

Tree and Stand Growth

Introduction

The first part of this chapter introduces the patterns of growth of individual trees. It includes primary growth (extension of shoots, leaves, and fine roots) and secondary growth (thickening of stems, branches, and roots). An explanation is provided for how trees prioritize growth allocation of carbohydrates (sugars) from the process of photosynthesis. The important aspect of "growing space" is presented, as well as how crown and stem morphology can differ among tree species. The nature of stem form and wood properties are also explained.

The second part focuses on stand-level patterns of growth and productivity in relation to climate, site, and stand development age. The methods are described for measuring productivity over time for both stands and individual trees.

The third part of this chapter is concerned with the complicating effects of thinning on stand productivity, primarily dealing with the growth and yield response.

Growth within Individual Trees

Carbohydrate Allocation in Trees

Trees, like all green plants, capture solar energy through photosynthesis (Salisbury and Ross, 1992; Larcher, 2001). This energy is briefly stored in the electrons of chlorophyll molecules and is then used to synthesize sugar (glucose) from carbon dioxide and water in the interior of the leaf. In the next step, simple carbohydrates are formed from sugar and are translocated throughout the tree. Some of these carbohydrates are used for respiration to meet the basic metabolic needs of the living cells and to catalyze the growth of new cells. Others are used as the building blocks for larger and more complex carbohydrate molecules, principally cellulose, hemicellulose, and lignin, which form the structure of cells and collectively make up most of the mass of a tree. Much smaller amounts of proteins and lipids are also formed.

The amount of carbohydrate produced by a tree depends mainly on the size of the crown (the total mass of foliage) and the ability of the roots to supply the foliage with water and nutrients (Larcher, 2001).

There are two basic types of growth in most trees. **Primary growth** consists of the extension of shoots and leaves aboveground and of fine roots belowground. Plants have stem cells (similar to those in animals), which are not genetically determined, so they can form a variety of cell types. In plants, stem cells are called meristems or meristem cells. New shoots and roots develop from apical meristem cells in the buds and root tips; they divide and differentiate into the many cell types that form leaves, stems, and roots. (The terms 'apex' and 'apical' refer to the tip of a plant shoot.) **Secondary growth** involves the increase in the thickness of woody stems, branches, and roots. This growth is initiated by cambium meristem cells that form a layer encircling the stem and branches of the tree; these meristem cells divide and differentiate into xylem and phloem cells. Just outside the phloem, there are bark cambium meristem cells that form new layers of bark. The growth rates of all of these tree structures (both primary and secondary) depend on the overall amount of carbohydrate produced by the photosynthesis of the tree.

As a tree's vigor increases or decreases over time, the rates of growth and other functions of the tree do not increase or decrease proportionally. A hierarchy in carbohydrate allocation exists among the parts and functions of the tree, and it is under strong genetic control (Fig. 17.1). The highest priority is to sustain the function of living cells by rebuilding protein molecules and repairing cell membranes. The use of energy for this purpose is called **maintenance respiration**. Most of this activity occurs in the foliage, to maintain the photosynthetic structures and chemical reactions. The next priority is primary growth, which produces the foliage and fine roots that are vital to the survival of the tree. An important aspect of allocation to primary growth is that it includes the height growth of the tree (that is, the extension of the shoot at the apex of the tree). Reproduction (growth of flowers, strobili, cones, fruits, and seeds) also

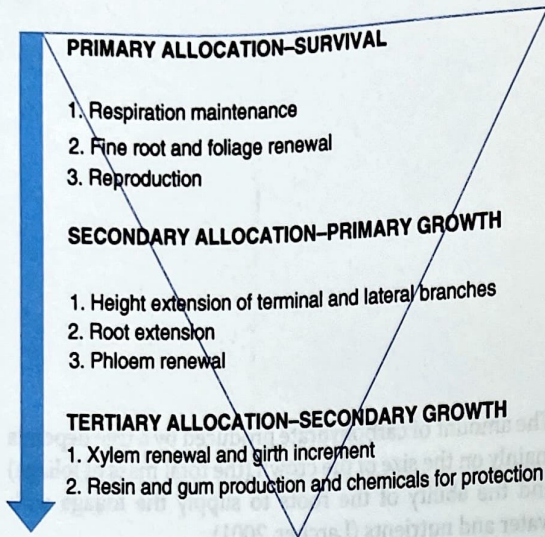


Figure 17.1 Priority allocation of carbohydrate in a tree.
Source: Mark S. Ashton.

has high priority and competes with shoot and root extension growth for carbohydrates. However, in some species, large seed crops are produced only periodically (**masting events**), with little or no allocation to reproduction in other years. Growth in diameter increment has been shown to be higher during non-mast years as compared to mast years.

The next priority is the storage of carbohydrates in stems, roots, and branches (and in the older foliage of evergreen species, as well). This storage plays a critical role in future allocation and growth because the sugars are stored in a stable condition as starch, but then can be mobilized back into sugars when needed. Secondary growth of the woody parts of the tree has relatively low priority. The functions that wood growth provide are: (1) to produce new layers of cells for transporting water and nutrients in the xylem, and sugars and other compounds in the phloem; (2) to provide for physical support of the tree by thickening the stem and roots. These functions are clearly important for the survival of the tree, but are provided by multiple years of functioning xylem and phloem. The dead xylem in stems, branches, and roots also gives additional structural support. The lowest priority in allocation is the production of defensive chemicals, such as resins in the wood of many conifer species, and tannins in the leaves of oaks and other species (Salisbury and Ross, 1992; Barbaroux, Breda, and Dufrene, 2003).

One carbohydrate allocation, **growth respiration**, relates to nearly all of the functions described, as it occurs anywhere that plant tissues are being constructed. This respiration occurs proportionally to the rate of growth of foliage, root tips, wood, bark, flowers, or seeds in any location in the tree. It cannot be placed in a specific priority level within the hierarchy. It should be

noted that there is no difference in biochemical process between growth respiration and maintenance respiration. Both of these terms are used so as to differentiate allocation of respiration energy between the two functions: growth and maintenance.

The Effect of Carbohydrate Allocation on Tree Growth

The priority rankings of different functions of the tree will show an overall pattern (as described in the previous section), but this description may make it appear that the tree is being controlled by a computer program. It is useful to see how these allocations really work over a growing season. They are controlled by a source-sink relationship of sugars that functions principally in the phloem and are mediated by plant hormones (auxins, cytokinins, gibberellins, abscisic acid). For example, when leaves are fully active and producing sugars from photosynthesis, they would be a source of sugars. Fine roots growing at this time would be using sugars to build cellulose and other molecules to construct new cells; thus, the roots would be considered a sink because the sugars are disappearing as they are combined to create cellulose and other structural molecules to build cells. The sugars would be flowing from high sugar concentrations in the leaves to low sugar concentrations in the root tips. Plant hormones control the activity of cell divisions within the various parts of the tree to turn them from sinks to sources and back to sinks (Salisbury and Ross, 1992; Larcher, 2001).

A deciduous tree in a temperate-zone climate exemplifies these changing activities during its growing season. In the spring, auxins initiate the growth of buds in the tree crown to produce shoots and leaves, and they begin to expand acting as strong sinks. The sugars are being mobilized from stored starch in large roots and the stem which are now acting as strong sources of sugars. Then, as leaves open and expand to full size, the source-sink patterns reverse. The leaves now become a source of sugar from photosynthesis, and the storage cells in the roots and stems act as a sink, converting sugar to starch and rebuilding the reserves for next year. Next, the cambium meristem is activated by auxins all along the branches and stem. Sugars are translocated down the phloem from the foliage to the sink in the wood cells. There, sugars are incorporated into the cellulose of new xylem and phloem cells, as well as made into defensive chemicals within the wood.

These patterns of growth are important for understanding how a tree grows. Consider a loblolly pine tree that is growing in a young, dense, loblolly pine stand, where the canopy has not closed yet. The tree's large crown would be able to supply sugars for all parts and functions of the tree. As the canopy begins to close,

bottom branches become shaded, and the total foliage would be reduced, so photosynthesis would decline. The weakest sink would be resin production, so this makes it more likely that the southern pine beetle would be able to bore through the bark into the phloem, stealing the sugars. If the tree had more sugars, then large amounts of pitch would block or kill the beetles. Stem diameter growth will then decline, especially in the lower part of the stem, which is last in line for the sugars that are allocated for the stem. However, the tree had continued to grow in height at the same rate as in past years. It had already obtained all the sugars that were needed from that which was stored from last year. However, if crown competition within the stand limits the crown size even further, the tree would not be able to store an adequate amount of sugars as starch for the following year. So, during the next growth season, the leader would not grow as much in height as in previous years. The crown size of this tree must be reduced to a very small size in order to not be able to provide the stored sugars for the growth of shoots and leaves in the crown; trees of this sort are not long for the earth, unless more growing space is given for the crown to expand. Of course, not all the pines will follow this trend. Pines that have taken the growing space away from those like this one, are going to remain strong and healthy. Only the strong survive. This means that those trees that start to lose the battle to secure crown growing space and resources will usually die. Those trees of the same species that obtain more growing space will win over their same-species competitors.

Tree Structure and Development

A great diversity exists among tree species in the structure (or architecture) of the stem and main branches. A division into two basic types can be made, to recognize an important structural difference. Some species have an **excurrent form**, with a main vertical stem that extends to the very top of the tree, and with branches that are distinctly smaller in diameter, growing in a roughly horizontal orientation. Other species have a **decurent form**, with branches that begin roughly horizontal but then curve upward to become vertical (see Oliver and Larson, 1996). The main branches on trees of decurrent species grow so large in size that they may nearly equal the diameter of the original main stem; in many cases, a main stem cannot be identified in the upper part of a mature tree (Fig. 17.2).

Nearly all canopy tree species exhibit excurrent form when they are saplings and poles, ascending toward the canopy. Most gymnosperms, such as pines, spruces, Douglas-fir, and ginkgo, maintain that form as they develop into large mature trees. Most angiosperms, such as oaks, maples, birches, and mahogany, lose the excurrent form as they grow beyond the sapling and pole stage.

(a)



(b)



Figure 17.2 The silhouette of a tree with (a) an excurrent form (Norway spruce); and (b) a decurrent form (horse chestnut). Source: (a, b) F. Cooper, Little Stick. Reproduced with permission from F. Cooper.

Factors that shift angiosperm species from excurrent to decurrent form appear to be related to: (1) repeated damage to the crowns, (2) timing of canopy exposure and full sunlight, or (3) initiation of crown flowering and fruiting. However, the division among structural types between the two main groups of trees is not complete. Some angiosperms such as yellow-poplar and sweetgum maintain the excurrent form to a very large size, unless the stem is damaged.

Stems and branches in both structural types are inherently negatively geotropic (which means that they grow away from the earth in an upward direction).

