability of tree roots to absorb moisture and exchange gases. Trees growing on compacted soils may have many of the same symptoms as those suffering from moisture stress. Construction, logging and road building equipment, and unmanaged domestic livestock can cause soil disturbance and compaction around tree roots. In campgrounds and other recreation areas, foot traffic and vehicles can cause significant compaction.

Soil compaction and disturbance can be avoided by careful planning when conducting construction or forest operations with heavy equipment. Protective measures during construction include fencing around trees to exclude heavy equipment, bridging roots when trenching, removing fill, and minimizing grading. Protective measures during timber harvest operations include using designated skid trails and specialized low ground pressure equipment (wide tracks or tires), minimizing wet weather traffic, operating equipment over logging slash and organic matter, and tilling compacted soil after harvest operations are completed.

TOLERANCE OF ENVIRONMENTAL CONDITIONS

Trees are constantly competing for available sunlight, water, and nutrients. Each species has evolved its own adaptations for survival in this competitive environment (table 1). They have different tolerances to environmental conditions and changes and consequently have competitive advantages and disadvantages.

Shade Tolerance

One of the most important characteristics of any tree species is its ability to grow under partially shaded conditions. Shade-intolerant trees grow quickly in sunny conditions but slow down once they are overtopped and shaded by other trees. Overtopped trees may eventually succumb to insects or disease. Ponderosa pine is a good example of a shade-intolerant species. Its growth slows to half its normal rate when 50 percent shaded, and it is likely to die in full shade.

Shade-tolerant trees, on the other hand, can grow and survive in full sun as well as in the shade of other trees. However, the price for this adaptation is that they usually cannot regenerate as easily or grow as quickly in full sun conditions as shade-intolerant trees. White fir is a good example of a shade-tolerant species. White fir seedlings cannot survive as well or grow as quickly in full sun as ponderosa pine seedlings. Since firs are shade tolerant, however, they often regenerate after shade-intolerant trees have shaded a site and can survive and grow in the shade of other trees for some time. When overtopping trees die and allow more sunlight in, white firs can continue to grow and replace them in the overstory. The life strategy of shade-tolerant trees is to outlast shade-intolerant trees rather than outgrow them.

Table 1. Comparative tolerances of common California trees, listed from most tolerant to least tolerant

Shade	Drought	Fire	Snow damage
white fir	Oregon white oak	ponderosa pine	red fir
red fir	California black oak	Douglas-fir	white fir
Douglas-fir	Jeffrey pine	sugar pine	Jeffrey pine
sugar pine	ponderosa pine	white fir	Douglas-fir
incense cedar	lodgepole pine	incense cedar	sugar pine
lodgepole pine	incense cedar	lodgepole pine	ponderosa pine
ponderosa pine	Douglas-fir		
black oak	sugar pine white fir red fir		

Trees exhibit a range of shade tolerance. Species like Douglas-fir are considered intermediate in tolerance. While they do best in full sunlight, trees with intermediate tolerance can survive in the shade and thrive if more sunlight becomes available. Very few species survive best in shade; Pacific yew is one example.

Drought Tolerance

Drought tolerance is the ability of a tree to survive under conditions of limited soil moisture. Drought tolerance is based on how well a tree can access soil moisture during dry times and its ability to control moisture loss through its leaves. Adaptations to water loss include waxy or hairy leaf surfaces, vertically oriented leaves minimizing the area receiving direct sunlight, lighter colored leaves to reflect light and heat, and stomata that close with moisture stress and are sunken or located on the underside of the leaf.

Fire Tolerance

Fire tolerance is the ability of a tree to survive fire. Generally, trees are more fire tolerant if they have thick bark and deep roots. Thick bark protects the living tissues of the tree, and deep roots are not as vulnerable as shallow roots that are closer to the heat on the soil surface. Mature trees with fewer lower limbs (self-pruned) are also more able to survive because they are less likely to transmit a ground fire up into their crowns.

Cold and Snow Load Tolerance

Cold tolerance is the ability of a tree to withstand frost or cold temperatures. Snow load tolerance is important at higher elevations. Conifers with short, flexible branches can generally shed heavy snow loads. Deciduous trees avoid both cold and snow by losing their leaves each fall, shedding their frost susceptible and snow accumulating tissues.

COMPETITION

A tree's genetic makeup determines its tolerance to environmental conditions. For example, a shade-intolerant drought-tolerant ponderosa pine is better suited to a sunny, dry site than a white fir, which is shade tolerant and drought intolerant. If planted at the same time, ponderosa pine seedlings would survive better and outgrow the white firs and come to dominate the site.

