4

Stand Dynamics: The Ecology of Forest Succession

Introduction

A forest stand may seem static but it is really a dynamic, ever-changing, living structure. After establishment, the choices made in silviculture are usually based upon altering stand-level processes (see description of defining stands in Chapter 3). **Stand dynamics** is the study of changes in forest stand structure over time, including stand behavior after disturbances (Reichle, 1981; Means, 1982; Oliver and Larson, 1996; Franklin *et al.*, 2002). In practicing silviculture, a forester must be able to predict what kind of vegetation will follow regenerative disturbances, and what patterns of development should be anticipated in the vegetation as the stand grows older. This chapter introduces the different kinds of stands and their developmental processes.

The chapter first defines the basic kinds of initiating disturbances which can be categorized as lethal or release. It then describes the stages of stand development after initiating disturbances for single-aged or single-cohort stands. The use of age-class and cohort terminology is clarified for the purpose of this book and its application in silviculture. Using this terminology, the nature of canopy stratification and development is progressively described and defined, starting with single-aged, single-species stands, then single-species, two- or three-aged (multi-aged), and then single-species, all-aged stands. Mixtures are then treated first as mixed-species, single-aged stands, then mixed-species, two- or three-aged stands, and lastly mixed-species, all-aged stands. The final part of this chapter compares this terminology and description of stand dynamics with paradigms of forest succession by other ecologists.

Initiating Disturbances and Sources of Regeneration

All silvicultural procedures are, at least to some degree, simulations of natural processes in which stands start, develop, and are replaced, gradually or suddenly. No plant starts or accelerates its development unless something dies or is killed, which then provides the plant open growing space. Established plants often exclude others by expanding, suppressing, or killing weaker ones. Some plants can endure beneath taller neighbors and thus share growing space with them. Silviculture imitates and regulates the processes involved.

An important distinction can be made between disturbances (Fig. 4.1) such as: (1) fire that can be said to "kill from the bottom up" because they are more likely to kill small plants than large; and (2) windstorms or pests that kill more large trees than small trees, and thus "kill from the top down." The natural disturbances that initiate new stands from the bottom up can be categorized as **lethal** to the groundstory (Zhang, Pregitzer, and Reed, 1999; Harper *et al.*, 2002; Winter *et al.*, 2002). For example, some fires burn so hot that virtually all preexisting plant life is killed. The other major kind of disturbance that kills from the top down, has been categorized as **release** because these disturbances include insect outbreaks and windstorms, which destroy the upper canopy but allow the release of the understory (Worrall, Lee, and Harrington, 2005; Svoboda *et al.*, 2010). Decisions about the regeneration of stands usually involve choices of the kinds of disturbance to simulate. See Chapter 5 for more details on the kind of disturbances and their relationship to the nature and origin of regeneration.

New trees can be recruited from many sources. Among these are seeds, nursery-grown plants, vegetative sprouts, and various forms of stored advance growth that have previously started beneath old stands (sources and processes of regeneration are described in Chapter 5).

Stages of Stand Development

After an initiating disturbance of any kind, trees of a single age class or cohort proceed from birth to death through a sequence of developmental steps (Oliver and Larson, 1996; Franklin *et al.*, 2002; Franklin, Mitchell, and Palik, 2007). These must be recognized if

The Practice of Silviculture: Applied Forest Ecology, Tenth Edition. Mark S. Ashton and Matthew J. Kelty.

Figure 4.1 **(a)** Fire-killed stand of lodgepole pine in western Montana. Natural regeneration of pines has started, and the fire eradicated the serious dwarf mistletoe infestation that caused the witches' brooms in the pines. *Source:* US Forest Service. **(b)** Stand of interior cedar–hemlock, British Columbia, that has been partially blown down by a convectional windstorm. *Source:* Mark S. Ashton.

understanding of stand dynamics is to be used to achieve management objectives by imitating, guiding, or altering natural processes in post-establishment silvicultural treatments (e.g., thinnings).

The first stage in stand development (Fig. 4.2) is called **stand initiation**. After a disturbance has created vacant growing space, the new trees that have become established in it (or preexisting larger ones that expand into it) do not fully occupy the space. Until they do, there is opportunity for additional plants to fill the empty spaces. Often, the plants that fill the newly vacant spaces are herbaceous annuals or other short-lived species that may come and go quickly.

Ultimately, both the aboveground and belowground growing space is filled with plants, mostly woody perennials in the case of forests. The tree crowns become closed in the horizontal dimension, and some of their lowest foliage starts to die because of shading by the upper foliage. This event starts the second stage of stand development, the **stem exclusion stage** (Box 4.1). During this stage, the trees start to compete with each other; the more vigorous ones encroach into the growing space of weaker trees that eventually die, usually from lack of light or soil moisture, in a process called **suppression**. Establishment of additional regeneration of tree species is also prevented.

Unless some disturbance wipes out the stand and starts a new stand initiation stage, an aging stand will gradually enter the **understory reinitiation stage** (Box 4.1). In this stage, scattered trees that have previously been successful in competition with other trees begin to be lost to pests, other damaging agencies, or cutting operations,

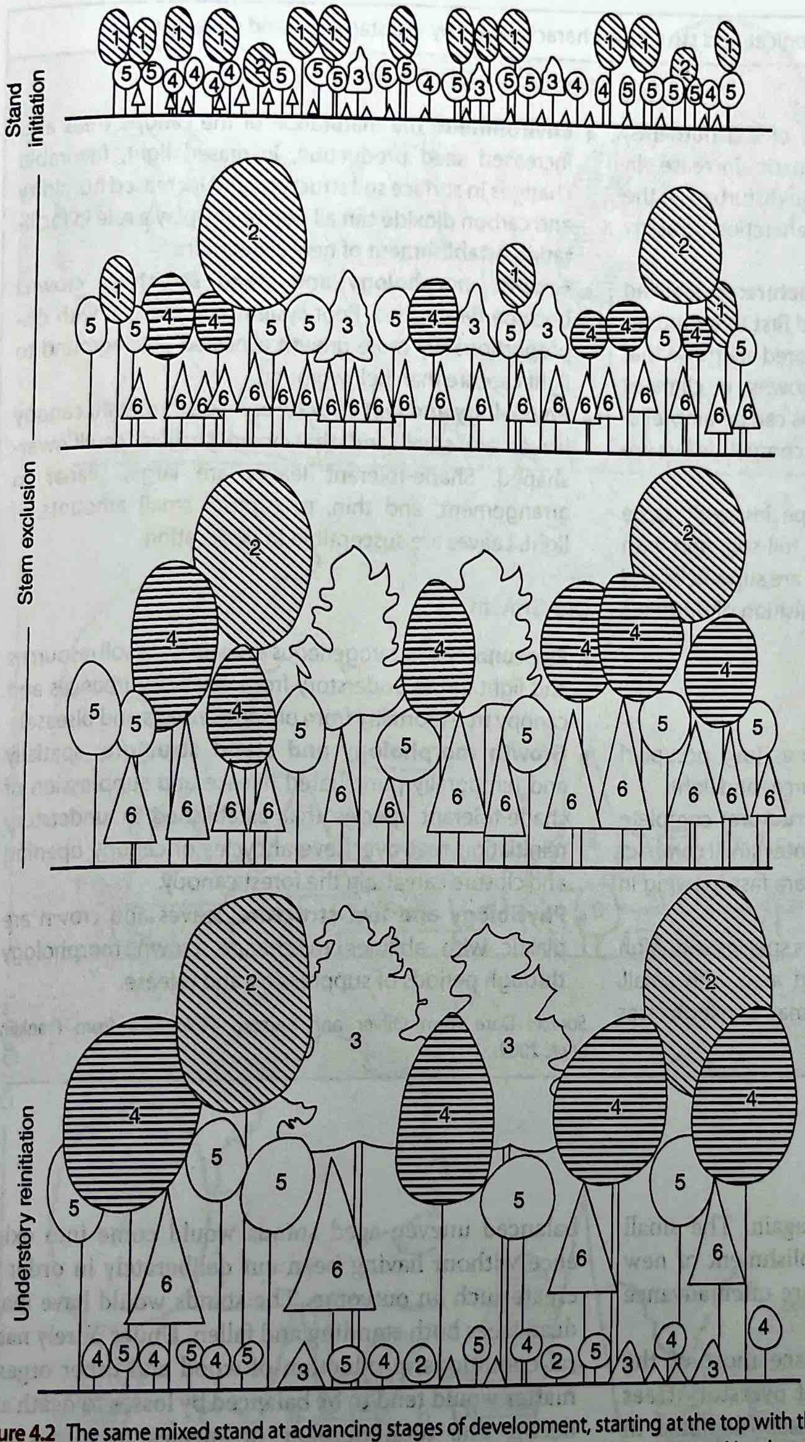


Figure 4.2 The same mixed stand at advancing stages of development, starting at the top with the stand initiation stage, then proceeding through the stem exclusion stage to the beginning of the understory reinitiation stage. Number and crown shapes identify the size of different species in the stand. Species: 1 – a short-lived pioneer that cannot tolerate shade after being over topped; 2 – a longer-lived pioneer that is a fast-growing emergent; 3 – a late-successional emergent with a delayed ascent to the tops of the canopy; 4 – a late-successional species with slow initial development that reaches the main canopy; 5 – a long-lived pioneer species with initial rapid development that is overtaken by species 4 but can withstand shade after being overtopped; and 6 – a very shade-tolerant late-successional species that usually remains in the lower strata. Figure 4.3 shows the same stand developing into old growth. *Source:* Yale School of Forestry and Environmental Studies.