In excurrent species, the shoot at the apex of the tree exerts strong **apical control** over branch growth. When a new shoot begins to develop from a bud on the main stem, it begins to grow vertically, but is quickly controlled by hormones translocated from the leader (the top shoot of a tree is often called the **leader**). This causes the branch to grow in the direction of the original orientation of the bud, usually somewhat above horizontal. Secondary growth of the branch is also controlled, and the new layer of wood is added to the branch at very low rates, even if it is a fast-growing, vigorous branch, and so the branch stays much smaller in diameter than the main tree stem. The influence of the leader at the apex of the tree is called **apical control**, which is a result of plant hormones that are produced in the leader and translocated to other parts of the tree. This control of branch growth is sometimes referred to as "epinastic control," although the term "epinastic" refers only to control of the angle of the branch, not the branch diameter growth rate. "Apical control" is the more commonly used term for the overall pattern.

If the leader of an excurrent species is cut off, some of the young branches just below the leader will be released from apical control, and one or more will curve upward and grow vertically. This occurs with any excurrent species when the leader is cut or broken. However, older branches that are lower in the tree are not affected by the loss of the leader; they maintain their horizontal or slightly upward orientation. In decurrent species, apical control appears to have much less effect on branches. Branches of these species also begin growth that is oriented with the initial bud angle when they are young, but then they routinely grow upward, with the branch tips eventually being almost equal to the height of the main stem tip, and nearly equal in diameter, as well.

The Concept of Growing Space

If a tree has growing space open in all directions, the branch growth of that tree will form a circular, symmetric crown. However, if growing space is limited on some sides of the tree by the crowns of other trees or other barriers, the crown will become asymmetric. Branches on the well-lit sides will produce a greater number of buds, and the shoots developing from those buds will have greater growth rates, compared to shaded branches. Thus, branches function somewhat autonomously from one another. Carbohydrates produced by the photosynthesis of foliage of each branch are not shared evenly among branches to maintain a symmetric crown. Vigorous branches export carbohydrates to support the current growth of stems and roots and to provide storage for future growth, but this export does not include other branches. When the stored carbohydrates are mobilized at the beginning of the growing season, more will be

translocated to the vigorous branches with more buds, which act as strong sinks for carbohydrates. Differing auxin concentrations in the various parts of the crown are the major mechanism for guiding the amount of sugar to the sites for growth. An old branch at the bottom of the crown, shaded by the branches above, will receive only a small portion of the stored carbohydrates because it has few buds. When photosynthesis produced by the branch can no longer meet its growth and respiration requirements, it will die. The same will happen with young branches high in the crown, if they are shaded by taller adjacent trees.

The development of asymmetric crowns improves the growth and survival of a tree by allowing it to efficiently capture free growing space. This can be observed at an edge between a forest stand and a field (Fig. 17.3). With most hardwood species (decurrent form), the edge trees will develop a longer crown on the field side with longer branches that have larger diameters, compared to the forest side. This highly asymmetric crown may become so unbalanced in weight that the tree will lean away into the open growing space. In these situations, it appears that the trees are phototropic (i.e., with the leader growing toward higher light intensity), but this is not the case. Phototropism has little effect on branch or stem orientation of trees past the seedling stage. As the heavier side of the crown begins to pull the tree over, the leader continually grows vertically. The growth of reaction wood in the stem (described later in this chapter) helps to bend the tree back to vertical, thus producing a curved tree. This happens with edge trees along streams or with trees growing in a stand with canopy gaps. With conifer species (excurrent form), a similar effect happens, but the most noticeable effect is the longer crown on the field side rather than a curvature in the stem. Because of the stronger apical control in conifer species, the branches on the field side do not increase in length or diameter to the same degree, so the effect will be only moderately larger diameter or longer branches. Generally, there is not enough differential weighting of the crown to cause the tree to lean.

The structural form of the root system is generally hidden from view, and so it is not as well understood as that of the aboveground portion of the tree. However, the main functions are quite clear: the fine roots take up water and nutrients, and the large woody roots anchor the tree in the soil, translocate water and nutrients, and store and translocate carbohydrates. In many tree species, the seedling produces a taproot that grows vertically beneath the stem, providing physical stability and uptake of water. Other roots grow horizontally, staying close to the soil surface where water and nutrients occur in high levels. They extend their roots in all directions, similar to that of branches. Fine roots proliferate where the combination of water, nutrients, and oxygen are



Figure 17.3 A photograph of the crown response to growth along a field edge. Source: Mark S. Ashton.

available, and they progressively thicken into woody roots. However, where fine roots encounter soils with few resources, they will slow in growth or die. Thus, asymmetric root systems develop and they appear to grow in a hydrotropic orientation (that is, toward greater water and nutrient availability), but this is not so. As with branches, it is a case of symmetric “exploration” of growing space, with differential survival in each direction based on the different amounts of resources in each direction.

Because roots do not have to support their weight, roots can extend much further than branches, beyond the edge of the tree crown. They can grow past the root systems of neighboring trees. When roots of neighboring trees of the same species grow across one another, a root graft can occur. As the roots enlarge through secondary growth, a union can form between the cambium, phloem, and xylem layers, such that water, nutrients, and carbohydrates are translocated from one tree to the other. In some single-species stands (mostly of conifer species), the trees that are clearly individuals aboveground have a single common root system belowground. This can be seen where tree stumps can remain alive for years after the tree has been cut. Dye that is injected into one tree stem will often be detected in a neighboring tree that was not injected with dye. There is some evidence from the tropics that trees can develop functional root grafts among different tree species, but only if the species are closely related. Similarly, there is evidence that

carbohydrates may be exchanged between Douglas-fir and paper birch (Simard *et al.*, 1997).

There is another aspect of carbohydrate allocation that was not described earlier in this chapter, which deals with the balance between the aboveground and belowground structure and function of woody plants. When water and nutrients are in limited supply on a forest site (as on a dry sandy soil), the translocation of carbohydrates from the aboveground tree to the root system is increased. This allows greater growth of fine roots, which increases water and nutrient uptake. The opposite occurs when soil resources occur at high levels. On a moist, high-nutrient site, more carbohydrates would be translocated to the shoots. This allocation maintains a physiological balance between fine root and foliage functions. This means that tree biomass is not balanced between aboveground and belowground; it will vary. In areas with high precipitation, the belowground biomass is generally only 20–30% of the total tree biomass. In arid regions, shrubs may have 50–70% or more of the total plant biomass in root systems.

Stem Growth

The stem of the tree is of greatest economic concern for timber production, and is also vital for supporting trees that are destined to grow to old-growth stature. Therefore, it is worthwhile to examine the details of stem growth in greater detail. The growth of woody portions

of a tree is so low in carbohydrate-allocation priority that if anything reduces the amount of photosynthesis, it will likely result in a reduction in stem growth, even though other parts of the tree might not be affected. This is why foresters can control the diameter growth by thinning the stand in order to allow the crown to grow larger. One rough but convenient index of the ability of the crown to supply sufficient carbohydrates for stem growth is the live-crown ratio (LCR), which is the stem length within the living branches divided by the total height of the tree, generally stated as a percentage.

Stem growth is based on current-year carbohydrate produced in the foliage of branches and exported to the stem. The annual ring is added as the outer layer of the stemwood, starting at the top of the tree and progressing downward. First, plant hormones activate the cambium to undergo cell division, and then carbohydrates provide the materials for the structure of the cells. It may take several weeks for the growth activity to progress from top to bottom of the stem of a large tree. The width of the new ring of wood generally increases, as it progresses from the top of the tree to the base of the live crown. For vigorous trees with large LCRs, the layer of wood continues to be added below the crown, but with declining ring-width. To understand this pattern of wood growth, it is helpful to think of the ring area rather than just the ring-width. The ring area added may remain constant along the stem, but the ring-width becomes thinner because it is being spread around an ever-increasing circumference of the stem as the wave of growth moves down the tree.

With vigorous trees in or above the main canopy, the mechanical stress caused by wind blowing on large crowns creates a hormone-mediated response that translocates more carbohydrates and creates additional diameter growth at the stem base (called **butt-swell**). On the other hand, low-vigor trees with low LCR (tree A in Fig. 17.4) have fewer carbohydrates available for wood production. A progressively thicker ring of wood is laid down along the stem within the live-crown portion of the tree, but then the ring width declines rapidly in the lower part of the stem. This is not just the result of an increasing circumference of the lower stem; the ring area of wood is reduced in absolute terms. In fact, trees with very low vigor may not have enough carbohydrates to add any new wood at the base of the tree. These trees will not complete an annual ring along the lower stem. Trees with such small crowns are generally in the lower canopy or in a very dense main canopy, and are not subject to mechanical bending from wind, so there is no response that provides additional diameter growth to produce a butt-swell either. Thus, the two factors that control the shape of the growth layer on a tree stem are (1) the total size and length of the crown, and (2) the degree of bending stress from wind.

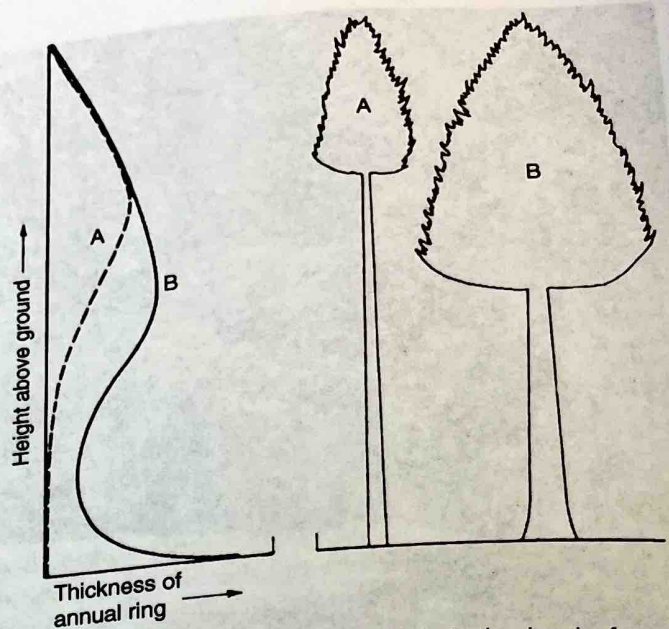


Figure 17.4 The variation in the thickness in the sheath of wood annually laid down on the central stem for a small-crowned tree (A) that is barely surviving, and a vigorous tree with well-developed crown and butt-swell (B). Note that there are peaks in ring thickness near the base of the crown of each tree. Source: Yale School of Forestry and Environmental Studies.

Effects of Stand Density and Thinning on Stem and Wood Characteristics

Stand density (the number and sizes of trees in a stand) is directly related to the degree of competition among individual trees. This competition affects tree vigor, apparent in the LCR, which in turn affects stem form and wood characteristics. These effects can be shown by comparing diagrams of three trees of the same conifer species and of the same age (Box 17.1) that have grown in stands with different histories of stand density.