As trees compete within the forest, some capture most of the site's light and moisture and become the largest and healthiest trees, while others die or grow very slowly. The success of a tree in competition with others can be judged by the size and shape of its crown (fig. 3). Dominant trees have crowns that extend above the general level of the canopy. They receive full light from above and partial light from the sides. Codominant trees have crowns at the level of the canopy. They receive full light from above but little from the sides. Intermediate trees have small crowns crowded into the general level of the canopy that receive some light from above but none from the sides. Suppressed trees have small crowns below the general level of the canopy and receive no direct light. Wolf trees have crowns nearly the full length of the tree because they have grown in completely open conditions, with full lighting all around. The lower branches continue to receive plentiful sunlight and so are retained rather than being discarded through self-pruning. Wolf trees can be aesthetically beautiful trees, but they tend to be too large limbed for high-quality lumber.

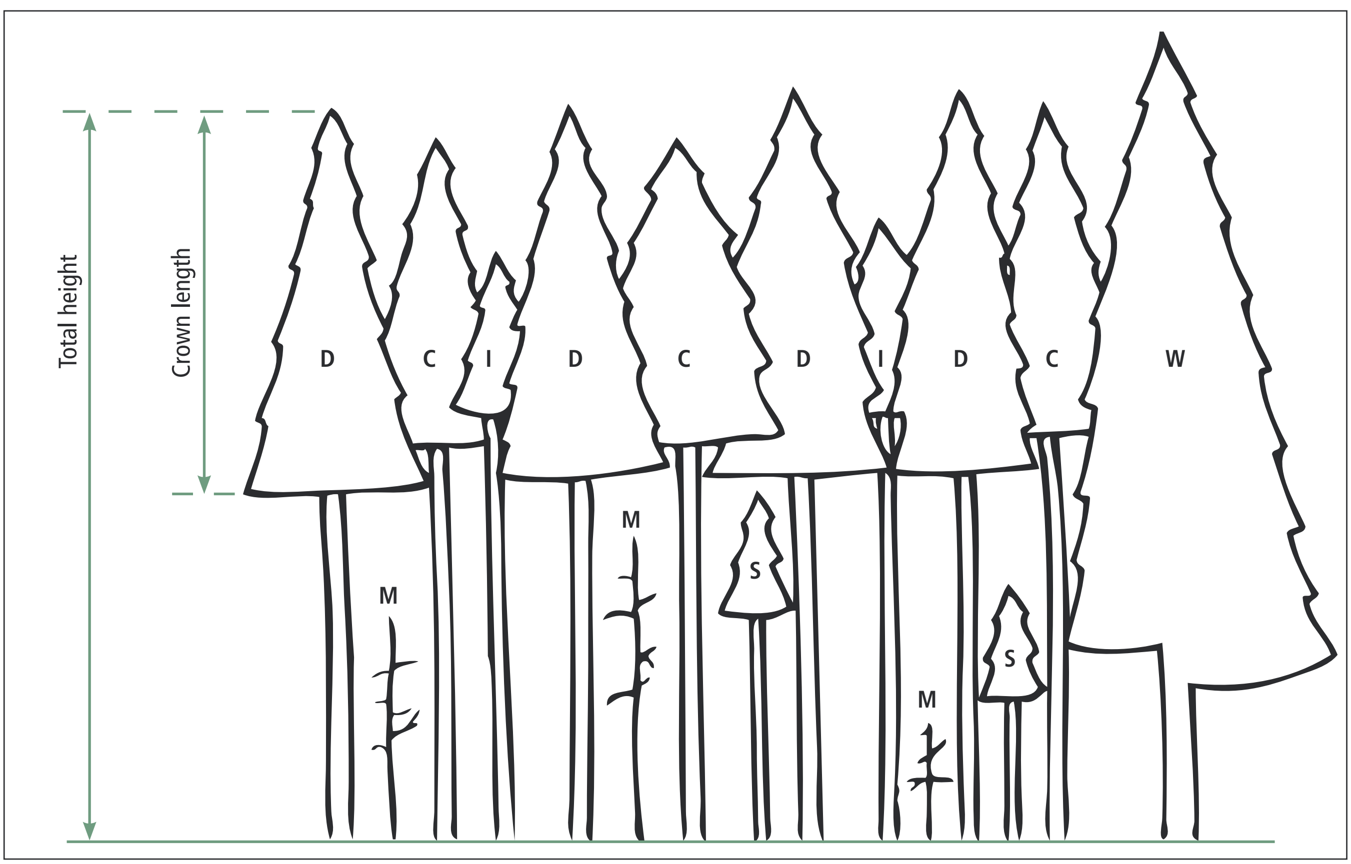
The management implications of tree growth and competition are profound. Forest harvesting that removes suppressed and intermediate trees retains those with the healthiest crowns that have the most potential for future growth. Conversely, harvesting only the biggest, healthiest trees (called high grading) often leaves behind unhealthy, suppressed trees with reduced potential for future growth. Removal of tree species that are most tolerant of site conditions can leave behind those least-adapted to the site, reducing the potential of the site to maintain a healthy forest over time.

