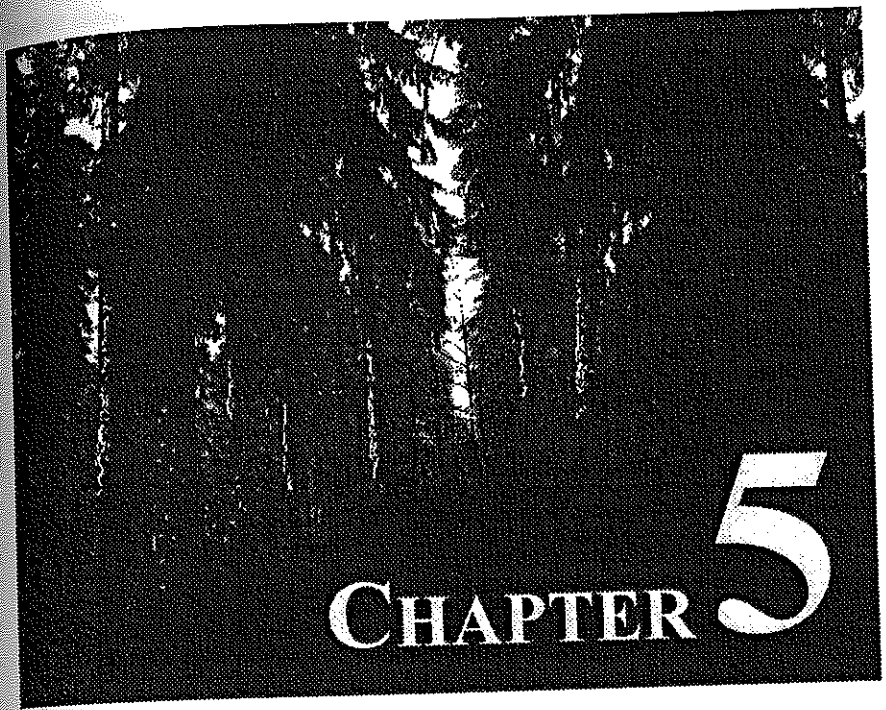


Overview of Stand Development Patterns

Introduction

Similar stand development patterns and processes appear after disturbances and change in similar ways with time in many parts of the world in stands of diverse species and distant locations. The same tree species dominate an area following a given type of disturbance within a geographic area, and the same species grow together and change the stand structure in similar patterns following the disturbance. These patterns and changes in stand physiognomy and species dominance result from competitive advantages gained by the new species following the disturbance and events occurring after the disturbance

These patterns and processes are expressed as stand structures (for definition, see Chapter 1). Two approaches have been recently used to study and manage forests: one is to concentrate on the processes of change following major (stand-replacing) and minor disturbances; the other is to concentrate on the stand structures which provide various values. Confusion between these two approaches has led to problems in both forest policy and management.

This chapter gives a descriptive overview of the general patterns and processes of forest development following both major and minor disturbances. It then describes the approach of concentrating on the various stand structures. Subsequent chapters then give more detailed, mechanistic explanations and quantitative descriptions of the patterns.

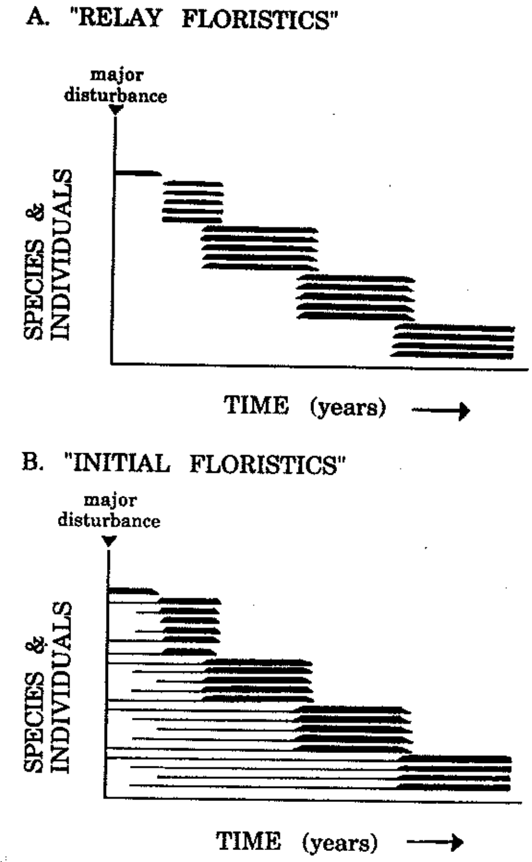


Figure 5.1 Schematic of two patterns assumed to occur in stand development. (*After Egler, 1954.*) (A) Traditionally, a "relay floristics" pattern has been assumed to occur, with one species or group invading and being replaced by successive species or groups. (B) An "initial floristics" pattern is actually more prevalent, whereby all species invade at approximately the same time after a disturbance but assert dominance at different times. The type of disturbance acts as an "environmental sieve" (*Harper, 1977*), giving some species a competitive advantage. (See "source notes.")