Stem Form

An open-grown tree clearly has a larger diameter at breast height (DBH) than the tree in a dense stand, but the differences in taper must be taken into account to determine accurate stem volumes. The measure of DBH is within the zone of butt-swell, and that can give exaggerated impressions of the growth of stem volume. It is unfortunate that trees are tall and people are short because it would be more reliable to take the basic measure of stem diameter at some point higher than 4.5 ft (1.4 m). In any case, methods exist to assess the degree of taper, which include both butt-swell and upper-stem taper. In the United States, the Girard form-class method is frequently used to determine taper by measuring the stem diameter at the height of 4.5 ft (outside bark) (1.4 m) and at the height of 17.5 feet (inside bark) (5.3 m), which is expressed as a percentage of the upper diameter

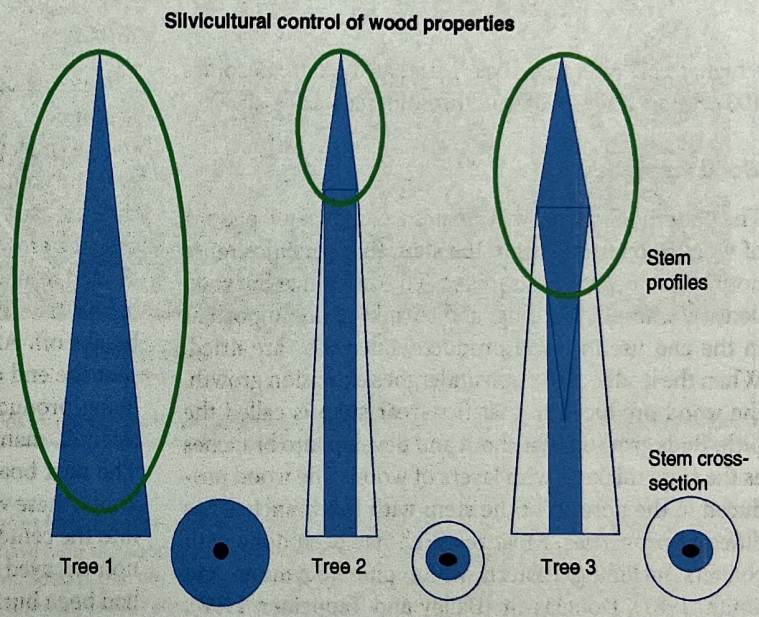
Box 17.1 Comparing stem growth and wood formation of trees with histories of different stand density.

Tree 1 has grown in a stand with such low density that the tree is open-grown (Fig. 1). Tree 1 has a live crown ratio (LCR) of 100%, meaning that the live crown extends to the ground. Tree 2 has grown in a much denser stand, and has an LCR of 20%. Tree 3 had initially grown in a stand with a density similar to that of Tree 2, until a thinning treatment substantially reduced the density, and Tree 3 then grew in the more open stand; its LCR is 50%.

In all three trees, stem diameter increases from the top to the bottom of the stem because the stem is progressively older (with more annual rings) from top to bottom. This is seen most readily in the open-grown tree (Tree 1), in which stem growth produces an annual ring that is nearly constant in width along the entire length of the stem (meaning that wood volume growth increases steadily along the

stem). This growth pattern produces a high degree of taper, and the stem form approximates the shape of a cone. This is because the crown is of sufficient size to allocate surplus carbohydrate to the weakest sink, the growth increment in girth. The stem of the tree growing in a dense stand (Tree 2) has increasing ring width within the crown, but declining ring width below the bottom of the crown. This will produce a stem with a conical shape within the live crown, and a more cylindrical shape (i.e., with less taper) in the lower stem. This is because little surplus carbohydrate makes it from the live crown to parts of the stem lower down (see Fig. 17.4). Tree 3 is intermediate with a renewal of growth increment down the stem because of crown expansion and increased carbohydrate production that can be re-allocated back down the bole.

Box 17.1 Figure 1 Stem and live crown profiles of an open-grown tree (1), a tree grown under high competition in a dense unthinned stand (2) and a tree grown in a dense stand that has subsequently been thinned (3). Blue indicates crown (juvenile) wood and white indicates mature wood. The same colors in the stem cross-section profiles represent mature and crown wood. Black circles represent the pith. *Source:* Mark S. Ashton.



divided by the lower diameter. Thus, both taper and bark thickness are included in the measure, which is used to modify the standard tree volume equations (Table 17.1).

When trees are grown rapidly with substantial taper, the shortcomings become obvious at the sawmill. A common method of sawing is to make cuts that are parallel to the axis (the pith) of the stem. The first cuts remove the **slab wood** (the outer planks with the butt-swell) to create a **cant** (essentially a square log). A good deal of the extra growth in a highly tapered tree will be lost in the slab wood. Furthermore, the annual rings (called the **grain** in the terminology of wood technology) are aligned with the taper of the stem, which is at an angle to the axis of the stem. Thus, the sawn boards have the grain at an angle to the board, a characteristic called **diagonal grain** or **cross grain**. These boards are prone to warping. Stems that are more cylindrical have grain

that is more closely aligned to the stem axis, and therefore to the sawn boards, so the problem of warping is reduced (Box 17.2).

Another consequence of the differences in stem taper in trees has to do with the risk of wind-throw. The high carbohydrate-allocation priority of stem height growth means that trees in stands of different densities (such as Trees 1 and 2 in Box 17.1) both have similar heights but substantially different diameters. This can cause a structural imbalance for trees in dense stands because the thin lower stem has little strength to overcome the wind stresses, even though the sail area of the crown is also reduced. A simple measure that is used to assess the risk of windthrow is the **height:diameter ratio** (H:D ratio). This ratio is calculated by dividing the total tree height by DBH, making sure that the same units (such as inches or centimeters) are used for both measurements. Tree 2 would have

Table 17.1 Girard form class values for several common North American tree species from the east. Values depict differences among regions and species. Greater values are associated with smaller-statured trees on more nutrient- or drought-stressed sites with lower productivity.

	Northeast	South	Lake states
Eastern white pine	80	–	78
Eastern hemlock	78	–	77
White oak	78	78	78
Red oaks	78	78	78
Yellow-poplar	80	81	80
Beech	84	82	82
Hickories	78	77	78
Cottonwood	78	78	78

Source: Mark S. Ashton.

a higher H:D ratio than Tree 1, and as the ratio becomes 100 or more, the risk of windthrow increases.

Wood Properties

The pattern of tree growth creates a complicated pattern of wood properties within the stem that becomes more noticeable once the log is milled. The differences in wood density, stiffness, warping, and shrinkage are important in the end use in wood products, once they are dried. When the leader of the tree undergoes extension growth, the wood produced in that first-year stem is called the **pith**. Buds grow on that shoot and develop into branches as the stem thickens with layers of wood. The wood produced in the portion of the stem with live branches has different properties. Most research has been done with conifers including eastern white pine (Seymour and Smith, 1987), Douglas-fir (Bailey and Tappeiner, 1998), and loblolly pine (Baldwin *et al.*, 2000). Generally, the wood in this area of the tree grows rapidly, producing wide annual rings, and the wood cells that are produced have lower density and are shorter (in the vertical dimension). They also have the propensity to bend or shrink because of the structure of the cell walls (Gartner *et al.*, 2002). These properties lower the value of wood for most uses. This wood has several names. The most common is **juvenile wood**, but this term leads to confusion because it seems to indicate that it is the wood grown in juvenile trees. That part is true, but it really means the wood in the juvenile part of a tree, regardless of the tree's age. So not only will juvenile wood exist around the pith of the young tree stem, it also is the wood growing on the part of the stem with live branches. The term **crown wood** is suggested as a better term; **core wood** or **pith-associated wood** have also been suggested as terms for the same thing. The crown wood is gradually encased by a transition to **mature wood** which has thin-

ner growth rings, higher density (in most species), and less probability to shrink or warp (Maguire, Kershaw, and Hann, 1991; Pape, 1991) (see the latter section of Box. 17.1).

One mistaken view that has long persisted is that the strength of wood is directly controlled by the rate of stem growth, and that conifer wood, such as hard pines and Douglas-fir, used for construction, is weakened by fast growth. This is based on the idea that the early wood (with lower density) is increased more with fast growth. However, thinning increases the ring width of course, but also usually increases the proportion of late wood (higher density). This is actually not a problem since the ratio remains the same. The problem is not the faster-growing wood of mature wood. The problem is the crown wood. Grading of lumber sometimes uses ring width but it really is just using this to eliminate the crown wood from construction grades.

Knots

The presence of knots in wood is a serious defect. The center core of any tree stem has branches that originated on the small young stem. The stem grows larger in diameter and continues to bury the old part of the branch while the new part continues to grow to form the branches in the tree crown. When the branch dies because of being shaded from other trees or branches higher in the crown, it will take some time until it begins to rot and then breaks off. After the main tree stem grows in diameter past the end of the dead branch, only then is clearwood being produced. When a large tree is being sawn at a sawmill, many of the outside boards will be clearwood. The next boards will contain black, partly decomposed knots; these were the slices of the dead branches. Farther into the center of the stem, there will be boards with red, non-decayed knots that are from the living branches that had been buried in the stem.

The problem of knots is so great that the silvicultural method of pruning branches was developed to eliminate the problem of knots in the main stem. The problems and methods to deal with knots are described in detail in Chapter 19.

Relationships of Crown Morphology to Stem Among Species

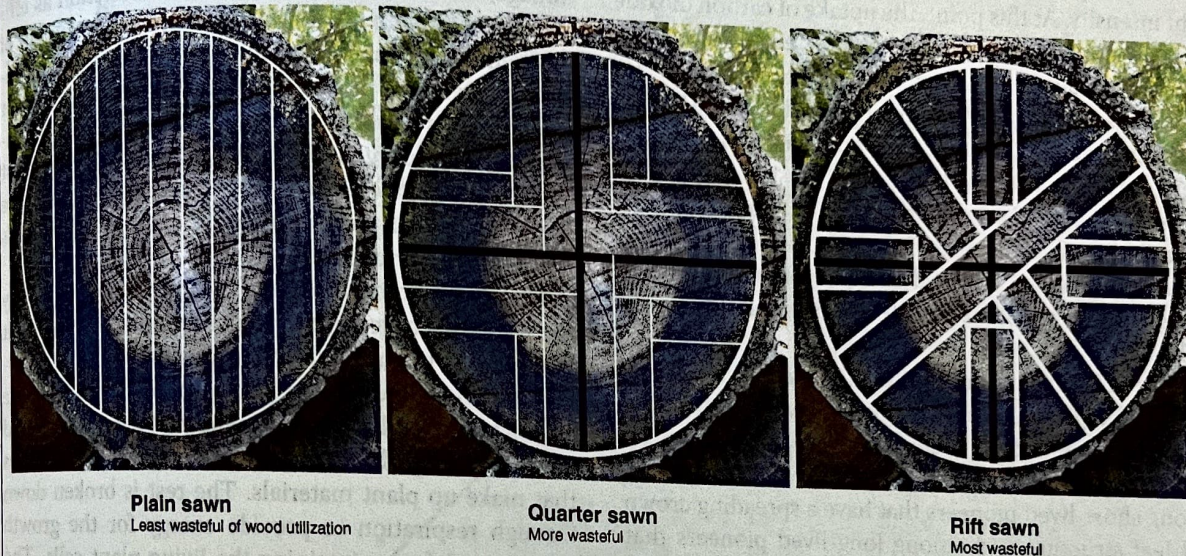
As can be predicted, tree species have different abilities to photosynthesize and allocate carbon for maintenance of living tissues (respiration), reproduction (flowering and fruiting), fine root growth, leaf production, height growth, and stem girth increment. Efficiency in growth allocation to stem increment can be gauged by a ratio of a measure of crown size (leaf area) to stem area. One such measure is the ratio of sapwood to leaf area (Table 17.2) (Tyree and Ewers, 1991). Fast-growing tree species can have a relatively high leaf area per sapwood

Box 17.2 The different kinds of sawn timber from the bole of a tree.