FOREST DEVELOPMENT

The development of a forest over time is called succession. In an ideal forest, succession would proceed steadily over time from bare ground to herbaceous plants to woody shrubs to fast-growing shade-intolerant trees to a climax forest. Forests in the real world do not follow this ideal course. Actual forest development is a result of myriad factors: climate, soil, competition, and the species present; events that occur, including natural disturbances such as fire, windstorm, insects, or disease; and human activities such as harvesting and fire exclusion. The forest that develops on your property is a product of all these interacting factors.

For example, cooler, shady sites at middle elevations in the Sierra Nevada would favor the growth of shade-tolerant drought-intolerant white firs. With frequent fire, however, the thin-barked white firs, which tend to hold their branches, are likely to be killed. However, ponderosa pine, which has thick bark and rapid self-pruning, tolerates frequent low-intensity fires quite well. Given an adequate seed source, open areas where firs are killed are more likely to reforest in ponderosa pine. Frequent low-intensity fires promote ponderosa pine growth and domination of the site over time, despite climate conditions that would favor white fir in the absence of fire. If the owner of this site selectively harvests ponderosa pine and prevents fire, the young white fir left behind in

Figure 3. Effects of competition within a stand. *Key:* C = codominant, D = dominant, I = intermediate, M = mortality, S = suppressed, W = wolf tree.



the forest understory will respond to the increased sunlight and reclaim the site. This has occurred over much of the Sierra Nevada and has created mixed conifer forests with a high proportion of white fir and less ponderosa pine than was historically present.