Box 4.1 A list of physiological, morphological, and structural characteristics by the stage of stand development.

Stand Initiation

- **Environment**: an immediate release of soil nutrients, increased soil moisture, and dramatic increase in amounts of light. The more severe the disturbance, the more opportunistic the species regeneration strategy favored.
- **Growth morphology and stand structure**: annual and biennial grasses and herbs are favored first to temporarily occupy the site. Woody species favored are those that are fast-growing, with expanding crowns. In climates where moisture is non-limiting, crowns can be umbrella-shaped and expansive, and can act to competitively suppress other species below.
- **Physiology and leaf structure**: species with large leaves, high photosynthesis rates in full-sun, and with fine fibrous surface root systems that are superficial and laterally branched for maximum acquisition of nutrients and water.

Stem Exclusion

- **Environment**: growing-space becomes fully occupied with strong competition for soil resources and light.
- **Growth morphology and stand structure**: complete crown closure and competition. Promotes small compact crowns with monopodial stems that are fast-growing in height.
- **Physiology and leaf structure**: favors species with high photosynthesis rates per unit crown area with small, thick leaves to reduce water loss but maintain high rates of light capture per unit leaf.

Understory Reinitiation

- **Environment**: the maturation of the canopy trees and increased seed production, increased light, favorable changes in surface soil structure, and increased humidity and carbon dioxide can all potentially play a role in facilitating establishment of new vegetation.
- **Growth morphology and stand structure**: crowns become flat-topped. Root systems are surficial with disproportionately more growth allocated aboveground to light capture than belowground.
- **Physiology and leaf structure**: shade intolerant canopy leaves are small and the crown shallow cauliflower-shaped. Shade-tolerant leaves are large, planar in arrangement, and thin, to capture small amounts of light. Leaves are susceptible to desiccation.

Old-Growth

- **Environment**: heterogeneous availability of soil resources and light in the understory from small disturbances and canopy tree mortality from old age (insects and disease).
- **Growth morphology and stand structure**: spatially and temporally punctuated release and suppression of shade-tolerant species that established in understory reinitiation that over several cycles of canopy opening and closure can attain the forest canopy.
- **Physiology and leaf structure**: leaves and crown are plastic with abilities to change crown morphology through periods of suppression and release.

Source: Data from Oliver and Larson, 1996 and from Franklin *et al.*, 2002.

and their crowns do not fully close again. The small vacancies thus created allow the establishment of new plants beneath the old stands. These are often advance regeneration of shade-tolerant species.

Unless something happens to replace most of the stand, the gradual process of death of overstory trees and replacement by younger age classes (depicted in Fig. 4.3) leads gradually into an **old-growth stage** (Spies, 2004) (Box 4.1). This stage commences when a majority of the original trees are gone and one or more of the new age classes or cohorts compose parts of the top canopy. It may continue on past the death of the last original trees. The number of different age classes increases, although it would be most unlikely that any balanced uneven-aged stands would come into existence without having been cut deliberately in order to create such an outcome. The stands would have many dead trees both standing and fallen. Under purely natural conditions, production of wood and other organic matter would tend to be balanced by losses to death and decay. The total number of species of plants may increase. Stratified mixtures typically develop, and foliage often extends from the ground to the top of the stand, at least in some parts of the stand. Franklin *et al.* (2002) go further in refining and describing several different stages within old growth that relate to the spatial complexity of structures and their developmental processes (see Box 4.1).

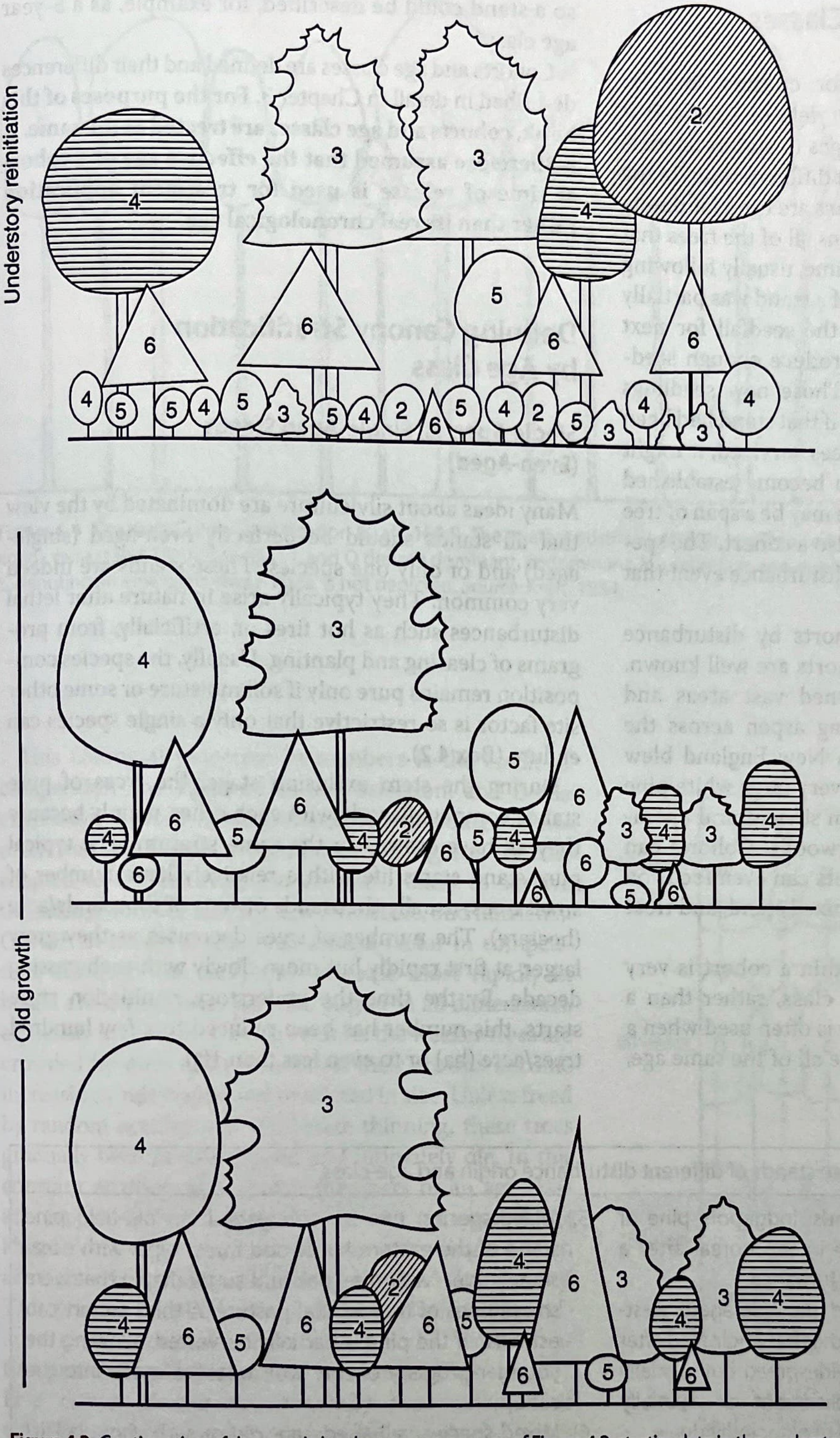


Figure 4.3 Continuation of the stand-development sequence of Figure 4.2, starting late in the understory reinitiation stage and extending into the old-growth stage. The five species have the same numbers as in Figure 4.2. Species 1 was too intolerant to become re-established in the understory. *Source:* Yale School of Forestry and Environmental Studies.