Plain sawing is the most common method of sawing a log (Fig. 1, left). It is also the simplest and involves a parallel series of cuts through the entire log. This is the least wasteful of the wood for producing sawn timber, but because the grain of the wood changes across the board, differences in the drying process can cause differences in tension which can lead to twisting and bowing. Flooring and other high-quality visual products can take on moisture from the air and then warp. Often, dry boards will absorb moisture from the atmosphere and will become distorted. Appearances are also variable because the wood was sawn in one direction only. This means the radial and tangential wood grain can be seen in the same or adjacent board.

Quarter sawing requires cutting the log radially along its length into four quarters (Fig. 1, center). Once quartered, it involves just plain sawing all the way through. This is the common method for producing flooring and other veneers and visual woods (especially oak) because the radial pattern of the growth rings is consistent across boards and warping is not such an issue because there is less variability in tension during the drying process.

Rift sawing is the most wasteful in producing sawtimber but the most visually appealing and the most resilient to warping and distortion (Fig. 1, right). All of the boards have been made by radial cuts through the stem. This is both time consuming and expensive.



Box 17.2 Figure 1 The three different kinds of methods for milling saw timber: plain sawn, quarter sawn, and rift sawn. Source: Mark S. Ashton.

Table 17.2 Leaf to sapwood area of select tree species from the US Pacific Northwest. Sapwood is the functional part of the stem that conducts water. Water-use efficient stems should have high sapwood area to leaf area ratio, meaning that a proportionally larger conductive system can supply a leaf area with water. Species that are from drier, more extreme sites, or that are more shade intolerant, have lower ratios than species from milder, wetter climates, or that are shade tolerant.

Species	Leaf area/sapwood area (m ² /cm ²)	Climate
<i>Abies amabilis</i> (Pacific silver fir)	0.64	Mild wet, shade tolerant
<i>A. grandis</i> (grand fir)	0.48	Mild wet, shade tolerant
<i>A. lasiocarpa</i> (subalpine fir)	0.78	Mild wet, shade tolerant
<i>A. procera</i> (red fir)	0.27	Mild, shade intolerant
<i>Juniperus occidentale</i> (western juniper)	0.18	Extreme desiccating, shade intolerant
<i>Picea engelmannii</i> (Engelmann spruce)	0.35	Mild wet, shade intolerant
<i>P. sitchensis</i> (Sitka spruce)	0.45	Mild wet, shade intolerant
<i>Pinus contorta</i> (lodgepole pine)	0.15	Extreme desiccating, shade intolerant
<i>P. ponderosa</i> (Ponderosa pine)	0.25	Desiccating, shade intolerant
<i>P. sylvestris</i> (Scots pine)	0.14	Extreme desiccating, shade intolerant
<i>Pseudotsuga menziesii</i> (Douglas-fir)	0.54	Mild wet, shade intolerant
<i>Tsuga heterophylla</i> (western hemlock)	0.46	Mild wet, shade tolerant
<i>T. mertensiana</i> (mountain hemlock)	0.16	Desiccating, shade tolerant

Source: Adapted from Waring *et al.*, 1982.

area, while long-lived species with large leaf areas have relatively lower sapwood areas.

There are also inherent ontogenetic changes in stem and crown physiology as a tree develops over time. As a tree grows from a seedling to sapling to pole to eventually a large canopy tree, its living body respiration increases relative to its leaf area (Fig. 17.5a). Seedlings that can withstand shade because of lower respiration rates, and therefore lower compensation points, become more shade intolerant with increased maintenance respiration when they grow taller and bigger in height and size. The compensation point is where the rate of photosynthesis equals the rate of respiration under a certain light intensity. At this point, the uptake of carbon dioxide through photosynthesis matches the release of carbon dioxide through respiration. Early successional species start off as seedlings with higher respiration maintenance rates, in large part because they are growing faster, and therefore are more shade intolerant than slower-growing, late-successional species. Differences in shade tolerance is similarly reflected in different species adaptations in crown morphology and leaf anatomy (Bond-Lamberty, Wang, and Gower, 2002; Poorter, Bongers, and Bongers, 2006) (Fig. 17.5b).

These relationships and differences among species at the physiological and morphological level also occur at the whole tree-crown architecture level. Crowns can remain the same shape as a tree grows. This is common among short-lived pioneers that have a spreading crown and leaf structure and among long-lived pioneers that have a compact crown. Late-successional species have crowns that change with time from columnar to shallow and expansive. The relationship between crown projection area and bole diameter of late-successional species therefore changes as the trees increase in height, and then mature and ascend into the forest canopy. Understanding the successional status of a tree species relative to other species is important in developing spacing guidelines for planting and thinning.

Stand Scale Patterns of Production

This section deals with tree growth (also called production or increment) at the stand level. Stands are collections of trees, but the measurement and analysis of stand growth per unit of land area reveals important patterns that cannot be seen from measurement of individual trees (Kelty, 1992; Reich *et al.*, 1997; Waide *et al.*, 1999). The basic biological measure of stand growth is the increase in biomass, generally in units of tons/acre/year (Mg/ha/yr). These units are in terms of oven-dried biomass to eliminate variations of moisture content that are not connected to growth.

The amount of sugar-producing foliage that a stand can maintain depends on species, and to a lesser extent, the ability of the soil factors to supply the foliage. Most evergreen species maintain more foliar surface than deciduous species, if only because the leaves persist longer than one growing season. Shade-tolerant species have more than the intolerants because their leaves can function at lower light intensity and thus form deeper crowns. Within a species, the total amount of foliage in a closed stand is much lower on a very poor site than on the best.

Poor sites produce less dry matter than good sites not so much because of major differences in the amount of foliage, but because the foliage cannot function as efficiently (Assmann, 1970). Deficiencies in the supply of nutrients and water from the soil can slow photosynthetic rates and the creation of new tissues. If water becomes unavailable because of depletion, low temperature, or soil-oxygen deficiency, photosynthesis must cease. High temperature can also cause stomatal closure and cessation of photosynthesis if evaporation exceeds the rate of water uptake.

The total photosynthesis of a forest stand (or of any ecosystem) is called gross primary production (GPP). It is measured in mass, which represents the glucose (carbohydrate) synthesized in photosynthesis. Some of the sugars produced by the photosynthetic process are used as the building blocks of cellulose and other molecules that make up plant materials. The rest is broken down through respiration to provide energy for the growth process and for maintaining the living plant cells. The annual increase in plant biomass is the net primary production (NPP), which is the GPP minus autotrophic (plant) respiration. Microbes, insects, and other organisms consume and decompose some of the plant matter that has been produced. They incorporate some of the plant matter into their growth and use much of it for their respiration; this is heterotrophic respiration. NPP minus heterotrophic respiration gives net ecosystem production (NEP), which is the increase in biomass of plants, animals, and microbes. This makes NEP difficult to measure. In most forests, biomass and respiration of organisms that consume plant material is quite small compared to the biomass and respiration of the trees and of the microbes in the soil and forest floor. NEP is often measured by NPP minus the rate of respiration from microbial decomposers (by measuring carbon dioxide). This assumes that the biomass of consumer and decomposer organisms doesn't vary over time, but of course it does vary with seasons.

The rate of GPP is dependent on the leaf area of the stand canopy. When measuring the leaf area per unit of land area, the measure is called leaf area index (LAI). Greater LAI provides the potential for high levels of GPP.

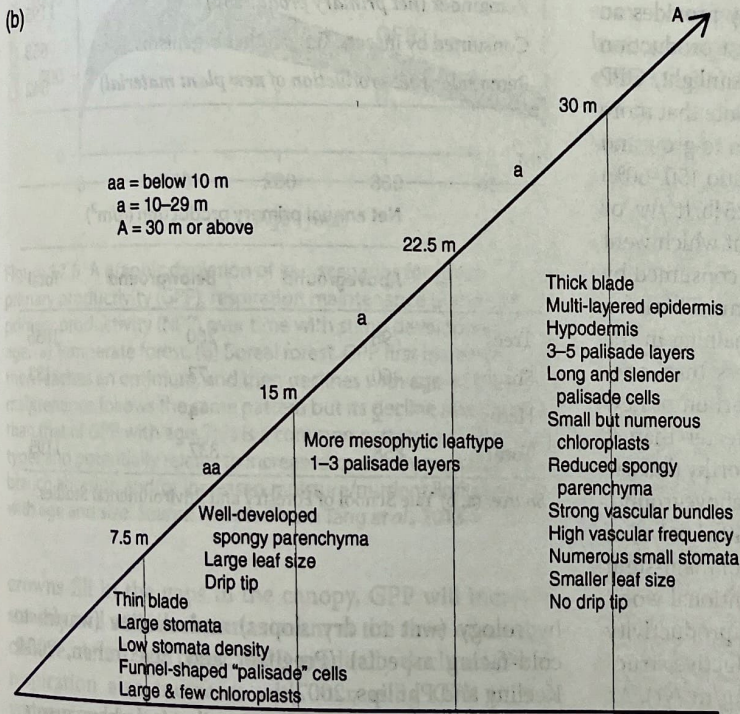
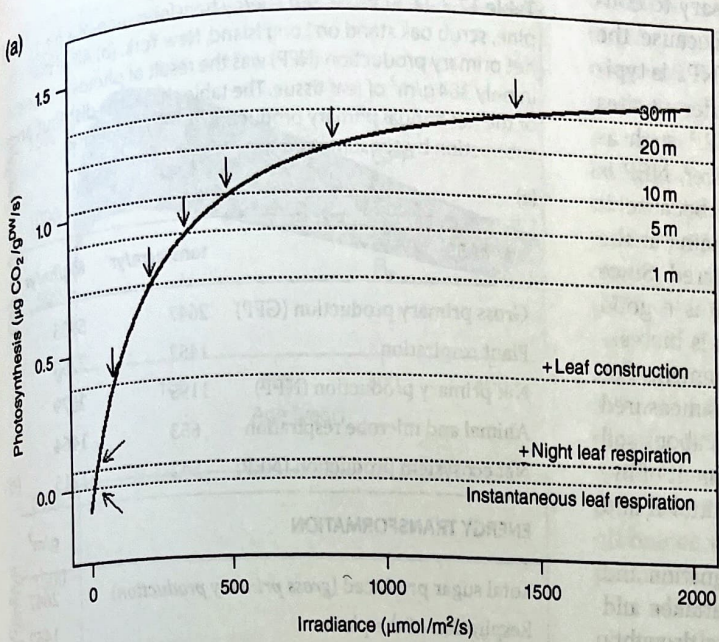