Development Patterns following Major (Stand Replacing) Disturbances

Successive changes in species dominance after a major disturbance have long been recognized by ecologists. Early interpretation of the pattern was that one or a few species invaded a disturbed area and predominated; as these altered the environment, other species invaded which achieved dominance, altered the environment, and allowed still other species to invade and eventually predominate (Clements, 1916; Cline and Spurr, 1942; Daubenmire, 1952; Oosting, 1956; MacArthur and Connell, 1966). This progressive change in species was referred to as *succession* and was believed to occur in an all-aged manner (Drury and Nisbet, 1973). The concept of one species invading after another in a "relaylike" manner is known as *relay floristics* (Fig. 5.1A). Eventually a species or group of species invades which predominates and replaces *itself* rather than being replaced by other species, creating a stable end point to succession ("steady state"), known as the *climax* (Cowles, 1911; Clements, 1916, 1936; Braun, 1950; Oosting, 1956; Dansereau, 1957; Odum, 1959; Daubenmire, 1968).

Other ecologists believed most plants existing in a stand invade shortly after a disturbance (Egler, 1954; Stephens, 1956; Raup, 1957, 1964; Olson, 1958; Johnson 1972; Drury and Nisbet, 1973; D. M. Smith, 1973; Henry and Swan, 1974; Niering and Goodwin, 1974; Oliver, 1978*a*, 1981), rather than throughout the life of a stand. According to this *initial floristics* pattern (Fig. 5.1B), species which predominate later have been present since soon after the disturbance but are often overlooked because of their small size, relatively few numbers, and, "to some extent, the preoccupation of botanists with the dominant species" (Drury and Nisbet, 1973). Elements of both initial and relay floristics are characteristic of forest development; however, the invasion pattern after a disturbance predominantly follows the initial floristics pattern.

Single- and Multiple-Cohort Stands (Even-Aged and Uneven-Aged Stands)

Stands developing after major disturbances have been described as "even-aged" stands, since all component trees have been assumed to regenerate shortly after the disturbance. In fact, trees may continue to regenerate for several decades where growth is slow before the available growing space becomes reoccupied, resulting in a wide age range in the stand.

The term *even-aged* is misleading for stands where there is a wide age range following a single disturbance. The group of trees developing after a single disturbance—whether major (stand-replacing) or minor—has been referred to as an *age class*, a *cohort* (Bazzaz, 1983), or a *generation* (Smith, 1984). In this book, a group of trees regenerating after a single disturbance will be referred to as a "cohort." The age range within a cohort may be as narrow as 1 year or as wide as several decades, depending on how long trees continue invading after a disturbance. Stands developing after a minor disturbance will be referred to as *single-cohort stands* instead of "even-aged stands." Stands where component trees arose after two or more disturbances (all but the first of which would be minor disturbances) will be referred to as *multiple-cohort* (or *multicohort*) *stands*, instead of the usual designation of "uneven-aged" or "all-aged" stands.

More is known about single-cohort stands than multicohort stands, probably because they are less complicated, they have been considered as part of "secondary succession" by ecologists, and they are more commonly managed by foresters.

Stages of Stand Development

Patterns of species dominance and changes in stand structures are not the result of obligatory laws which forest stands must follow. While they can be somewhat—but not completely—anticipated, they are simply the result of interactions of plants and are emergent properties of the tree interactions. For purposes of this discussion, the development patterns following a disturbance will be divided into stages (Fig. 5.2; Oliver, 1981). These stages are similar to the descriptions of Isaac (1940), Jones (1945), Raup (1946), Watt (1947), Bloomberg (1950), Horton (1956), Daubenmire and Daubenmire (1968), Reiners et al. (1971), Day (1972), Harris and Farr (1974), Bormann and Likens (1979), Crow (1980), Hartshorn (1980), Wallmo and Schoen (1980), Peet (1981), Alaback (1982*a,b*, 1984*b*), Brady and Hanley (1984), Felix et al. (1983), Nakashizuka (1984*a,b*), Whitmore (1975, 1984), and Peet and Christensen (1987).

Stand initiation stage. After a disturbance, new individuals and species continue to appear for several years.