Defining Cohorts and Age Classes

For the purposes of planning for cuttings and for forecasting the future growth and yield of stands, it is important for foresters to assign ages to stands or parts of stands that have begun growth at different times in the past. The terms **cohort** and **age class** are used for dating the ages of stands. A cohort contains all of the trees that had been established at a specific time, usually following a forest disturbance. For example, if a stand was partially burned, killing half of the trees, the seedfall for next year's regeneration would likely produce enough seedlings to cover the entire stand. Those new seedlings would be called a cohort. However, if that stand had been burned so badly that only a few trees survived, it might take 30 years for the seedlings to become established across the stand. Even though there may be a span of tree ages from 1 to 30, these trees are also a cohort. The specific age is not important, it is the disturbance event that creates the new cohort.

Foresters tend to describe cohorts by disturbance type, date, and species. Some cohorts are well known. The 1988 Yellowstone fires burned vast areas and produced a huge cohort of young aspen across the landscape; the 1938 hurricane in New England blew down many stands and created a very large white pine cohort. Cohorts are also created in silvicultural operations, such as planting or shelterwoods. Cohorts can include mixed species, and foresters can even focus on just a particular species within a mixed stand, and treat it as a cohort.

If the range of ages of trees within a cohort is very narrow, it is often called an **age class**, rather than a cohort. The age-class terminology is often used when a stand is composed of trees that are all of the same age, so a stand could be described, for example, as a 5-year age class.

Cohorts and age classes are defined and their differences described in detail in Chapter 3. **For the purposes of this book, cohorts and age classes are treated as the same. It is therefore assumed that the effective age of a cohort at time of release is used for treatment application rather than its real chronological age.**

Defining Canopy Stratification by Age Class

Single-Species, Single-Aged Stands (Even-Aged)

Many ideas about silviculture are dominated by the view that all stands should be perfectly even-aged (single-aged) and of only one species. These stands are indeed very common. They typically arise in nature after lethal disturbances such as hot fires or, artificially, from programs of clearing and planting. Usually, the species composition remains pure only if soil moisture or some other site factor is so restrictive that only a single species can endure (Box 4.2).

During the stem exclusion stage, the trees of pure stands compete fiercely with each other, mainly because they all have crowns in the same stratum. The typical pure stand starts life with a relatively large number of small trees, usually thousands or tens of thousands/acre (hectare). The number of trees decreases as they grow larger, at first rapidly but more slowly with each passing decade. By the time the understory reinitiation stage starts, this number has been reduced to a few hundred trees/acre (ha) or to even less than 100.

Box 4.2 Examples of North American stands of different disturbance origin and age-class.

1) Single-species, single-aged stands: lodgepole pine of the interior west and jack pine in the boreal after a severe and widespread lethal disturbance.
2) Single-species, two- or three-aged (multiple-aged): western larch of the Rocky Mountains that has originated after sub-lethal severe fires that are widespread but spatially variable promoting the establishment of spatially clumped cohorts and the survival of older individuals.
3) Single-species, all-aged: pure eastern hemlock of moist temperate northern hardwood forest that has recruited over a long period from frequent periodic small wind and ice storms that open up the canopy.
4) Mixed-species, single-aged: recruitment and release of a single cohort after a heavy single cutting of all stems in a mixed-species oak–hickory stand.
5) Mixed-species, two- or three-aged: an old-field pine stand of the eastern hardwood forest type, with occasional older "wolf tree" oak and sugar maple that were shade trees of the original pasture. A third cohort can establish if the pine is partially harvested, allowing the younger progeny of the "wolf trees" to move into the canopy.
6) Mixed-species, all-aged: an old-growth Douglas-fir/western hemlock forest of the Pacific Northwest that has multiple openings of varying sizes that originated from different canopy disturbance events promoting the release of intimate mixtures of tree species growing at different rates.

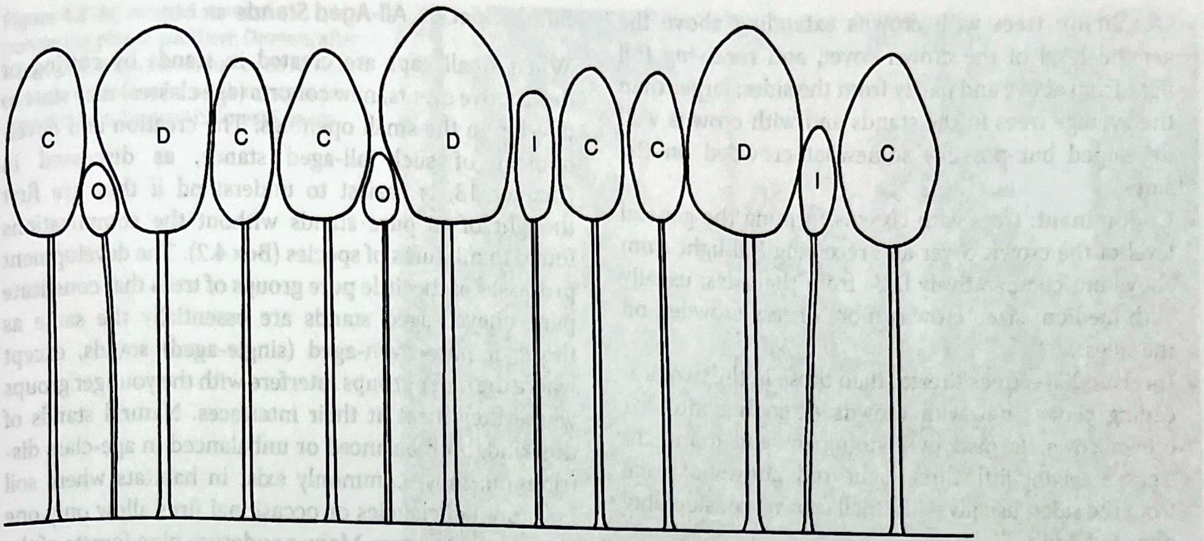


Figure 4.4 The Kraft Crown Classification (Kraft, 1884). The relative positions of trees in different crown classes in a single-aged (even-aged), pure stand. The letters D, C, I, and O denote dominant, codominant, intermediate, and overtopped crown classes, respectively. E, denoting an emergent crown class, is not depicted. *Source:* Kraft, 1884.

This continual reduction in numbers is the result of competition and rigorous natural selection, and is the expression of one of the most fundamental biological laws of silviculture. Those trees that are most vigorous or best adapted to the environment are most likely to survive the intense competition for light, moisture, and nutrients. Growth in height is the most critical factor in competition, although the trees that increase most rapidly in height are almost invariably the largest in all dimensions, especially in the size of the crown. As the weaker trees are crowded by their taller associates, their crowns become increasingly misshapen and restricted in size. Unless freed by random accidents or deliberate thinning, these trees gradually become overtopped and ultimately die. In this constant attrition, the weaker members of an age class are progressively submerged, and the strongest forge ahead. Very few trees ever recover a leading position after they have fallen behind in the race for the sky. This process is called **crown differentiation.** The relative crown positions of trees within this differentiation process can be categorized into classes (Figs. 4.4, 4.5). Five crown classes are generally recognized. This classification of tree crowns is called the Kraft Crown Classification, after the nineteenth-century German forester who devised it. It is useful only for single-species stands, or for stands composed of different species with identical regimes of height growth. The five classes are as follows.

- **Emergent**: trees with crowns extending well above the general level of the canopy so much so that the bottom of the crown is above the canopy.

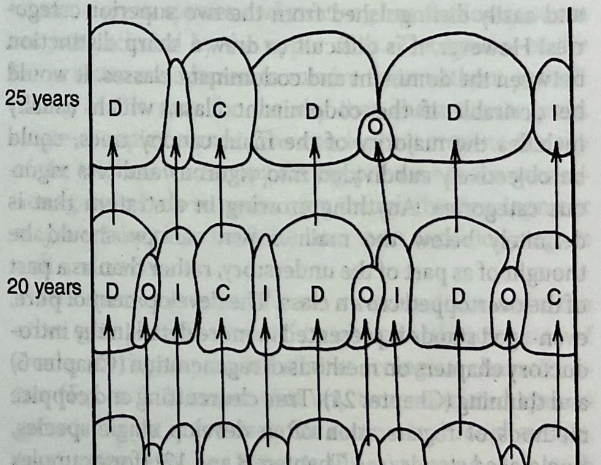


Figure 4.5 The process of differentiation into crown classes as a result of competition in a pure, single-canopied, single-aged stand, showing how some trees that were initially dominants may lose in the race for the sky. *Source:* Yale School of Forestry and Environmental Studies.