Figure 17.5 (a) A graph depicting photosynthesis, respiration, and compensation point with tree size (height) from seedling to canopy tree for a yellow-poplar (*Liriodendron tulipifera*). The curve is the instantaneous rate of photosynthesis (as measured amount of CO_2 assimilated per dry weight of plant per second) plotted as a function of irradiance (amount of sunlight as measured in $\mu\text{moles}/\text{m}^2/\text{s}$). The horizontal dashed line at the bottom reflects the instantaneous rate of leaf respiration. The dotted horizontal lines represent the cumulative respiration rates first of night respiration, then leaf construction, and then of whole plant growth at various sizes (1–30 m; seedling to tree). The intersection between the rates of respiration for the different size classes and the photosynthesis curve are the compensation points (the point where respiration rate = photosynthesis rate). If a plant or tree is growing in a light environment where its rate of photosynthesis is below the compensation point then it will die. Shade-tolerant species have relatively lower compensation points in low light as compared to shade-intolerant species. This is particularly the case for seedlings, but as seedlings become trees, all species become more shade intolerant because their compensation points increase to match the increased respiration rates of larger individuals. Source: Givnish, 1988. Reproduced with permission from CSIRO Publishing. (b) A graphic illustrating change in leaf morphology with tree height from seedling to canopy tree. Leaves within all species change from thin and large to thick and small on progressing from understory to canopy conditions, but the more shade-tolerant species show the more dramatic changes. Fast growing shade-intolerant or drought-sensitive species will place less emphasis on expensive structures and thicknesses that make species withstand drought or shade. Source: Adapted from Roth, 1984 with permission from Springer.

but a supply of water and nutrients is necessary to convert the captured sun energy to glucose. Because the activities of fungi and insects are so variable, NPP is typically used to compare forest growth from different sites or ages. Often it is just a component of NPP, such as aboveground NPP or just stemwood. However, NEP is becoming an important practical measure because it is the plant biomass (live or dead) that remains at the end of a year, after decomposition has occurred. Since biomass is approximately 50% carbon, NEP is a good measure of carbon sequestration rate, which is increasingly becoming an objective of forest management. For inventories (as opposed to research where it is measured precisely but at high cost) some assumptions about soil decomposition must be made, with measurement of living and dead trees being the main factor (Whittaker and Marks, 1975).

One of the early studies of energy transformation and biomass production was conducted by Whittaker and Woodwell (1969) in a 45-year-old stand on a droughty site on Long Island, New York. This study provides an example of the details of basic annual forest production (Table 17.3a). In this case, with plenty of sunlight, GPP would have been limited by water supply. Note that more than half of GPP is used in plant respiration to grow and maintain plant cells. This is a common ratio (50–60%) in forests. Nearly half of this NPP (0.25 lb/ft²/yr or 1195 g/m²/yr), including a major part of that which went into such temporary tissues as leaves, was consumed by insects, fungi, and other dependent organisms. This left a net production (of new plant material remaining in the stand) of 0.11 lb/ft²/yr (542 g/m²/yr) (or less than one-fourth of the gross production). The proportion of new root tissue on this dry site is probably greater than it would be in forests on most sites. It is noteworthy that the shrubs and herbs grew more below than aboveground, but the trees did not. Only 0.03 lb/ft²/yr (149 g/m²/yr) of the annual tree production was in the form of main-stem wood; furthermore, the efficiency of conventional wood utilization is low in relation to the massive productivity of forests. Acorns, cones, and other reproductive structures accounted for 0.004 lb/ft² annually (22 g/m²/yr). As is the case with most forests, the tree stratum produced much more substance than the subordinate vegetation (Table 17.3b).

Where resources are non-limiting or less limiting (high rainfall year round, high sunlight, high-fertility soils) and where climates are cool but not frozen, NEP can be very large, as in the Pacific Northwest. Warm, wet climates (tropical wet forests) can have much higher GPP than cool, wet climates, but they also have higher plant and animal respiration rates making the NEP lower. These patterns in biomass and energy transformation can be seen and measured across landscapes that change

Table 17.3 (a) Biomass and energy transformation of a pitch pine, scrub oak stand on Long Island, New York. (b) All of the net primary production (NPP) was the result of photosynthesis in only 384 g/m² of leaf tissue. The table shows the distribution of the net annual primary production (g/m²) before the subtraction by consumption.

(a)		
BIOMASS	tons/acre/yr	Mg/ha/yr
Gross primary production (GPP)	2647	5935
Plant respiration	1452	3255
Net primary production (NPP)	1195	2679
Animal and microbe respiration	653	1464
Net ecosystem production (NEP)	542	1215
ENERGY TRANSFORMATION		g/m ²
Total sugar produced (<i>gross primary production</i>)		2647
Respiration of the plants		1452
Remainder (<i>net primary production</i>)		1195
Consumed by insects, fungi, other organisms		653
Remainder (<i>net production of new plant material</i>)		542

(b)			
	Net annual primary production (g/m ²)		
	Aboveground	Belowground	Total
Trees	796	260	1056
Shrubs	60	73	133
Herbs	2	4	6
Total	858	337	1195

Source: (a, b) Yale School of Forestry and Environmental Studies.

hydrology (wet to dry slopes) and climate (warm- to cold-facing aspects) (Pregitzer and Euskirchen, 2004; Keeling and Phillips, 2007).

In general, evergreen forests and stands have greater NEP than deciduous forests and stands. Forests and stands with higher proportions of shade-tolerant species have higher NEP than those with higher proportions of shade-intolerant species (Pregitzer and Euskirchen, 2004).

Age-Related Changes in Stand Production

Gross and net production rates do not remain constant as a stand ages. Seedlings in a newly established even-aged stand will expand their crowns rapidly. As the

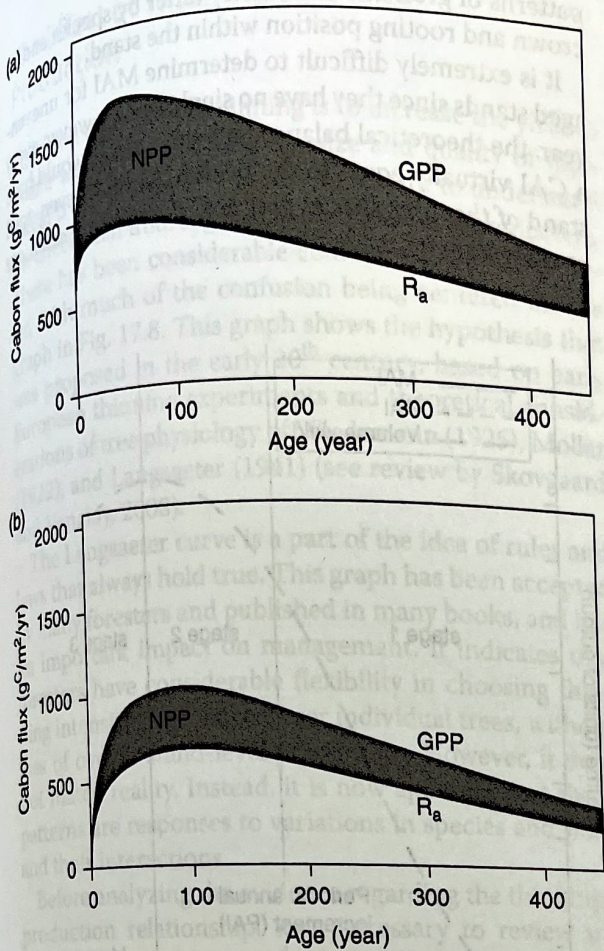


Figure 17.6 A graphic depiction of two scenarios for gross primary productivity (GPP), respiration maintenance (R_a), and net primary productivity (NPP) over time with stand development age. (a) Temperate forest. (b) Boreal forest. GPP first increases, then reaches an optimum, and then declines with age. Respiration maintenance follows the same pattern but its decline rate is less than that of GPP with age. This is a common pattern in all forest types and potentially relates to increased crown shyness from branch abrasion and/or increased moisture/nutrient limitations with age and size. Source: Adapted from Tang *et al.*, 2013.

crowns fill in the gaps in the canopy, GPP will increase steadily and will reach a maximum at the time of canopy closure. After that point, GPP gradually declines. Plant respiration also increases with increasing GPP in the young stand, but then levels off at the time of canopy closure and remains constant or gradually declines (Ryan, Binkley, and Fownes, 1997) (Fig. 17.6). This pattern of GPP and plant respiration rate results in NPP increasing from stand establishment to canopy closure, and then declining with increasing age. This pattern of NPP is widely seen in forests with strong stressors that become more limiting with age (e.g., wind, ice, soil moisture, and soil-nutrient availability) (Fig. 17.6).

The mechanisms that control this growth pattern are not fully understood, and the growth pattern itself is somewhat surprising. Canopy closure occurs rather early

in many stands. Why should young vigorous stands begin growth declines so early? This process has been observed in mixed-species and single-species stands; most studies of the process focus on single-species stands to reduce complexity and variability. The initial increase in GPP is clear, as leaf area increases because of crown expansion into openings among seedlings. GPP peaks and is maintained at a steady rate when complete canopy closure occurs but the subsequent decline of GPP has a number of possible causes. With many species, leaf area index (LAI) declines as a result of narrow gaps that develop between adjacent crowns (sometimes referred to as “crown shyness” or “canopy disengagement”). When the canopy first closes, branches interweave between adjacent crowns. As the trees grow taller, they sway in the wind and crown edges abrade, breaking off branch tips. The result is a canopy with many small permanent gaps that reduce the overall LAI.

In addition, other factors may arise that reduce the photosynthetic rate of LAI, rather than reduce LAI. In some combinations of species and sites, nutrients may become sequestered in standing tree biomass to the extent that there are insufficient soil nutrients available for root uptake. Nutrient stress would then reduce the photosynthetic rate. Similarly, hydraulic limitations in tall trees at older stand ages may reduce water availability to the canopy, again reducing photosynthetic rate, particularly on dry sites.