Stem exclusion stage. After several years, new individuals do not appear and some of the existing ones die. The surviving ones grow larger and express differences in height and diameter; first one species and then another may appear to dominate the stand.

Understory reinitiation stage. Later, forest floor herbs and shrubs and advance regeneration again appear and survive in the understory, although they grow very little.

Old growth stage. Much later, overstory trees die in an irregular fashion, and some of the understory trees begin growing to the overstory.

How rapidly a forest changes from one of the above-described stages to another varies greatly. In some cases—as in balsam fir/red spruce stands—a disturbance may intervene before the later stages are reached (Sprugel, 1976; Osawa et al., 1986). Where there is a partial overstory the pattern may differ slightly.

Development of single-cohort stands growing after major disturbances will first be discussed because it is the least complicated pattern. The development of multicohort stands created by minor disturbances will then be discussed. Major disturbances are not necessarily more prevalent, and in some regions they may rarely occur; however, for purposes of this discussion, they allow a "starting point" for describing forest development.

Stand initiation stage

A major disturbance kills all large trees but may not destroy the forest floor herbs, shrubs, advance regeneration, buried seeds, and roots—depending on the type of disturbance.

A major disturbance radically changes the forest floor and soil environments, even if it does not destroy them. There are losses of evapotranspiration and litter input as well as great changes in pedochemical and biological processes. Many pedologic changes such as alteration of the soil profile (Lyford, 1964*b*) or releasing of nutrients (Bormann and Likens, 1981) from the upper soil are almost immediate; however, others occur over several years as the newly dead roots and other organic matter decompose and reduce the cation exchange sites and alter the soil structure. Such disturbances do not necessarily reduce the soil's productivity. The disturbance may actually have a rejuvenating effect in soils undergoing podzolization (Ugolini et al., 1989). The rate of these pedologic changes after a major disturbance depends on the climate, soil texture and structure, nature of the overstory, nature of the disturbance, and other factors (Bormann and Likens, 1981).

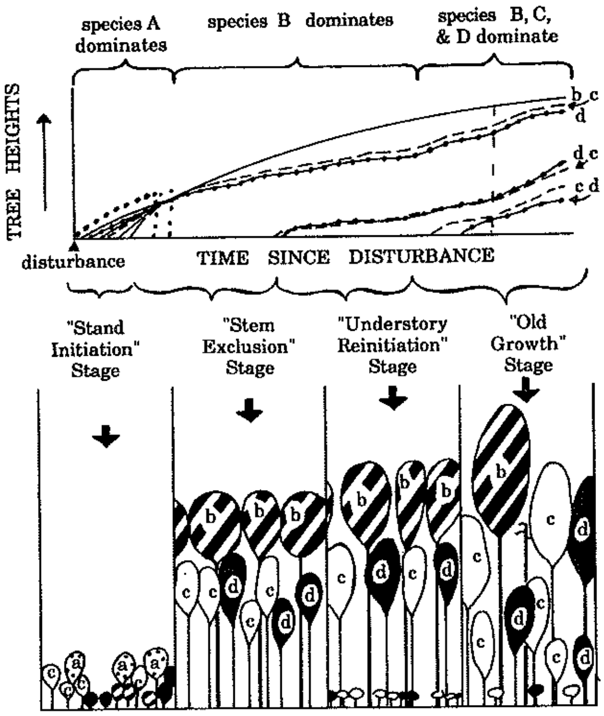


Figure 5.2 Schematic stages of stand development following major disturbances. All trees forming the forest start soon after the disturbance; however, the dominant tree type changes as stem number decreases and vertical stratification of species progresses. The height attained and the time lapsed during each stage vary with species, disturbance, and site. (*Oliver, 1981.*) (See "source notes.")