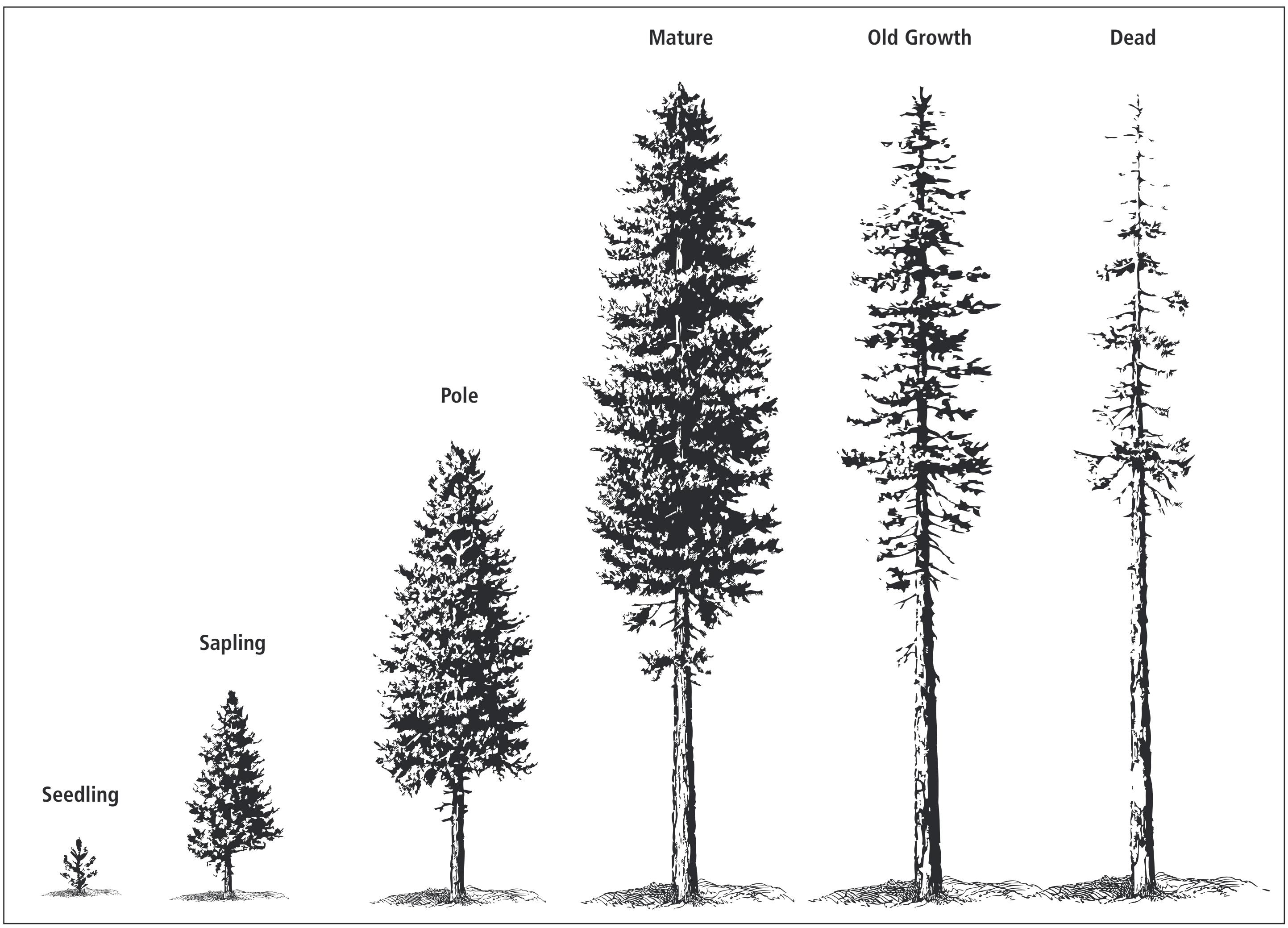
STAND DEVELOPMENT

A group of trees growing together under similar conditions (soils, slopes, and species composition) and managed in the same way is called a stand. Forests are comprised of stands, which may be defined in many ways on the basis of species composition, age, or location. Like the forest as a whole, stands grow in a somewhat predictable manner through a series of stages. These stages include stand initiation, stem exclusion, understory initiation, and old growth (fig. 4).

Stand Initiation Phase

After a significant disturbance such as an intense fire or clear-cut harvest, a new stand will establish through planting or natural seeding of the area. The stand initiation phase is the period in which new trees are becoming established on a site. This typically takes from 20 to 50 years, depending on various factors at the location. Planting reduces the time for stand initiation. With no control over competing vegetation, shrubs and grasses can capture available moisture and reduce seedling survival and slow tree growth, increasing the amount of time for stand initiation.

Figure 4. Stages of tree and forest stand development.



Stem Exclusion Phase

Once the site is fully occupied by trees and they begin to compete with each other, the stand is said to be in the stem exclusion phase. This phase can continue for 50 to 150 years, during which dominant trees shade out less-competitive trees and very few new plants can successfully become established on the forest floor. Stems are excluded because the trees already on site are utilizing all the available sunlight, moisture, and nutrients.

Understory Reinitiation Phase

Eventually some of the trees in the stand die, leaving openings for new tree seedlings, shrubs, and herbs to establish in the understory. This phase is called the understory reinitiation phase.

Old Growth Phase

In an old-growth stand there is a balance of older trees dying off and being replaced by new trees growing up from the understory. Older trees with large branches and cavities, dead trees, rotted and partially rotted large wood debris on the ground, and a highly developed forest canopy are all characteristics of old-growth stands.

Although wildlife is found in forests at every stage of stand development, wildlife found in old-growth forest is of particular concern to forest managers. Old-growth wildlife species are dependent on the complex structure found in old-growth forests, including large trees, snags (standing dead trees), intermediate-size trees, downed logs, and forest canopy. These old-growth characteristics are difficult to recreate in a young stand. The northern spotted owl is one example of a species that depends on old growth. The owl does not build its own nest cavity and so requires large old trees or snags with cavities to nest in; it requires intermediate-size trees for roosting and downed logs for nesting and cover for the small mammals the owl preys on. Managing a forest to maintain old-growth tree species requires leaving as much of this structure intact as possible.

While the owl requires old-growth stands for nesting habitat, it feeds on wood rats and other animals that live in brush fields and less dense stands within foraging distance of the nesting stand. Thus a diversity of forest stand conditions across a landscape is required for spotted owl and other wildlife.

MANAGEMENT IMPLICATIONS

The management implications of the differences in tree growth characteristics, tolerances, and stand or forest development patterns are innumerable. As a rule, the astute forest manager will “work with nature” when planning and implementing practices. For example, thinning and stand improvement prescriptions should be based on favoring the best-growing trees of species that are most suited to the site in question. When visualizing the desired future forest, it is necessary to have a clear picture of the potential of the site. It is impractical, for example, to expect shade-intolerant species to successfully regenerate and grow in the absence of sufficient light. For this reason, silvicultural systems have been generally adopted for specific forest types. A useful exercise for any forest landowner is to seek out examples of stands and forests in the forest type that is natural for their property that can represent feasible target conditions for their future forest.

The forest landowner should also recognize that under natural conditions, forests are not uniform in structure, function, or appearance. That is, they are comprised of stands in different stages of development, and within a forest there can be “too much” of any stand type. Managing for diversity across the landscape usually yields more benefits in terms of productivity, wildlife habitat, and other values than does managing for any single stand condition.

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