In forest management, much of the interest in stand growth is focused on the commercial part of the tree, which often is just the stemwood. Biomass production of stemwood follows the same general pattern as total NPP, with an increasing growth rate in young stands to a maximum at canopy closure and then a declining growth rate. However, the decline in older stands is more pronounced for stemwood than for NPP. The cause appears to be related to both the stand differentiation process and to the low priority in carbohydrate allocation to the woody parts of the tree, especially diameter increment (as described earlier in this chapter). The cause can be understood with the idea of crown efficiency of individual trees.

Crown efficiency refers to the rate of stemwood growth of a tree to its crown projection area or its leaf area. In a young even-aged stand before canopy closure, trees of a particular species will have similar efficiencies. After canopy closure, the stand will differentiate into a range of sizes from large dominant trees to small suppressed trees. Large trees develop large crowns that have many branches. Wood in general has low allocation priority, and branches (leaf-bearing stems) get first allocation of carbohydrate for growth and respiration, before non-leaf-bearing stems. Thus, bole-wood production declines in large trees. Suppressed trees have low photosynthetic

rates because of shading (low light levels) so they produce only small carbohydrate levels used mostly for replenishing foliage and fine roots; this in turn will cause very low allocation to stems. Suppressed trees often do not complete xylem growth down the stem. In contrast, a stand of similar-sized trees with moderate crown sizes will be most efficient in stemwood production per unit of crown. However, the largest trees in a differentiated stand are the most vigorous trees with the greatest absolute stemwood growth rate. These are often the trees that are favored for future growth in managed stands, but they have a lower stemwood growth rate per unit of crown area or leaf area.

It is important to note that the maximum time of stand biomass production is not really related to age, even though "age-related" is the term commonly used to describe the growth pattern. The pattern is controlled by the time of canopy closure. In natural stands, the timing of canopy closure is affected by initial stand density, site quality, and species. Foresters can change the timing by controlling early stand density, and controlling competing vegetation, or speeding up the process of canopy closure and increasing LAI by using fertilization.

Measuring Growth

Traditionally in forestry, there are three measures that have been used to gauge stemwood growth of individual trees and stands: (1) mean annual increment (MAI); (2) periodic annual increment (PAI); and (3) current annual increment (CAI). Measures of volume increments of the stem are usually the norm but it is easier to calculate DBH as a proxy. Periodic or current annual increment area is a better measure of growth than diameter increment because of the increase in bole diameter over time.

Mean annual increment is the average annual growth increment over the total age of the tree or stand. For example, a tree that is 15 inches (38 cm) DBH, and is 15 years old has an MAI of $15/15 = 1$ in/yr (2.5 cm/yr). Periodic annual increment is the average growth increment over a period of years. It is usually taken to be the most recent 5 years. Current annual increment is the growth for the most recent year of growth.

The point where the MAI and PAI meet is referred to as the biological rotation age (Fig. 17.7). It is always where MAI reaches a peak. This is the age at which the tree or stand would be harvested if the management objective is to maximize long-term yield. It is a key value for determining how much can be harvested annually if a forest is managed to produce a sustained yield of timber and how long the rotations should be to maximize production. It is also important to recognize that stand-level averages of MAI and PAI do not reflect individuals but the stand average. Individuals can have very different

patterns of growth because they differ by species and by crown and rooting position within the stand.

It is extremely difficult to determine MAI for uneven-aged stands since they have no single age. However, every year, the theoretical balanced all-aged forest would have a CAI virtually equal to the peak MAI of an even-aged stand of the same species grown to the same rotation age on a similar site.

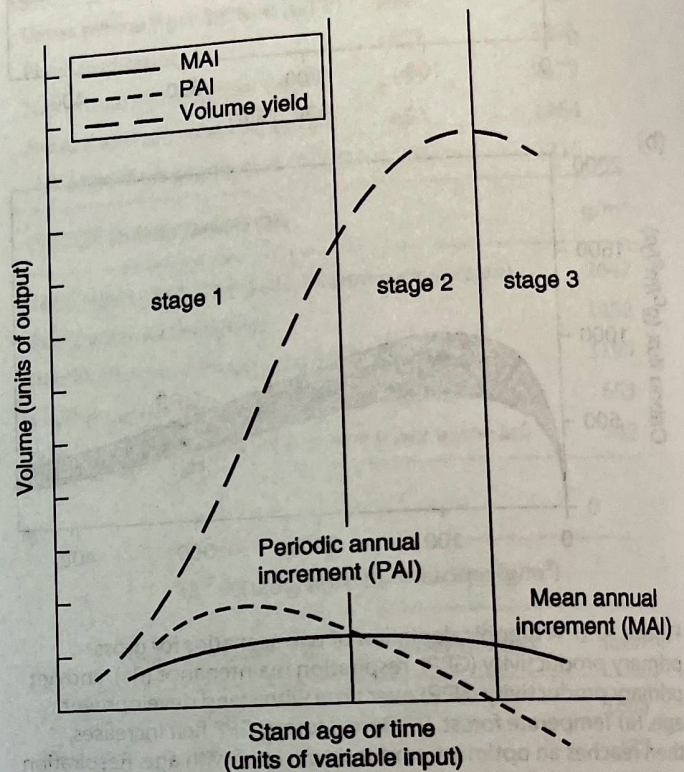


Figure 17.7 A graph depicting the stand-level mean annual increment (MAI) and periodic annual increment (PAI) over the course of development. The long-dashed line indicates the volume yield over time. The maximum point on the curve of PAI is the same as the inflection point on a graph of yield versus time. The inflection point is the point corresponding to the fastest change in yield. In most circumstances the most economic rotation period (highest net present value) is always shorter than the biological rotation. The culmination of MAI is often regarded at the biological rotation of a stand (as depicted by the line demarcating stage 1 from 2). The curves originate from zero because they are based on total dry-matter production. If they were based on board-foot volume with some large minimum top diameter for logs, the origins of the curves and their peaks would shift far to the right. If the measurement units define product objectives, the age of maximum MAI is the optimum rotation length where the objective is to maximize production from a limited land base. If the PAI of a given stand exceeds the simultaneous MAI, this means that the stand has not yet reached the culmination of MAI; one may also make an educated guess about the amount of MAI, and the time of its culmination. PAI becomes negative after the age when decay and mortality becomes equal to growth, as in very old stands. MAI would decrease to zero only when the very last tree of the initial stand was gone. Source: Mark S. Ashton.

The Effect of Thinning on Stand Production

The main objective of thinning is to increase the yield of usable wood by increasing the size and quality of individual trees. However, it is also important to understand the effects that thinning has on the stand-level production. There has been considerable confusion about this matter, with much of the confusion being centered on the graph in Fig. 17.8. This graph shows the hypothesis that was proposed in the early 20th century, based on early European thinning experiments and theoretical considerations of tree physiology of Wiedemann (1925), Moller (1922), and Langsaeter (1941) (see review by Skovgaard and Vanclay, 2008).

The Langsaeter curve is a part of the idea of rules and laws that always hold true. This graph has been accepted by many foresters and published in many books, and has an important impact on management. It indicates that foresters have considerable flexibility in choosing thinning intensity to produce larger individual trees, without loss of overall stand-level production. However, it does not match reality. Instead, it is now apparent that these patterns are responses to variations in species and sites, and their interactions.

Before analyzing the evidence regarding the thinning–production relationship, it is necessary to review the methods. The measures of volume production can vary, but nearly all studies have used merchantable wood volume. European studies follow a standard that includes all aboveground wood (stems and branches, with bark included) that is larger than 3 in (7 cm) in diameter. By using this low diameter specification, most of the wood is included. Specifications for studies in the US and other regions vary greatly.

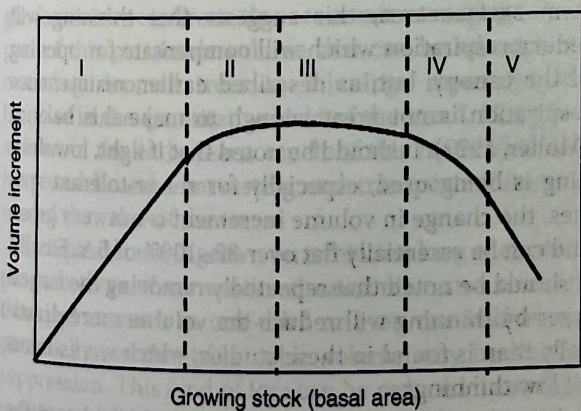


Figure 17.8 Langsaeter's curve. The hypothesized pattern of stand volume growth at different levels of stand density, as measured by basal area. This pattern (often called Langsaeter's curve) is no longer accepted as the pattern for most species or sites. Source: Yale School of Forestry and Environmental Studies.

There are practical reasons for setting these limits, but they are problematic, and may cause some of the conflicting evidence about the relationship of stand density to production. In high-density stands, diameter growth is slower for all stems and branches. Therefore, dense stands will have a smaller proportion of the total amount of wood counted in the assessment of production. This is especially important in the very dense stands used in European studies. Total wood biomass would be the best biological measure. It would clear up some of the confusion, but use of merchantable volume has the advantage of keeping a focus on yield. Having both measures would be ideal.

The studies that have been conducted to test the so-called Langsaeter hypothesis consist of even-aged stands of a single species (or predominantly one species). Plots are thinned to varying densities, as measured by basal area (BA). The densities are often described as a percent of the mean BA that occurs in unthinned stands. One requirement for this kind of study is to specify the sizes of trees to be removed within each plot. As described earlier in this chapter, trees in different crown positions have different growth efficiencies. Overtopped trees have the lowest efficiencies. If thinning experiments do not carefully remove trees of similar crown positions for each thinning intensity, then the results will be difficult or impossible to interpret. The response of trees of different crown status will vary greatly after thinning. Most studies have used low thinning, which selects the smallest trees first for removal, and then moves up in size until the desired stand density is reached. Useful comparisons could not be made if large trees were cut, leaving the low-efficiency small trees to respond to release from thinning.

The initial reinterpretation of the evidence from European studies was from Assmann (1970), who provided an early form of meta-analysis in his review of the early experiments. In addition, a number of studies in the US have been conducted that reflect current thinking (Fig. 17.9) (Long and Smith, 1990; Jokela, Dougherty, and Martin, 2004).

The main pattern is of consistent decline in volume production with increase in thinning intensity. The slope and curvature of the line differs among species, but the declining trend is consistent. The reductions in volume increment are shown in Table 17.4, using the stand density of 50% of the unthinned basal area for each species.

The major consequence is that thinning to promote larger individual tree size is done at the expense of losing stand volume growth. With the Langsaeter hypothesis, it appeared that there was no tradeoff between individual tree growth and stand growth, but there actually was, and is, a tradeoff.