New plants—trees, shrubs, and herbs—grow from seeds, sprouts, advance regeneration, and other mechanisms into the growing space made available by the death of the previous overstory (Dyrness, 1973; Johnson, 1981*a,b*; Canham and Marks, 1985). Only certain individuals are able to grow on a given area, depending on the type of disturbance, competing vegetation, availability of seeds from surrounding areas, suitability of microsites for growth, and predation by animals. Those which grow rapidly at first reoccupy the available growing space. Their advantage over other species which invade later often allows them to dominate and/or exclude other species for many years or centuries—often until the next disturbance (Nichols, 1935; Hough and Forbes, 1943; Chapman, 1942; Spurr, 1954; Niering and Egler, 1955; Raup, 1964; Dyrness, 1973; Strang, 1973; Henry and Swan, 1974; Niering and Goodwin, 1974; Whitmore, 1974; Hanley et al., 1975; Ashton, 1976; Keeley, 1979; Veblen et al., 1980; Strang and Johnson, 1981; Hibbs, 1983; Felix et al., 1983; Frelich and Lorimer, 1985; Thomas and Agee, 1986; Aplet et al., 1988). As a result, the species composition of each stand is largely the result of the type of disturbance which initiated it; i.e., the disturbance determines which species have the initial advantages immediately after the disturbance (Ahlgren, 1960; Buckman, 1964; Pase, 1971; Tappeiner, 1971; Drury and Nisbet, 1973; Cattelino et al., 1979; Johnson, 1981*a,b*; Oliver, 1981; D. M. Smith, 1982; Tappeiner and McDonald, 1984; Adams and Adams, 1987). When germinating seeds are favored by a disturbance, the species composition of the ensuing stand will also depend on which species are producing seeds during the years immediately following the disturbance (Frissell, 1973). Soil, climate, and other gradients also influence which species have a competitive advantage. The concept that a single area can be occupied by different, relatively stable groups of species (Botkin, 1979; Sprugel, 1991) is different from early assumptions that each area returns to a single equilibrium vegetation composition soon after disturbance (Clements, 1916).

Also contrary to older interpretations of forest development, tree species often invade newly disturbed areas without other, nonwoody species having preceded them to modify the soil and microclimatic conditions (Niering and Egler, 1955; Hack and Goodlett, 1960; Ohmann and Ream, 1971; Purdie and Slatyer, 1976; Johnson, 1981*a,b*). Tree species have even been found invading newly available growing space within a few years after the soil was uncovered by a retreating glacier (Sigafoos and Hendricks, 1969; Oliver et al., 1985).

A given environment permits only certain individuals to grow on an area. This process of species limitation is referred to as an environmental sieve (Harper, 1977), and the composition of the stand is restricted by those species able to "pass" the environmental sieve. Disturbance types, microclimates, and soil conditions may all be considered environmental sieves. The environmental sieve may change slightly during stand initiation, since some plants slightly modify the environment—such as by creating slight shade which allows other plants to germinate and grow which could not become established in direct sunlight.

Some invading plants grow rapidly at first and complete their life cycles before other plants crowd them out (Marks, 1974; Cook, 1978; Zamora, 1982; Alaback, 1982*a,b*; Oliver et al., 1985). Annuals and biennials have a competitive advantage immediately after a disturbance where time since disturbance is considered as a gradient. Tree species such as fire and bitter cherries (Marks, 1974; Stubblefield, 1978) invade early and set seeds after several years. Douglas-firs, oaks, and some other species can begin growth at the same time as the rapidly growing ones, but are not so numerous, do not grow so rapidly at first, and do not produce seeds until they become older (Oliver, 1978*a*; Wierman and Oliver, 1979). Consequently, they do not dominate the site at first.

Still other plants—such as red alders, tulip poplars, and vaccinium shrubs—grow rapidly at first and maintain a dominant position for a long time (Stubblefield and Oliver, 1978; O'Hara, 1986). Some trees such as western hemlocks can either predominate the site soon after a disturbance or become dominant later in their lives, depending on the site and the other plants on the area (Franklin and Dyrness, 1973; Atkinson and Zasoski, 1976). Individuals will continue to invade an area so long as growing space is available. The invasion period can vary from a few years to many decades, depending on how rapidly the newly growing stems reoccupy the growing space. Factors leading to a short invasion period are soil and site conditions favorable to rapid growth; a rapid appearance of new plants in the disturbed area—either because the seeds, root collars, or advance regeneration survived the disturbance or because seeds came in rapidly from adjacent areas; the presence of species which naturally grow rapidly and in directions which occupy the most growing space when young (e.g., lateral expansion of branches is often more important than height growth during this stage); a high frequency of plants so that the growing space is filled by each plant growing only a small amount; and the absence of animal predators or harsh conditions which kill invading plants.

The age range of invading plants, therefore, is limited by the time it takes the growing space to become reoccupied. Actually, the age range of the cohort may become somewhat narrower as the stand grows older if the last arriving plants are outcompeted and killed by more dominant ones. In forest development each individual is considered, regardless of whether it is a genetically different individual (a genet) or simply a clone (a ramet) of another or previous plant. Consequently, age is considered as time of initiation of sprouts rather than time of germination of the original seed, which may have occurred several generations earlier. Advance regeneration is also commonly aged from the time it is released rather than when it germinated, which may have been over 50 years earlier.