- **Dominant**: trees with crowns extending above the general level of the crown cover, and receiving full light from above and partly from the sides; larger than the average trees in the stands and with crowns well developed but possibly somewhat crowded on the sides.
- **Codominant**: trees with crowns forming the general level of the crown cover and receiving full light from above but comparatively little from the sides; usually with medium-sized crowns more or less crowded on the sides.
- **Intermediate**: trees shorter than those in the two preceding classes but with crowns extending into the crown cover, formed by codominant and dominant trees; receiving little direct light from above but none from the sides; usually with small crowns considerably crowded on the sides.
- **Overtopped**: trees with crowns entirely below the general level of the crown cover, receiving no direct light either from above or from the sides. Synonym: "suppressed."

This qualitative classification is simple and can be applied without measuring heights or crown widths. The intermediate and overtopped classes are well defined and easily distinguished from the two superior categories. However, it is difficult to draw a sharp distinction between the dominant and codominant classes. It would be desirable if the codominant class, which usually includes the majority of the main canopy trees, could be objectively subdivided into vigorous and less vigorous categories. Anything growing in a stratum that is definitely below the main crown canopy should be thought of as part of the understory, rather than as a part of the overtopped crown class. The development of pure, even-aged stands is presented in more detail in the introductory chapters on methods of regeneration (Chapter 6) and thinning (Chapter 21). True clearcutting and coppice methods of regeneration often develop single-species, single-aged stands (see Chapters 8 and 12) (for examples see Box 4.2).

Single-Species, Two- or Three-Aged Stands (Multi-Aged)

It is possible to have stands in which a new cohort or age class starts beneath an old one that is entirely or partially eliminated, allowing the new one to continue its development. Natural fires may create such stands (Box 4.2). They can be of pure- or mixed-species composition. Chapter 11 describes the use of irregular shelterwood and seed-tree regeneration methods in establishing these kinds of multi-aged stands. If the stands are pure, each new cohort develops with the same differentiation into crown classes (described in the previous section).

Single-Species, All-Aged Stands

When small gaps are created in stands by cutting or destructive events, new cohorts (age classes) may start to develop in the small openings. The creation and development of such all-aged stands, as discussed in Chapter 13, is easiest to understand if they are first thought of as pure stands without the complications found in mixtures of species (Box 4.2). The development processes of the little pure groups of trees that constitute pure uneven-aged stands are essentially the same as those of pure even-aged (single-aged) stands, except where the older groups interfere with the younger groups where they meet at their interfaces. Natural stands of this kind, both balanced or unbalanced in age-class distribution, most commonly exist in habitats where soil moisture deficiencies or occasional fires allow only one tree species to grow. Many ponderosa pine forests of the western interior epitomize this condition (Fig. 4.6). Most all-aged stands are actually mixtures of species.

The management of uneven-aged stands is complicated even if they are pure, especially if attempts are being made to mold them into self-contained sustained-yield units. These efforts usually involve manipulation of diameter classes and efforts to create reverse-J-shaped diameter distributions. The management of these stands is much less complicated where the trees and groups of trees are thinned to enhance growth, and harvested when mature without attempting to change age-class structure. These treatments involve what is aptly called the selection method of regeneration and are considered in much more detail in Chapter 13.

Mixed-Species, Single-Aged Stands

Unstratified Canopies

It is possible, but uncommon, for two or three species of the same age to grow in height at the same rate for long periods. If they do, they can be thought of, and managed, in the context of the single-canopied structure almost as if they were pure stands (Guldin and Lorimer, 1985). Ordinarily, however, one species tends to suppress its associates; very small differences in height growth become greater as the leaders forge ahead and the laggards suffer. For example, this can happen in mixtures of loblolly pine and shortleaf pine; loblolly pine generally gets ahead, unless dry site conditions cause loblolly pine to slow in growth. In central Europe, mixtures of the tolerant species beech, spruce, and fir must be thinned constantly to keep the beech or spruce from exterminating the fir. In fact, trees that drop out of the single-canopy stratum are usually eliminated or are promoted into the upper canopy by release operations (see Chapter 20 on release operations).

An additional concept about stand development patterns of single canopies relates to the fact that different

Figure 4.6 An all-aged stand of ponderosa pine in southern Oregon, after a group of mature trees has been removed to make a vacancy for establishment of regeneration. *Source:* US Forest Service.

species grow at different rates. Often, mixed stands are mosaics composed of little pure stands arising from a small, pure patch of young trees. Because each patch develops independently (except at the edges), it is possible for each species to grow at its own rate. A process can be postulated in which each patch might be reduced to a single tree in a mixture that became stratified in some late stage of development. Patch-wise mixtures of this kind are most likely to arise from deliberate planting, usually in squares. Patchy variations in soil or microenvironmental conditions may cause them to start from natural seeding, but the randomness imparted by seed dispersal and other factors usually causes species to be intermingled.

Stratified Canopies

Single-aged stratified mixtures develop when different species represented by advance regeneration, sprouts, new seedlings, or combinations of the three, start off together upon release by some major disturbance such as a windstorm, insect outbreak, or heavy cutting. Although these mixtures are usually thought of as originating from natural regeneration, they can also start with the planting of mixtures of species.

The developmental processes of stratified mixtures of species are different from those of simple pure even-aged (single-aged) stands or cohorts. There is differentiation of tree heights into horizontal canopy strata or stories, one above the other, with one species or a group of similar species in each stratum. Note that this kind of differentiation is not simply dividing into Kraft crown classes within a single canopy stratum; it is dividing within various canopy strata of many species.

The sorting into strata begins in the stand initiation stage (Fig. 4.7) and becomes most pronounced in the stem exclusion stage. Competition is most intense among trees within a given species and stratum, but the lower strata are not excluded by the upper ones. The species of the lower strata are adapted to survive there without participating in the race for the sky that characterizes pure, single-canopied stands. The species that arose to the top of the total crown canopy during previous forest generations generally do so again, even though this development may not take place until the later stem exclusion stage is well underway.

The species groups of each stratum differ from the other groups in the rate of height growth, tolerance of shade, rooting depth, and similar ecological characteristics (Fig. 4.8). It is rare that any two associated species grow in height at precisely the same rate throughout life, even when they are not actually competing with each other. If they are intimately intermingled, the species with the most rapid rate of juvenile growth in height will gain ascendancy over the slower-growing species, which will lag even farther behind because of the lack of light beneath the canopy.

In the simplest kind of stratified mixture, each species ultimately tends to occupy a different stratum of the total crown canopy. In general, there will be as many strata as there are groups of species that differ from one another in height growth and tolerance. The stratification is not always perfect or readily apparent. Even when the stratification is well differentiated, a few individuals of a species that goes with one stratum may by chance have grown upward into a higher stratum or have been left behind in a lower one. Furthermore, the observer