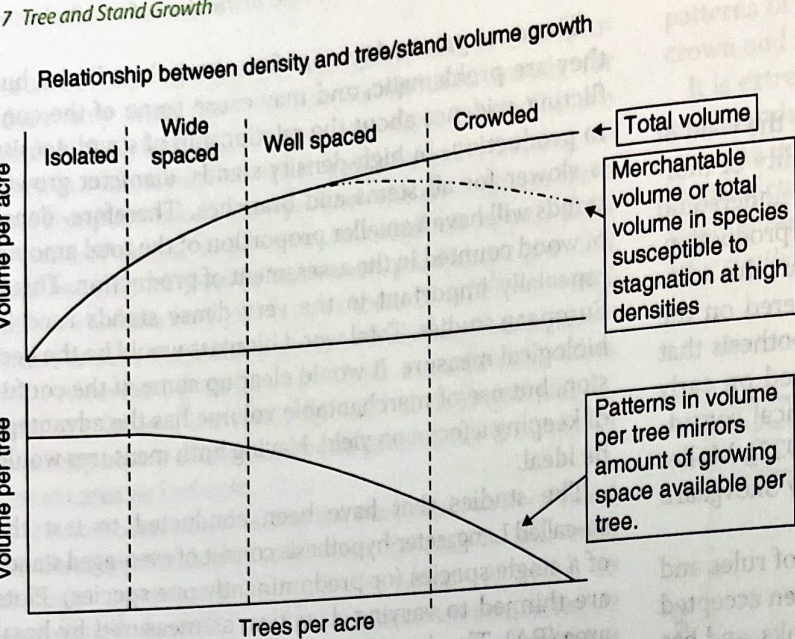


Table 17.4 Gross woody volume reduction from thinning by select timber tree species.

Species	Volume reduction at 50% BA compared to unthinned BA	Reference
European beech	-10	Assmann, 1970
Norway spruce	-10	Assmann, 1970
Scots pine	-25	Assmann, 1970
Sessile oak	-25	Assmann, 1970
Douglas-fir	-25	Curtis, 1967
Eastern white pine	-30	Seymour and Smith, 1987
Loblolly pine	-15	Nelson, 1964
Red pine	-20	Martin and Ek, 1984

Source: Yale School of Forestry and Environmental Studies.

The second pattern occurs on dry sites, as noted by Assmann (1970). Overtopped trees in these stands are using water and nutrients, but they produce very little wood increment. They are just surviving, renewing foliage and roots, but not increasing in wood. By removing these trees, resources now made available below-ground (water and nutrients) are used by trees in upper canopy positions. Growth then increases with light thinning because the canopy is not opened by the removal of the understory trees. With greater thinning, the negative effects of the growth of canopy opening outweighs the more efficient use of soil resources, and

Figure 17.9 These graphs should replace the flat line hypothesis and Langsaeter's curve. Top: the general trend shows that stand volume increases with stand density and basal area reach a maximum allowable density. Bottom: with increased stand density because of increasing competition for growing space. Evidence supports these trends rather than the Langsaeter curve in Figure 17.8. Source: Adapted from Smith *et al.*, 1997 and from Daniel *et al.*, 1979.

the declining pattern occurs. This effect has been observed in oak stands in the eastern US. In the removal of understory trees on dry sites (light, low thinning), growth increases in the overstory, but no overstory increase occurred in areas with higher precipitation (Breda, Grainer, and Aussenac, 1995). The same pattern occurred with understory removal of hardwoods growing beneath pines in dry and moist sites (Kelty, Gould, and Twery, 1987).

There are a number of reasons why the Langsaeter curve was accepted for so long. The range of thinning in many early studies was limited, starting with very dense unthinned stands and reducing to 80% of BA. Many research plots in the early days were not replicated and there was likely no consistent response across different studies with these limitations. Also, Moller was influenced by the relationship of respiration to stem surface area; this suggests that thinning will reduce respiration which will compensate for opening of the canopy, but, as described earlier, maintenance respiration is not great enough to make this balance (Moller, 1922). It should be noted that if light, low thinning is being used, especially for shade-tolerant species, the change in volume increment is not very great, and can be essentially flat over 80–100% of BA. Finally, it should be noted that repeatedly removing the largest trees by thinning will reduce the volume more drastically than is found in these studies, which were almost all low thinnings.

A study of loblolly pine (Nelson, 1964) shows the impact of site. Unthinned stands develop much higher volume growth and higher BA on good sites. This demonstrates the importance of not relying only on BA percent. In retrospect, there does not seem to be a reason

to have thought that all species on all sites would follow a similar quantitative response to thinning.

The Effect of Thinning on the Economic Yield of Stands

Practical understanding of thinning procedures depends on knowing how they can be applied to increase the economic yield, even though they do not substantially increase, and may even slightly decrease, gross production. The general approach is to allocate the production to some optimum number of trees of highest potentiality to increase in value; the other trees are systematically removed in such a sequence as to obtain maximum economic advantage from them. The various advantages that can be gained are as follows:

- 1) salvage of anticipated losses of merchantable volume;
- 2) increase in value from improved diameter growth;
- 3) yield of income and control of investment in growing stock during rotation;
- 4) improvement of product quality;
- 5) opportunity to change stand composition to prepare for the establishment of new crops;
- 6) reduced risk of damage or destruction by insects, disease, fire, or wind.

Salvage of Anticipated Losses

The gross production of wood by a stand should not be confused with the actual yield in terms of usable volume removed in cuttings. Not all the cubic feet of wood produced by the growing stand remain stored on the stump until the end of the rotation. In fact, a high proportion of the total production will be lost from death and decay of the large numbers of trees that do not survive the struggle for existence. From the economic standpoint, any part of this perishable volume that can be salvaged by removing doomed trees in thinnings represents an increase in the quantitative yield of the stand. However, at least in the early years, much of this material is not harvested because harvesting and transportation costs exceed the value of the trees.

If a typical stand is grown on a rotation long enough to produce trees of conventional sawtimber size without thinning, as much as one-third or even one-half of the potentially merchantable cubic volume may be lost to suppression. This kind of loss can be reduced by ending rotations when such mortality becomes serious, but this approach makes it hard to get trees of the diameters often desired. Diameter growth can be increased by widening the initial spacing of the stand, but this maneuver prevents suppression loss, partly by leaving growing

space vacant and thus merely preventing the production that would become loss. Thinning is the best solution to this dilemma and is therefore practiced whenever other considerations do not preclude it.

Thinnings designed to anticipate and salvage losses from natural suppression are the only proven means, other than site improvements, of increasing the yield of total cubic volume or tonnage from a stand. Only part of the prospective losses can be recovered unless stands are annually gleaned for dead and dying materials no matter how small. Unless the site is ameliorated such as by fertilization, the practicalities of timber harvesting dictate that the harvested yield can be increased only by decreasing the gross production of the stand.

Not all of the material removed in anticipation of loss will need to come from small trees of the suppressed and intermediate crown classes. By using crown and selection thinning, it is possible to take out part of this volume in larger trees, thus forestalling the death and stimulating the growth of their subordinates. Selection thinning must be used carefully in this way because frequently the lower crown class trees will not respond well to release, and the overall growth of the stand will be reduced.

Increase in Value from Improved Diameter Growth

Up to this point, the discussion of the effect of thinning on the quantitative yield of a stand has dealt mainly with production of cubic volume. However, not all units of cubic volume of roundwood are equally valuable; those that come from large trees are generally of greater value than those from small trees. One of the most important objectives of most kinds of thinning is to reduce the stocking of a stand so that it eventually has fewer trees, but of larger average diameter than it would without thinning.

The most general reason for the greater unit value of trees of large diameter is that the cost per unit value of ultimate product is less for processing them than for small ones (Fig. 17.10). This relationship applies to the cost of handling each tree or log individually during harvesting and subsequent processes. The monetary return for growing a tree, stumpage, is the difference between the value of the ultimate unit of product and the cost of harvesting, transporting, and processing it. The forest owner who grows 100 units of cubic volume in fat trees saves handling costs for the buyer and is thus entitled to a higher price than one who grows 100 units in a greater number of slender trees. Of all the economic reasons for thinning, this one is usually the most important.

A second reason for trying to improve diameter growth is that wood quality usually increases with tree diameter. This is mainly because the outer rind of wood has fewer knots and grain irregularities than the central

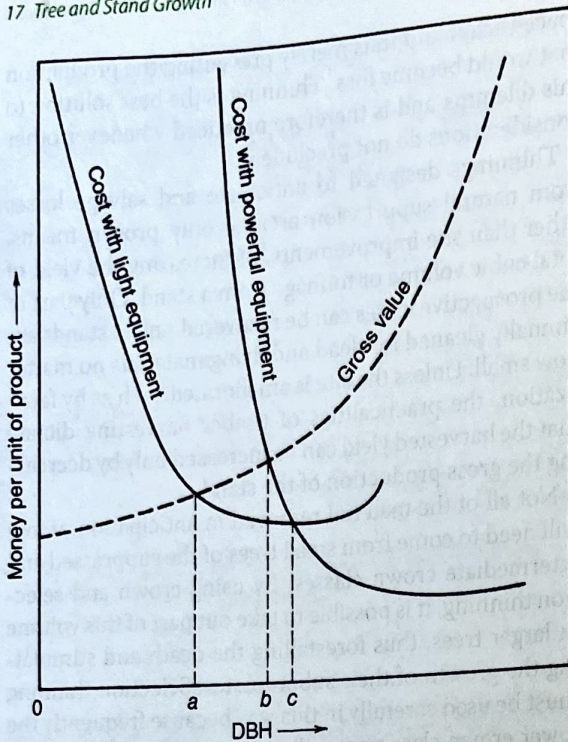


Figure 17.10 The effect of the diameter of a tree on the cost of processing it, and the value of the product, per unit, when the harvesting and processing are done with two different sets of equipment. The set of light equipment is low in capacity and cost; the powerful equipment is high in initial investment and hourly operating cost. Points a and b are the smallest diameters at which it becomes economical to use each set of equipment. For trees larger than diameter c, it would be logical to use the more powerful set. Net value at any diameter is the vertical distance between the appropriate curve of cost and that of gross value. Note that certain costs, such as those of roads or of handling trees collectively in bundles, are not affected by tree size. The curve of gross value would be nearly horizontal for such products as fuelwood or that which is chipped for pulp or other reconstituted products. Gross value can also decline with increasing tree size if the incidence of rot or similar defect increases with age or size. Note that the ideal thinning program would be one in which trees are caused to move as swiftly as possible into diameter classes that can be harvested most profitably and also with equipment appropriate to those sizes. Source: Yale School of Forestry and Environmental Studies.

core; ordinarily, it also has superior anatomical and mechanical properties. The outer wood is usually stronger, more easily worked, longer-fibered, less subject to warping, and in most ways much easier to use than the inner wood. With some species, the inner wood improves when it turns to heartwood, but this change also depends on diameter growth. The more outer wood that can be added by increasing diameter growth, the greater is the inherent value of the wood.