The stand initiation stage—before the growing space is fully reoccupied and new stems quit initiating—is the time of very high numbers of plant species (Isaac, 1940; Alaback, 1982*a,b*, 1984*b*; Zamora, 1982; Felix et al., 1983; Hibbs, 1983; Oliver et al., 1985). Long-lived tree species have not had time to outcompete other species and reduce the diversity. It is also a period when many animals are found, since the variety of plants and seeds provides an abundance and diversity of food. The palatable, succulent upper canopy of young plants is still accessible and provides hiding cover close to the ground and a variety of spatial patterns for territorial establishment.

There may be elements of relay floristics during plant initiation. Some species grow only on extreme sites after other species have altered or increased the growing space (Connell and Slatyer, 1977; Agee and Dunwiddie, 1984; Peet and Christensen, 1987). Also, some short-lived herbaceous and woody plants may die and relinquish their growing space before a disturbance kills them (Johnson, 1981*a,b*; Hibbs, 1983). Other species invade in a relaylike manner when this growing space is made available. This relinquishing of growing space is similar to the death of overstory trees in the old growth stage. Herbaceous and shrub communities may at times pass through initiation, exclusion, reinitiation, and senescent processes similar to a forest stand, but over the course of a few months or years during the stand initiation or understory reinitiation stages of a forest stand.

Stem exclusion stage

Before the available growing space is reoccupied, plants are expanding in an *open growth* condition, unhampered by competition with other individuals. After the available growing space is reoccupied, new individuals do not become established successfully. Those plants with a competitive advantage in size or growth pattern are able to expand into growing space occupied by other plants and reduce their growth rate or kill them. The stage when this occurs is referred to as the *stem exclusion stage* both because new stems are prevented from successfully invading and because some existing stems die and thus are excluded from the stand.

Parts of a stand may be in the stem exclusion stage, with some trees dying from competition, while other, more open areas are still in the stand initiation stage because of spacing, species, and site irregularities. In fact, a given stand may take several decades before all parts make the transition from the stand initiation stage to the stem exclusion stage.

As the plants begin competing with each other, they form a layer of living foliage several meters thick in which their leaves are able to obtain sunlight (Assmann, 1970). Being in a slightly lower portion of this layer—in low shade—does not put these plants at a distinct disadvantage when young. At first there is not a pattern of height by species within the foliage layer. This period with all trees within the same layer at the beginning of the stem exclusion stage is called the *brushy stage* (Gingrich, 1971).

The foliage layer rises as the trees grow taller, and leaves cannot survive in the diminished sunlight beneath it. Plants which cannot grow tall enough to stay within this foliage layer often die (Isaac, 1940; Alaback, 1982*a,b*; Oliver et al., 1985). The shaded forest floor becomes devoid of living plants and consists of brown, dead leaves, twigs, and stems.

During rising of the foliage layer, growth characteristics of the different species manifest themselves, causing varied stand development patterns. In some cases, early dominance is a strong indication of which species will maintain dominance in the stand (O'Hara, 1995*a*; O'Hara et al., 1995). In other cases, a species can become dominant even if it begins at a relatively low canopy position in the "brushy stage" (Oliver, 1978). For simplicity, the various growth patterns of stands with only one species will first be described, although perfectly pure stands rarely occur. Afterward, mixed species stands will be described.

Single-species stand development patterns. When growing space is available in the stand initiation stage, all trees would expand at an equal rate in an ideal stand with trees of the same genetic potential and age, on a uniform site, and with uniform spacing between trees so that each tree occupies the same growing space. Each tree would continue to increase in size in the stem exclusion stage, but would not increase in amount of growing space it occupies. Because all trees would be identical, none would have a competitive advantage which would allow it to expand by taking growing space away from a neighbor. Each tree would eventually expand until all photosynthate was consumed by its own respiration to keep its increased size alive, and it would no longer grow. If all trees behaved uniformly in this manner, the stand would eventually quit growing and become a *stagnant stand.* Absolute stagnation does not occur in nature because stands do not exist as ideally as described above. Uniform, crowded stands of some species—such as lodgepole pines—can approach stagnation and be only 2 m (3 ft) tall at 18 years while adjacent, less crowded stands of the same age can be almost 4.5 m (15 ft) tall (Mitchell and Goudie, 1980). The stagnated condition seems to be more pronounced on poor sites and in stands with high numbers of trees, although more widely spaced stands on more productive sites can also stagnate. The uniform age and spacing of forest plantations may be creating stands which approach stagnation more commonly than do naturally grown forests.