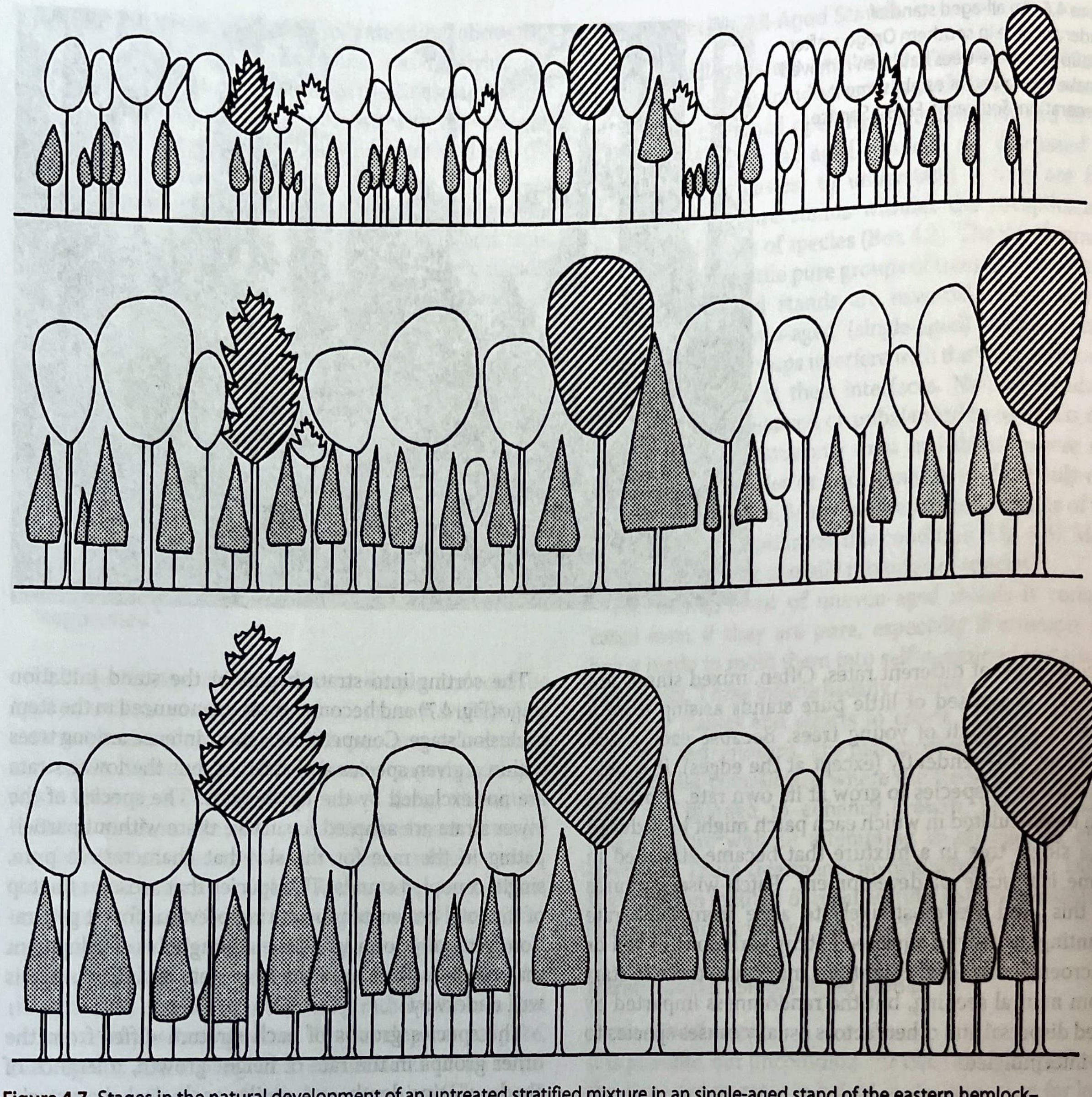


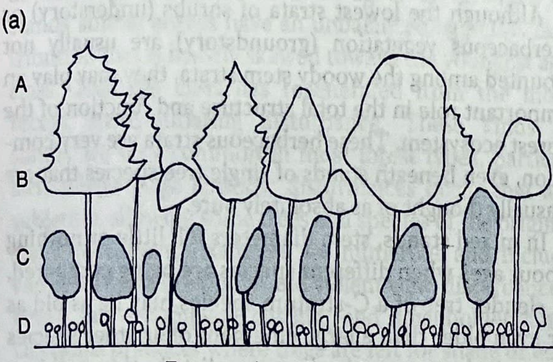
Figure 4.7 Stages in the natural development of an untreated stratified mixture in an single-aged stand of the eastern hemlock–hardwood–white pine type. The upper sketch shows the stand at 40 years with the hemlock (gray crowns) in the lower stratum beneath an undifferentiated upper stratum. At 70 years (middle sketch) the emergents (hatched crowns) have ascended above the rest of the main canopy, except for the white pine, which has only started to emerge. The lower sketch shows the stand as it would look after 120 years with the ultimate degree of stratification developed.*Source:* Yale School of Forestry and Environmental Studies.

standing beneath a stratified mixture will have to look closely and exercise some imagination to perceive the different strata. Stratified mixtures have been widely reported on throughout North America, specifically: western US (Cobb, O'Hara and Oliver, 1993; Deal, Oliver, and Bomiann, 1991); eastern US (Oliver, 1978; Kelty, 1989; Fajvan and Seymour, 1993).

The different strata can be designated A, B, and C downward, a terminology first applied in the forests of the moist tropics, where the concept of the stratified mixture originated (Fig. 4.9). The A-stratum may be continuous, but is more often composed of scattered, isolated emergents that either grow faster or continue growing longer than their associates. Sometimes the emergents are simply called "emergents" and then the A-stratum is regarded as the highest fully closed canopy layer. Each stratum can also be designated by the name of the most characteristic species within it, as when a pure Douglas-fir stratum is above one of pure western hemlock, or an oak stratum is above a sugar maple stratum, which is above beech.

An understanding of the structure and development of stratified mixtures provides a way of dealing with many kinds of complex stands. These are usually found where soil moisture and other site factors are so favorable that many species can grow, although they can also occur on less favorable sites. On sites that contain many tree species, it is very difficult to maintain pure, single-canopied stands. Frequently, a single species is not capable of fully

Figure 4.8 A single-aged mixture of northern hardwoods, about 90 years old, in the Adirondack Mountains of New York. The emergents are the white pines at the left, and some white ashes in the middle, which are still nearly leafless in this spring picture. Sugar maples and yellow birches form the main canopy stratum with American beech in the understory stratum. *Source:* Yale School of Forestry and Environmental Studies.



Even-aged stratified mixture

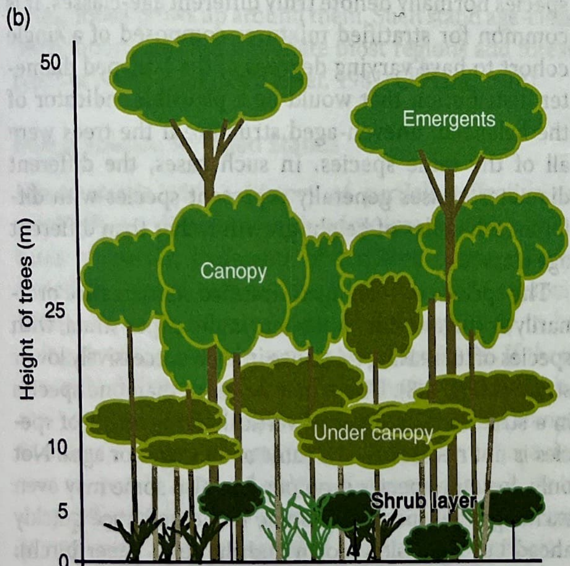


Figure 4.9 Two different categorizations of forest strata. (a) A single-aged, mixed-species, stratified stand showing four strata: A – canopy, B – subcanopy, C – understory, and D – groundstory. *Source:* Yale School of Forestry and Environmental Studies. (b) A second-growth tropical rainforest as an example of a single-aged mixture with the following strata: emergent, canopy, under canopy, and shrub layer. *Source:* Mark S. Ashton.

occupying such sites, and stands turn into stratified mixtures unless costly treatments are applied to reduce the invaders.

If the soil factors are not seriously limiting, the vegetation collectively intercepts more of the photosynthetically active light than a pure stand of some shade-intolerant upper-stratum species (Kelty, 1989). The vertically distributed foliage in a stratified mixture represents a sequence of sun- and shade-leaves that are more fully adapted to do this, than the rather similar array of leaves within a single species. However, in some habitats the lower stratum species can be undesirable or not permanently adapted to the site, and so a single species would be better adapted. For example, the exclusion of fire on some dry, fire-prone sites has sometimes allowed the establishment of lower-stratum species that cause excessive buildup of forest-fire fuels, or might rob the upper stratum of water, causing growth decline of the desirable species.

Plants follow many different strategies for exposing their leaves to solar radiation and claiming growing space. Most annual plants are designed to expend all of their carbohydrates on herbaceous roots and shoots that fill a small amount of growing space quickly, with no provision made for woody stems and roots, and none for the future except for seeds. Perennial herbaceous plants tend to develop enduring control of small amounts of the soil space, but avoid investing substance in the woody stems needed for races toward the sky. Trees and other woody perennials have a wide variety of strategies. Shrubs invest so little in building sturdy stems that the sizes of their crowns are limited. The stems of woody vines are designed almost entirely for conduction of water and dissolved substances.