One of the most common and valuable ways of using trees is as lumber or solid-wood products. There is probably no other way of producing structural materials that is more economical of the world's energy supply. Unfortunately, it is not correspondingly economical,

either of the wood itself or of the time required to grow trees of suitable sizes. Both of these problems can be mitigated by thinnings designed to grow trees of larger diameter in shorter time.

The waste of wood in lumber production is in the sawdust, slabs, and edgings generated when round stems are sawn into square-edged boards. Given the ordinary requirement that boards be of certain minimum thicknesses, the proportion of wood that is wasted is greater in trees of small diameter than in large ones. In fact, there is usually some minimum diameter of stemwood below which the material is simply left in the woods; the proportion thus abandoned in severed tops is also inversely related to diameter. One exception is the production of small-dimension products which often results in utilization to a very small minimum diameter. In this case, a large number of small trees will have less total branchwood than a smaller number of large-diameter trees.

The board-measure log rules that are used in North America are, in effect, computational devices designed to estimate the volume of lumber that will remain after round logs are sawn into square boards. One cubic foot of wood (0.028 m^3) could be converted into 12 board feet (0.005 m^3) only if a tree were a square timber throughout its length and could be sliced into boards without sawdust or other waste. Cubic volume is, in other words, round and not square. The ratio of board feet to cubic feet ranges from roughly 5 in trees about 8 in ($\sim 20 \text{ cm}$) DBH to a nearly stable value of 7, or slightly more in trees that are more than 20 inches ($\sim 30 \text{ cm}$) DBH. If trees are grown for lumber and the cubic volume growth is fixed, this difference in proportion of waste is another reason to seek improved diameter growth. Even if the waste is used for reconstituted wood products, loss of potential value still takes place.

Not all units of board measure are equally valuable. Those that are in wide boards are worth considerably more than those in narrow ones. This is yet another advantage that accrues to improved diameter growth.

Merely because the calculations are easier, the results of thinning trials are often interpreted in terms of common mensurational units, especially cubic volume, without any consideration of the distribution of diameters in the stands. In fact, many thinnings have purposely tried to duplicate the distribution of diameters before and after thinning for statistical convenience in determining volume growth changes. The purpose of most regimes of stand management is to maximize the production of net value and not just volume.

Rough comparisons can be made between possible treatments by observing the distribution of numbers of trees or of volume by diameter classes. Another simple test parameter is the average diameter of a fixed number of the largest trees per unit area, such as the 100 largest/acre (ha). It must be borne in mind that the average

diameter of a whole stand is automatically increased by removing some of the smaller trees.

To reap the rewards of cutting large trees late in the rotation, it is necessary to cope with the high cost per unit volume of harvesting and utilizing small trees in earlier thinnings. This difficulty can be mitigated partly by using different equipment and logging methods for the small trees than are later used for the large. The kind of equipment that is most efficient for handling final crop-trees is usually not the best for the thinnings; such equipment is ordinarily heavier, more cumbersome, more costly, and more expensive to operate for a given length of time.

The problem can also be evaded by delaying the thinnings until the trees to be removed are grown large enough to handle economically. Another evasion is to confine the first removals to any large- or medium-sized trees of poor potentiality and to ignore the small ones until they become larger. Trees that are destined never to be worth harvesting can be either left to die of suppression or killed by the cheapest means available.

The ideal solution is to manipulate the equipment and sequence of thinnings so that the equipment is matched with the sizes of trees to be removed, and as many trees as possible are cut when they have grown into the range of diameter that can be harvested efficiently. The objective should be to maximize the total value from harvesting the entire crop of one rotation rather than to minimize the cost of each separate operation in the whole sequence of cuttings.

Increase in stem diameter is so advantageous that it is generally best to thin stands down to the lowest density that will not cause poor tree form or other unacceptable side effects. Deliberate sacrifice of production of gross tonnage or total cubic volume is often desirable; sacrifice of production of merchantable volume may or may not be desirable, depending on the relative merits of growing large trees and securing a large total yield of wood of any sizes. Some countries are sufficiently concerned about maintaining high wood production such that they prohibit thinning so heavily that yield of merchantable cubic volume is sacrificed. The stand structures that result from heavy thinnings sometimes have other advantages, such as foraging areas for the red-cockaded woodpecker in the southeastern US and the maintenance of hardwood browse for large herbivores in many areas.

Yield of Income and Control of Investment in Growing Stock During Rotation

An unthinned crop of trees is an asset that increases in value throughout the rotation but remains frozen under passive management. No cash income is realized, yet carrying charges accumulate that must be paid for by the crop. After some trees have become merchantable, thinning can become a form of continual asset management.

The early returns from thinning will lead to longer rotations if the overriding goal of management is timber. Money from the early part of the rotation is worth much more than income received later in the rotation, because of the compounding effects of discount rates. The periodic removal of the poor earners and encouragement of the good earners is a means of decelerating the speed at which the growth rate of the overall stand value inevitably declines. The rate declines between thinnings and can be elevated again by each thinning. When it becomes impossible to restore the rate to the desired level, according to this mode of analysis, it is logical to replace the stand with a new one and thus end the rotation.

In applying this idea, it is best to allocate growing space to the trees that earn the most. This allocation requires estimates of the earning capacity of trees of different classes of diameter, crown class, and stem quality. Once a few calculations are made and the basic relationship between tree characteristics and earning capacity is formulated, it is then necessary to use intuitive judgment in determining which trees to cut or leave because the detailed computations are too complicated to apply tree by tree. It is especially difficult to take differences in tree quality into account. The easy assumption that all trees of the same diameter in a stand are of the same value can impair application of the principle.

Thinning can be applied in such a manner as to reduce the investment in growing stock and increase the value of gross growth by removing trees of low earning potentiality and increasing the growth of those of high potentiality. Because growing stock can be reduced without greatly reducing volume growth, this becomes a way of eating one's cake and having it too.

In whole forests that are young and immature because of earlier heavy cutting in a locality, thinnings and other intermediate cuttings may provide the only source of income for long periods. Thinning helps meet two financial tests that are often applied to long-term investments in timber production. Both tests involve compound interest and affect decisions about rotation length. Consequently, the two different tests often get confused with each other.

The first test requires an adequate rate of compound-interest return on all out-of-pocket costs of establishing the crop and carrying it to maturity. The second test requires that the rate of interest earned on the stumpage value of the trees or stands will not fall below some desired rate. The rate demanded under the first test, which involves whole rotations and hard cash, may be higher than that of the second, which operates over shorter periods and merely involves income temporarily forgone. These are separate tests, and the choice must be made as to which analysis should be used for thinning decisions.

In the first test, the cost of establishing a stand and all subsequent costs are carried at a compound interest rate

until the end of the rotation. Thinning helps meet this test by providing income during the rotation which is also compounded to the end of the rotation. By the reckoning involved, the money received at age 20 may be worth twice that at age 35. The compounded costs of stand establishment early in the rotation can be offset by early thinning returns rather than letting them mushroom until the end. If the thinning enables trees to grow larger and more valuable, or increases the total yield, the net income against which the charges can be made is increased. If these improvements make it financially prudent to have longer rotations, the average annual expense for regeneration in the whole forest is reduced, and so the overall result can be still further improved.

The second test involves the crucial task of improving the return on the large investment represented by the liquidation value of merchantable growing stock in managed forests. For example, if an owner requires a rate of return of 8%, each dollar left in growing stock at the beginning of the decade must grow to \$2.16 in value during the decade to justify having left the tree or stand. In this test, unlike the first, any money invested in growing the tree does not count; only that money for which it could have been sold at the beginning of the period is considered.

The second test embodies one of the most useful ways of determining which trees to cut and which to leave in thinning. Those trees that cannot be made to increase enough in value to yield an acceptable rate of return on their own value are removed. Those that can are not only left but they are also granted enough additional growing space that the compound interest that they earn is increased. The trees most likely to continue yielding the desired rate of return for the longest time are those of highest quality and rate of growth. In a pure application of this approach, the first trees to be cut would be those of low quality or slowest growth, although they would theoretically not be cut until they had acquired a positive value.

Regardless of how rotation length is determined, thinning provides ways of extending rotations and also of lending some flexibility to their control. The rotation necessary to grow trees of a given size can be shortened; larger and more valuable trees can be grown on rotations of fixed duration. Short rotations do not necessarily have the financial values that are so often ascribed to them, especially if all of the financial factors involved are considered. If thinnings have produced enough revenue to amortize establishment costs, yield an adequate income, and maintain good rates of growth, there may be little need to rush into the risk and expense of starting a new crop that will be some years in regaining full occupancy of the site. The forest manager who refrains from thinning may be condemned to short rotations, frequent regeneration problems, and limited opportunity to maneuver to meet

all sorts of emergencies and changes in markets or management objectives.

Improvement of Product Quality

The value of a fixed total production can be enhanced simply by favoring the trees of best potential quality and discriminating against the poor ones. This effect of thinning on wood quality is vastly more important than any other. The superior diameter growth induced by thinning usually improves wood quality because the large trees tend to be of better quality than small ones. The general effect of thinning on wood quality is not harmful, in spite of some opinion to the contrary.

Control of Stand Composition and Effects on Regeneration

The opportunity to intervene in the development of the stand during the rotation produces a number of other economic benefits. It enables continuing control of undesirable species that were not eliminated during the period of regeneration. If mixed stands of dissimilar species are being deliberately maintained, thinning may represent the only means of taking adequate advantage of those species that tend to mature earlier than the major components. The long period of control over stand composition enables the forester to prepare for natural regeneration by reducing the seed source of undesirable species and fostering that of the good. Thinning also builds up the physiological vigor, mechanical strength, and seed production of the individual trees of the final crop, so that there is wider choice among methods of regeneration cutting. Unthinned stands are likely to have to be replaced during an abbreviated period of establishment, even when more gradual replacement might enable greater use of the financial potentialities of the crop.

Reducing Risk

Thinning can reduce the risk of the stand being destroyed or reduced in value by a variety of causes. One of the main effects of thinning is to increase the vigor of the trees by giving each tree more growing space. Increased vigor increases the tree's ability to respond to most insect attacks. Production of secondary compounds helps protect the tree from many types of herbivory, and the additional vigor allows those trees capable of a second flush of foliage to recover from defoliation. More vigorous trees are also able to withstand reductions in photosynthesis without succumbing to the overriding needs of respiration.

Thinning also increases protection from abiotic agents. Salvaging potential mortality reduces the fuel load that leads to catastrophic fires. Thinning leads to reduced height/diameter ratios and greater wind firmness.

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