Actually, some trees outgrow others in a stand because even single-species plantations are rarely uniform in site, tree age, spacing, or genetic potential. Even in apparently stagnated lodgepole stands studied in eastern British Columbia, some trees were found to be outgrowing others—albeit at a rate of less than 1 cm/year. As some individuals outgrow others, they take away available light space by shading foliage and physically abrading foliated branches of adjacent trees. The reduced growing space of the tree being outcompeted forces it to put less of its reduced photosynthate into growth, and it declines in growth while the dominating one may not. The result is crown *differentiation,* with some trees becoming larger at the expense of others (Guillebaud and Hummel, 1949).

Trees in pure, single-cohort stands usually have their crowns within a single horizontal layer, although the more vigorous trees' crowns can extend higher within the layer and the foliage of suppressed trees may live lower in the layer. In mixed-species stands, there are often several distinct layers of tree crowns. Each horizontal layer is referred to as a *stratum.* Single-cohort, single-species stands generally contain a single stratum when in the stem exclusion stage. The degree of dominance and suppression within each stratum has been described by classifying trees into four crown classes (Kraft, 1884; D. M. Smith, 1986). These crown classes are distinct from canopy strata discussed later (Fig. 5.3).

Dominant. Crowns extend above the general level of crown cover of other trees of the same stratum and are not physically restricted from above, although possibly somewhat crowded by other trees on the sides.

Codominant. Crowns form a general level of crown stratum and are not physically restricted from above, but are more or less crowded by other trees from the sides.

Intermediate. Trees are shorter, but their crowns extend into the general level of dominant and codominant trees, free from physical restrictions from above, but quite crowded on the sides.

Suppressed (overtopped). Crowns are entirely below the general level of dominant and codominant trees and are physically restricted from immediately above.

Trees in single-species stands expand their crowns horizontally and intercept more sunlight as they become larger. Consequently, they constantly compete with neighbors and either dominate (and eventually kill) them, or are dominated (and killed) by them.

This death from suppression is referred to as *natural thinning* or *self thinning* (Peet and Christensen, 1987). The dominant (survivor) then grows until it comes into contact with the next-closest tree, these trees compete, and eventually one dominates (and survives). Trees tend to become somewhat regularly spaced in a stand as they grow older. Stands sometimes have irregular waves of mortality separated by times of relatively little mortality of the remaining trees.

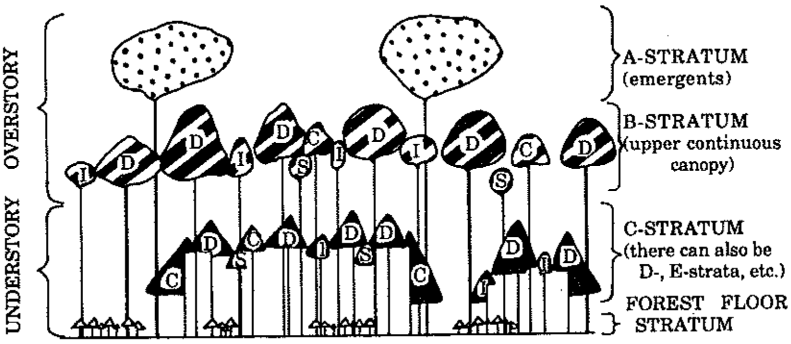


Figure 5.3 The relative positions of canopy (or crown) strata and crown classes. Canopy strata are the horizontal layers of tree crowns which are separate from higher and lower layers. Crown classes refer to trees within each stratum [D = dominant; C = codominant; I = intermediate; S = suppressed (overtopped), as defined in text]. Trees of each crown class can be found in each stratum. (*After Richards, 1952; Oliver, 1978a; D. M. Smith, 1984, 1986*).

Mixed-species stand development patterns. Most stands in North America contain more than one species, even where a single species has been planted. The growth patterns of mixed stands vary greatly, depending on environmental conditions and the physiological predispositions of the interacting species. Some general patterns emerge, however (Larson, 1992; Kelty et al., 1992).

Some tree species grow rapidly when young and dominate the stand. Species growing in this way are referred to as *pioneers*. A species such as western hemlock can either act as a pioneer species or dominate a stand much later after a major disturbance (Franklin and Dyrness, 1973; Atkinson and Zasoski, 1976). Other species—such as yellow poplars (Beck and Della-Bianca, 1981) or Douglas-firs (Isaac, 1940)—act as pioneers and continue to dominate the stand for many decades or centuries. Quaking aspens and grey birches behave as pioneers but have short natural life spans; they die even before becoming dominated by other species—having already set seeds for perpetuation of the species (Oliver, 1978*a*). Bitter, pin, and fire cherries behave as pioneers but are soon overtopped by other species and die in the understory after an initial period of domination (Marks, 1974; Stubblefield, 1978; Hibbs, 1983). Red maples and black birches can act as pioneers in mixed stands with red oaks and dominate the stand for the first few decades; then they become overtopped and continue to live for many decades in subordinate positions (Olson, 1965; Stephens and Waggoner, 1970; Oliver, 1978*a*). Where species are tolerant enough of shade to survive in subordinate positions completely overtopped by other species, the forest can have a *vertical stratification* of foliage layers (Richards, 1952; D. M. Smith, 1962, 1986; Grubb et al., 1963; Walter, 1971; A. P. Smith, 1973; Mueller-Dombois and Ellenberg, 1974; Beard, 1978; Oliver, 1978*a*; Yamakura, 1987).