Most pioneer tree species have weak stems that are designed to expose large amounts of foliage to sunlight rapidly. Usually, they either collapse of their own weight when young or are overtaken by species with stronger stems that start height growth more slowly. However, some quick starters, such as yellow-poplar and some hard pines, continue height growth for long periods and dominate the top stratum for whole rotations (see Chapter 5 for a more detailed description of functional grouping of species by kind of regeneration and growth strategy). It should be noted that every tree species has a limiting total height, greater on good sites than on poor, which should guide decisions about how to handle mixtures of species.

Many ideas about silviculture are based on the view that all useful species of trees grow quickly and steadily in height for whole rotations, but this is not true. A large number of tree species grow very slowly in height, or do not even grow in height at all, until they have built root systems that are adequate to supply water to the crowns (e.g., longleaf pine, oaks). When that is completed, the young trees can initiate rapid height growth, if growing space is available. However, if these trees have not been released from taller trees, they may remain stunted, but retain the potential for rapid growth for many years or even decades. Also, there is the interesting situation in which some shade-tolerant species may grow fairly rapidly in height for a time, but then lapse into very slow growth after being overtaken by faster-growing species (e.g., hemlock).

As a result of these phenomena, there can be remarkable reversals in the position of different species in the different strata. Northern red oak, for example, grows at a steady, moderate rate that cannot be accelerated; after several decades, associate species such as red maple and black birch that had previously gone ahead, then slow down and lapse into the lower strata (Oliver, 1978). Some species, such as the white pines and spruces (Fajvan and Seymour, 1993), may linger below the top of the canopy and ultimately emerge above it, simply because they survive or continue growing in height longer than their associates.

Stratified mixtures were first recognized by Richards (1952) in the wet evergreen and moist deciduous tropical forests, which are practically incomprehensible without this means of analyzing their structure. The fact that stratified mixtures can be even-aged has been learned in the temperate zone where trees have annual rings (Kelty, Larson, and Oliver, 1992). From these, it has been possible to reconstruct the patterns of height growth that lead to whatever structural arrangement exists at any developmental stage (Oliver, 1981). The myriad of such patterns that must exist in moist tropical forests is almost unknowable until ways are invented to determine ages of the trees. In one case, Terborgh and Petren (1991) were able to reconstruct the development of stratified mixtures in a datable series of even-aged stands that became established annually, as new soil was laid down while a tropical river shifted its course sideways each year. Even-aged stratified mixtures are now a very important legacy of land clearance and then recolonization after agricultural abandonment. Native mixtures of second-growth forests now comprise the majority of forest across Eurasia and North America (Whitney, 1994). Even-aged second-growth forests are also becoming an important forest type across Latin America, where agricultural lands are reverting back to brush and early second-growth (Wright, 2005; Chazdon *et al.*, 2009).

Efforts to apply the Kraft Classification of crown dominance to stratified mixtures usually cause confusion about the past and future development of individual trees without adding much that is useful to tree description. However, trees of the same species do compete strongly with each other (Kittredge, 1988), and sometimes the different crown classes can be discerned within a stratum.

Although the lowest strata of shrubs (understory) or herbaceous vegetation (groundstory) are usually not counted among the woody stem strata, they may play an important role in the total structure and function of the forest ecosystem. These herbaceous strata are very common, even beneath stands of single tree species that are casually thought of as absolutely pure.

In mixed stands, stem diameters tell little or nothing about ages when different species are being compared. A slender tree of a C-stratum species may be as old as or even older than a large emergent of another species above it. Large gaps in diameter distribution within a species normally denote truly different age-classes. It is common for stratified mixtures composed of a single cohort to have varying degrees of the J-shaped diameter distribution that would be a plausible indicator of the balanced, uneven-aged structure if the trees were all of the same species. In such cases, the different diameter classes generally represent species with different schedules of height growth rather than different age classes.

The species of even-aged stratified mixtures are ordinarily arranged with intolerants in the upper strata, with species of increasing tolerance in each successively lower stratum (Fig. 4.8). There may be more than one species in a stratum. The order of vertical arrangement of species is not necessarily the same at all stages or ages. Not only do some species drop out, but also some may even exchange their positions. Some intolerants race quickly ahead but soon slow down and die (e.g., paper birch); other intolerants grow rapidly and steadily, and live on to old ages (e.g., ash, yellow-poplar, Douglas-fir). The more shade-tolerant species almost always start slowly and accelerate later (e.g., oak). The very shade-tolerant ones may endure as practically dormant seedlings or saplings and then shoot for the sky, but only when there is a gap in the canopy (e.g., hemlock). Some species grow rather rapidly at first and then slow down and lapse into the understory (e.g., red maple). In other words, in mixed-species stands, the stand development is clearly *not* like that of a pure even-aged stand.

Collectively, the various strata often fill the growing space so long, that the stem exclusion stage may extend for long periods of time. Even if one of the upper layers is completely eliminated, a lower one will usually take over any vacant space. If there are no major lethal disturbances, vacancies gradually develop in the lower strata; the understory reinitiation stage starts and ultimately leads into a very complex, uneven-aged, old-growth stage.

Mixed-Species, Two- or Three-Aged Stands (Multi-Aged)

This text considers mixed-species stands that have two or three age classes to be multi-aged. These kinds of stands almost always have an unbalanced age-class distribution that is heavily skewed toward the youngest age class. This age class has regenerated from the most recent stand-initiating disturbance. These kinds of stands are very common in most forest types, particularly where large episodic disturbances occur that are sublethal, allowing some trees and species of the original stand to survive. Examples are numerous and include variable crown fires, large and violent wind disturbances, heavy but incomplete cutting, and smallholder land-clearance practices where trees are left for shade or economic value and then when the land is abandoned a young forest grows up around them. Such stand age-class distributions perhaps dominate most regions and forest types of North America (Oliver, 1981; O'Hara, 2014).

Mixed-Species, All-Aged Stands

Mixed stands with a history of partially effective or patchy forest disturbances develop into complex mixtures of species, fragments of stratified mixtures, and varieties of age classes or cohorts (Fajvan and Seymour, 1993). All stages of stand development are likely to be going simultaneously in some part of the stand. If there are truly different age classes or cohorts, there will be real variations in the height of the top of the main canopy in different parts of the stand. If shade-intolerant species that are normally found only in the upper strata exist in very different diameter classes within a stand, the stand is very likely to be composed of more than one cohort.

Where site conditions produce mixed stands, this chaotic kind of structure is characteristic of undisturbed old-growth stands. The same is true of **high-graded stands** from which the best trees have been cut, except that the best species and largest trees may have already been eliminated in an earlier cutting.

The intermingling of trees of very different ages often obscures and complicates processes by which different species sort themselves into different strata. Older individuals of species normally found in some lower stratum often reach the uppermost levels and the stands become irregularly uneven-aged. The best silvicultural solution for managing such stands lies in diagnosing the processes taking place in each separate part and treating it accordingly. Even though they may exhibit some semblance of a J-shaped curve for diameter distribution, they almost never approach the balanced all-aged condition. That condition is actually artificial; it is created by deliberate silvicultural action and not by random events of nature.

Old-growth forests that are mixed-species and all-aged are usually in forest types where return intervals between large disturbances are very long (>250 years), and where late-successional tree species that attain the canopy die from individual small events (e.g., windthrow, lightning strikes, pathogens, insect defoliation). Such forests are found in everwet climates outside of the hurricane or cyclone regions. Examples of mixed-species, all-aged, old-growth forests have been illustrated as profile diagrams in the older literature describing the floristics of primary (undisturbed) tropical rainforests in Southeast Asia and the Amazon (Fig. 4.10).

Relationship of Stand Dynamics to Other Interpretations of Vegetational Development

Compared to the paradigm of stand dynamics, there are other interpretations of vegetation change over time (Shugart, 1984; McIntosh, 1978; Cattelino *et al.*, 1979). The concept of natural succession formulated by Clements (1936) once dominated American ecology. An oversimplified version of this concept holds that pioneer vegetation of an initial **Stage 1** colonizes an area from which all preexisting vegetation has been eliminated. **Stage 1** soon dies and is replaced by a **Stage 2**, which is composed of other species that start under **Stage 1** and are relatively shade tolerant (Fig. 4.11). Ultimately, **Stage 2** is similarly replaced by **Stage 3**, and there may be additional stages leading to a stable, endlessly self-replacing stage called the **climax**. The originator of the concept made it far more complicated and sophisticated, but many of the disciples have oversimplified it.