Sometimes a species grows so much taller than the others in a mixed stand that it appears to emerge above them. Such stems are referred to as *emergents* (Fig. 5.3). Emergent trees are also found in tropical forests (Richards, 1952) and probably developed similarly as in temperate forests. The emergent stratum in a forest is also referred to as the *A-stratum* (Smith, 1984; Oliver, 1978*a*). An individual which acts as an emergent when intermixed with slower-growing species may appear in the upper continuous stratum—the *B-stratum*—when grown with more trees of the same species. Pioneer species such as aspens can be described as emergents before they die when they are isolated among shorter species. Isolated white pines in eastern hardwood forests often appear as emergents (Oliver, 1978*a*), as do isolated western larches in mixed coniferous stands in the northern Rocky Mountains (Cobb, 1988). Sometimes, isolated western hemlocks or Douglas-firs can act as occasional emergents in mixed stands dominated by red alders (Stubblefield and Oliver, 1978).

Two species can have similar enough growth patterns that they interact as a single species, with each asserting dominance and killing the other depending on subtle differences in ages, microsites, and spacings which give one or the other a competitive advantage. Loblolly and longleaf pines behave this way on certain sites in the southeastern United States. A slightly greater shade tolerance of the loblolly pines allows them to maintain fuller crowns and larger limbs and to grow larger in diameter than surrounding longleaf pines.

Different species growing together can also have quite different growth rates, resulting in a predictable pattern in which one species overtops the other. When the overtopped species is not able to live in the shade of the other, it dies (Lorimer, 1981). Douglas-firs usually become overtopped by red alders when the two are grown closely together. Since Douglas-firs cannot live in the shade of alders, the Douglas-firs die. Consequently, Douglas-firs are rarely found beneath an alder canopy (Stubblefield and Oliver, 1978).

If the overtopped species is able to survive in the reduced light beneath the dominating species, it can form a lower canopy stratum. Such stands are commonly referred to as *stratified, mixed-species stands.*

A dominating species can relegate other species to lower strata by shading them with high shade so that their height growth slows down, and by physically abrading the others' terminals during windstorms (Oliver, 1978*a*; Wierman and Oliver, 1979; Kelty, 1986; Larson, 1986). Once in the reduced light beneath the main canopy, the tree may survive but generally grows very slowly. Eventually the continued growth of the upper stratum trees and the curtailed growth of the lower make the dominating trees much larger (Fig. 2.1; D. M. Smith, 1962, 1986; Gibbs, 1963; Stubblefield and Oliver, 1978; Wierman and Oliver, 1979). Such stratified, single-cohort, mixed stands have been mistaken for uneven-aged stands which grew in a relay floristics pattern (Oliver, 1980; Johnson, 1981*a,b*). The smaller trees in the lower strata have been incorrectly assumed to be younger and in the process of overtaking the larger, apparently older stems in the upper stratum (Meyer and Stevenson, 1943; Phillips, 1959; Minckler, 1974; Mueller-Dombois and Ellenberg, 1974).

Progressively lower strata are referred to alphabetically (Fig. 5.3):

A-stratum (emergents). Trees above the highest continuous canopy

B-stratum. Upper continuous canopy

C-stratum, D-stratum, etc. (understory strata). Progressively lower strata beneath the B-stratum, although each one is not necessarily as continuous as the B-stratum; these strata may not be present

Forest floor stratum. Trees and shrubs very close to the soil surface; usually not more than 2 m (6 ft) tall.

During the initial brushy stage, all trees exist within the same stratum. They first appear to differentiate into dominant, codominant, intermediate, and suppressed crown classes (O'Hara et al., 1995). The crowns of some species can live beneath others. In these cases, the overtopped trees do not die; instead, they form lower strata beneath the B-stratum as differentiation proceeds (Smith, 1984).

Within each stratum, the trees tend to differentiate further into crown classes. It is important to distinguish between crown classes and strata. Crown classes can occur within each stratum as the trees differentiate. The behavior of each tree varies greatly depending on both its stratum and its crown class. For example, a suppressed shade-tolerant tree such as hemlock in the B-stratum of a pure hemlock stand will behave much differently upon release than would a dominant hemlock in the C-stratum of a mixed stand.