Climax vegetation has been regarded by some as an ultimately perfect state of nature in which all organisms are represented and all physical and biotic factors are in perpetual balance. It was once postulated that this perfect condition required freedom from disturbance, although it has been conceded more recently that

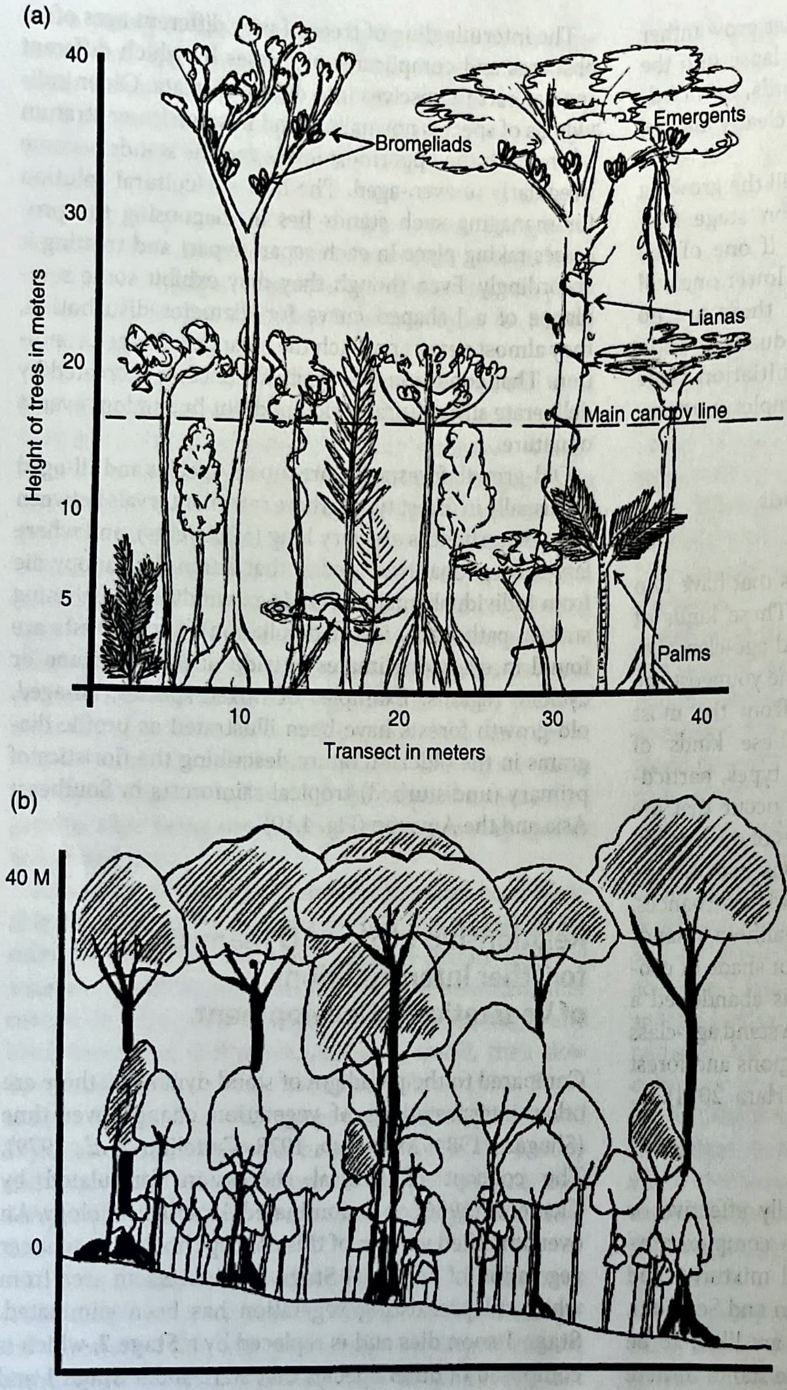


Figure 4.10 Profile diagrams for rainforests. (a) French Guyanan rainforest dominated by slow-growing late successional leguminous trees. Trees with bold outlines depict canopy and emergent species. The dotted line denotes the canopy layer and above. *Source:* Adapted from Richards, 1996. (b) A mixed dipterocarp forest growing on fertile soils in Sarawak. The canopy is less broken with few emergents and a dominance of mixed dipterocarp tree species in the canopy (darker shading). *Source:* Adapted from Ashton, 1964. For scale, 10 m is about 33.3 ft.

perpetuation of the essentially uneven-aged state depended on the occasional creation of small gaps in the growing space. In fact, the terms **gap** and **patch dynamics** have been coined to describe the study of patterns of establishment and subsequent development of vegetation in all vacancies of any size in the growing space (Pickett and White, 1985). In this sense, the term **forest stand dynamics** as used in this book is a kind of gap or patch dynamics, except that gaps or patches filled by single cohorts are called stands.

The Clementsian natural succession model does describe at least the early stages of development after most vegetation has been killed by severe disturbances, but it does not cover other sequences very well. According to the stand dynamics principles proposed by Oliver and Larson (1996), the stages of stand initiation, stem exclusion, and understory reinitiation represent early stages of the natural succession just described, and the old-growth stage covers all of the subsequent steps leading to the climax stage.

Figure 4.11 Successional development in which an old senescing stand of western larch in western Montana is dying and being replaced by subalpine fir and a few Engelmann spruce. *Source:* US Forest Service.

Enthusiasm for the simple Clementsian concept of natural succession and the climax stage as the sole pattern of vegetational development has declined, mainly because of two things. First, it was observed that fires and other major disturbances were so common, even in nature, that in many localities, the theoretical climax vegetation never had time to develop. Second, it became apparent that more complex ideas were necessary to account for the behavior of intimate mixtures of species and the effects of disturbance that killed only some of the plants growing in a unit of space.

The concepts of stratified mixtures and the principles of stand dynamics covered earlier in this chapter represent attempts to deal with the effects of partial disturbances and the interaction of different species. Each of the individual strata of a single-cohort stratified mixture often represents one of the sequential stages envisioned in the Clementsian concept of succession, with the species of the earliest stage being those of the A-stratum.

Some ecologists have applied the term **initial floristics** to the simultaneous appearance of many different categories of plant species in what is here termed the stand initiation stage. These ecologists call Clementsian succession **relay floristics**. The members of a single cohort that develop into a stratified mixture arise through initial floristics. Each one of these terms describes one of the various ways in which vegetation develops; the two concepts are complementary rather than conflicting, because each fits a different disturbance pattern. Relay floristics usually fits developments following disturbances such as hot fires that wipe out nearly all of the vegetation. Initial floristics is associated more with regeneration from sprouts and advance growth as well as new seedlings that start development following an initiating disturbance by wind or other agencies that kill stands from the top downward (see Chapter 5 for further details).

Another way of viewing stand development over time emphasizes the accumulation of biomass and chemical nutrients after a destructive regenerating disturbance. This perspective is very much a biogeochemical one (Bormann and Likens, 1981). The regeneration step is called **reorganization**, the buildup of biomass is referred to as **aggradation**, and the state in which the accumulation of biomass and nutrients comes into equilibrium with losses is the **steady state**. These stages are analogous to steps of stand initiation, stem exclusion, understory reinitiation, and old growth that relate to changes in tree populations.

There is no single universal pattern; in fact, there are more patterns than terms to describe them. In managing any category of stands, the forester should know as much as possible about their past and future development. It is good to be wary of preconceived ideas about standard patterns because there are more developmental sequences than are described in this book. Oliver and Larson (1996) cover this topic in more detail.

Choice of Developmental Patterns

Silvicultural choices can be thought of as determining what kind of stand developmental process or stage of natural succession is most desirable in a given situation.

In the Pacific Northwest, for example, the forester must often decide whether to perpetuate pure stands of Douglas-fir, or allow them to be succeeded by stratified mixtures of Douglas-fir, western hemlock, and redcedar. In the Lake Region, the choice may be between the pioneer aspen association and a climax stage such as the spruce–fir association. In the southeast US, decisions must be made about whether to let old-field stands of loblolly pine revert to pine–hardwood mixtures. In almost every kind of forest, it must also be recognized that some wildlife species may depend on stands that have some dead trees and other features of old-growth stands.

Several generalizations of wide, but not universal, application may be introduced at this point. In the first place, the most valuable commercial species tend to be relatively intolerant but comparatively long-lived trees representative of the early or intermediate stages in natural succession. Species such as pines, Pacific Coast Douglas-fir, yellow-poplar, and white ash definitely fall in this category. It is no coincidence that intolerant species are important commercially because they are the ones most likely to lose their lower branches through natural pruning. It is of significance that some of them are adapted to reproduce mostly after major disturbances that happen infrequently. If these are to survive from one major disturbance to another, they must be long-lived; as a result, they are likely to develop the economically desirable attributes of large stem size and resistance to decay.

Late-successional forest types, characterized by species such as hemlock, true firs, and beech, are frequently composed of branchy trees that produce less valuable wood. Because of their shade tolerance, they can reproduce almost continuously; thus the ability of individuals to endure for long periods is not so crucial in the survival of the species. Many pioneer species have even less capacity for individual longevity. However, they usually exhibit good natural pruning, and the necessity that they grow rapidly to seed-bearing age is an economically desirable attribute, although they usually have weak wood of low density.

Natural succession proceeds most rapidly and vigorously on the better sites, that is, on soils that are both moist and well aerated. It is sometimes impossible to resist the invasion of additional species without expensive silvicultural treatments. Furthermore, good sites are hospitable to the growth of so many species that silvicultural treatment becomes complicated and difficult. These considerations often have the paradoxical effect of making silviculture most efficient on sites of intermediate quality where uncomplicated stands can be maintained without strenuous effort. In fact, on poor sites occasionally it may be virtually impossible for succession to proceed beyond an intermediate stage, which is sometimes referred to as a **physiographic climax**. For example, pure stands of jack pine or red pine occasionally represent valuable physiographic climaxes on certain dry, sandy soils in the Lake Region.

It has been claimed that late-successional or old-growth types may be more resistant to, and more cheaply protected from, fire, insects, fungi, wind, and weather than earlier stages. In those cases where this advantage exists, it results more from the diversity of species and age classes than from age or position in the successional scale. Similar advantages sometimes prevail in mixed stands with a variety of age classes that are still typical of earlier successional stages.

It is often postulated that natural climax or old-growth communities are in a stable and favorable equilibrium with the physical and biological environment. Perfect stability and complete favorability do not exist, so it is in terms of relative degrees of each quality. For example, the balance achieved by long-continued natural processes, operating more or less at random, is not necessarily more favorable to the trees than to the organisms that feed upon them. The more artificial dynamic equilibrium produced by prudent silviculture may be less stable but ought to be more favorable from the standpoint of the integrated effect of all socioeconomic factors. If the dynamic equilibrium created by treatment ultimately balances at some disastrous condition, the silviculture was hardly prudent.

The naturalistic doctrine of silviculture did not arise from any clearly demonstrated disadvantages of early or middle stages of natural forest succession. It developed largely from disappointments with attempts to create unnatural types, particularly with exotic species or native species not adapted to the sites involved. In more recent times, it has been advanced as a result of concern for wildlife diversity and the need for conservation of natural areas.

References

Ashton, P. S. 1964. *Ecological Studies in Mixed Dipterocarp Forest of Brunei State*. Oxford Forestry Memoirs, 25.

Bormann, F. H. and Likens., G. E. 1981. *Pattern and Process in a Forested Ecosystem*. Springer Verlag, New York. 253 pp.

Cattelino, P. S., Noble, I. R., Slayter, R. O., and Kessell, S. R. 1979. Predicting the multiple pathways of plant succession. *Environmental Management*, 3(1): 41–50.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E., and Miller, S. E. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology*, 23: 1406–1417.

Clements, F. E. 1936. Nature and structure of the climax. *Journal of Ecology*, 24: 252–284.

Cobb, D. F., O'Hara, K. L., and Oliver, C. D. 1993. Effects of variation in stand structure on development of mixed-species stands in eastern Washington. *Canadian Journal of Forest Research*, 23: 545–552.

Deal, R. L., Oliver, C. D., and Bomiann, B. T. 1991. Reconstruction of mixed hemlock–spruce stands in coastal southeast Alaska. *Canadian Journal of Forest Research*, 21: 643–654.

Fajvan, M. A. and Seymour, R. S. 1993. Canopy stratification, age structure, and development of multicohort stands of eastern white pine, eastern hemlock, and red spruce. *Canadian Journal of Forest Research*, 23: 1799–1809.

Franklin, J. F., Mitchell, R. J., and Palik, B. 2007. *Natural Disturbance and Stand Development Principles for Ecological Forestry*. USDA Forest Service General Technical Report NRS-19. Newtown, PA. 44 pp.

Franklin, J. F., Spies, T. A., Pelt, R. V., Carey, A. B., Thornburgh, D. A., Berg, D. R., Lindenmayer, D. B., Harmon, M. E., Keeton, W. S., Shaw, D. C., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, 155: 399–423.

Guldin, J. W. and Lorimer, C. G. 1985. Crown differentiation in even-aged northern hardwood forests of the Great Lakes Region, USA. *Forest Ecology and Management*, 10: 65–86.

Harper, K. A., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: a landscape scale study. *Silva Fennica*, 36: 249–263.

Kelty, M. J. 1989. Productivity of New England hemlock-hardwood stands as affected by species composition and canopy structure. *Forest Ecology and Management*, 28: 237–257.

Kelty, M. J., Larson, B. C., and Oliver, C. D. (eds.). 1992. *The Ecology and Silviculture of Mixed-Species Forests.* Kluwer Academic Press, Norwell, Mass. 287 pp.

Kittredge, D. B. 1988. The influence of species composition on the growth of individual red oaks in mixed stands in southern New England. *Canadian Journal of Forest Research*, 18: 1550–1555.

Kraft, G. 1884. *Zur Lehre von den Durch Forstungen. Schlagstellungen und Lichtungshieben*. Hanover, Germany.

McIntosh, R. P. 1978. *Phytosociology*. Academic, New York. 416 pp.

Means, J. E. (ed.) 1982. *Forest Succession and Stand Development Research in the Northwest*. State University, Forest Research Laboratory, Corvallis, OR. 171 pp.

O'Hara, K. L. 2014. *Multiaged Silviculture: Managing for Complex Forest Stand Structures*. Oxford University Press, Oxford, UK. 213 p.

Oliver, C. D. 1978. Development of northern red oak in mixed species stands in central New England. *Yale University School of Forestry & Environmental Studies Bulletin*, 91. 63 pp.

Oliver, C. D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management*, 3: 169–182.

Oliver, C. D. and Larson, B. C. 1996. *Forest Stand Dynamics*. John Wiley and Sons, New York. 520 pp.

Pickett, S. T. A. and White, P. S. (eds.). 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York. 472 pp.

Reichle, D. E. 1981. *Dynamic Properties Afforest Ecosystems*. Cambridge, New York. 683 pp.

Richards, P. W. 1952. *The Tropical Rainforest, an Ecological Study*. Cambridge University Press, Cambridge, UK. 450 pp.

Richards, P. W. 1996. *The Tropical Rainforest, an Ecological Study*. 2nd ed. Cambridge University Press, New York. 600 pp.

Shugart, N. H. 1984. *A Theory of Forest Dynamics, the Ecological Implications of Forest Succession Models*. Springer-Verlag, New York. 304 pp.

Spies, T. A. 2004. Ecological concepts and diversity of old-growth forests. *Journal of Forestry*, 102: 14–20.

Svoboda, M., Fraver, S., Janda, P., Bače, R., and Zenáhlíková, J. 2010. Natural development and regeneration of a Central European montane spruce forest. *Forest Ecology and Management*, 260: 707–714.

Terborgh, J. and Petren, K. 1991. Development of habitat structure through succession in Amazonian floodplain forest. In: E. D. McCoy and H. R. Mushinsky (eds.). *The Structure of Habitats*. Chapman & Hall, New York.

Whitney, G. G. 1994. *From Coastal Wilderness to Fruited Plain: a History of Environmental Change in Temperate North America*. Cambridge, New York. 451 pp.

Winter, L. E., Brubaker, L. B., Franklin, J. F., Miller, E. A., and DeWitt, D. Q. 2002. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. *Canadian Journal of Forest Research*, 32: 1039–1056.

Worrall, J. J., Lee, T. D., and Harrington, T. C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea–Abies* forests of Crawford Notch, New Hampshire, USA. *Journal of Ecology*, 93: 178–190.

Wright, S. J. 2005. Tropical forests in a changing environment. *Trends in Ecology & Evolution*, 20: 553–560.

Zhang, Q., Pregitzer, K. S., and Reed, D. D. 1999. Catastrophic disturbance in the presettlement forests of the Upper Peninsula of Michigan. *Canadian Journal of Forest Research*, 29: 106–114.