A stratum can contain one species or several species of similar height growth rates and shade tolerances. In both single and multicohort stands, trees of a single cohort can be found in more than one stratum. In a multicohort stand, a stratum can contain trees of one cohort or of several cohorts.

There are, of course, many variations of the stratification patterns. Sometimes a species has such a height growth advantage that it can stratify above other species under almost any conditions, as tulip poplars outgrow white oaks (O'Hara, 1986). In other cases—such as in mixtures of cherrybark oaks and sycamores (Clatterbuck et al., 1987; Oliver et al., 1989) or Douglas-firs and red alders (Stubblefield and Oliver, 1978)—rapid early height growth of one species can be offset by later sustained height growth of the other species. Which species dominates depends on whether the initial spacing is wide enough for the initially slow growing species to avoid being overtopped before it outgrows the other. Relatively few species occupy the upper strata even in stands containing many species, as has been found in deciduous forests in eastern North America (Putnam et al., 1960), as well as in tropical humid forests of the Amazon (Hubbell and Foster, 1986; Balslev and Renner, 1989; Hartshorn 1989*b*) and southeastern Asia (Ashton, 1989).

In a few cases a species can grow upward from a lower stratum in mixed, single-cohort stands after the structure of the stand appears stabilized. In these cases, the species emerging into the overstory generally is very tolerant of shade and has tough lateral branches. As winds cause the tree to sway, its branches rub and batter against those of other species and break them.

The numbers of species and individuals decline during the stem exclusion stage. This stage contains the fewest plant species (Alaback, 1982*a,b*; Oliver et al., 1985). Comparatively few species of animals are found in forests in this stage because there is very little living foliage near the forest floor to serve as food, cover, and habitat diversity. Some animals specifically live in these stands, however. The Kirtland's warbler makes its nests in these young jack pine stands in the Lake States (Walkinshaw, 1983).

Understory reinitiation stage

As the overstory grows older, new herbs, shrubs, and/or trees appear in the forest floor (McKinnon et al., 1935; Sprugel, 1976; Alaback, 1982*a,b*; Henderson, 1982; Oliver et al., 1985). These are usually species capable of living under low intensity, high shade and can be the same as or different from species in the overstory and those shrubs and herbs which grew during stand initiation. Less is known about the understory reinitiation and old growth stages.

Time of this understory reinitiation varies from only about 60 years in shade-intolerant southern pines (Peet and Christensen, 1987) or stressed stands to over 150 years in stands of shade-tolerant conifers (Oliver et al., 1985).

Why understory stems appear later in a stand's age and not earlier has not been extensively studied. Foresters have generally recognized it as a time when the overstory "loses its grip on the site" but have not explained the causal mechanisms. In some cases, more light reaches the understory as the suppressed overstory trees die and/or as the remaining trees become taller, sway more in wind, collide with neighboring trees, and abrade their outer branches (Sprugel, 1976). A higher carbon dioxide concentration near the forest floor may also increase the photosynthetic efficiency of understory plants. Pedogenic processes may create more growing space near the forest floor.

Some species seed continually into an understory even during the stem exclusion stage. The seeds may germinate, but the seedlings grow very little and are so small that they are not readily visible. These seedlings may die within a few years, creating an ephemeral understory of seedlings and creating wavelike populations as they seed in at periodic intervals of good seed years and stand conditions (Hett and Loucks, 1968, 1971, 1976; Hett, 1971).

Still other species have seeds which stay dormant in the soil for many years. These seeds can germinate after subtle changes in growing space during the understory reinitiation stage (Krugman et al., 1974; Marquis, 1975*a*; Osawa, 1986). Many shrub and herb stems initiate from rhizomes and root sprouts during the understory reinitiation stage.

Plants in the forest floor stratum in the understory reinitiation stage do not grow rapidly in the small amount of high-shade sunlight reaching them for photosynthesis. They grow even less in height relative to their total biomass accumulation than would trees growing in full sunlight. The reinitiated understory beneath a forest stays quite small, and thus visibly distinct from older trees in upper strata, for many years.

Lower strata of a single-cohort, mixed species stands can contain the same tolerant species as the advance regeneration. The stand can be mistakenly assumed to be all-aged, with each successively lower strata being younger because the trees are smaller; and the advance regeneration are sometimes assumed to be climax trees during the understory reinitiation stage, since these trees are expected to grow to the overstory (Braun, 1950; Scott, 1962).

In a literal sense, the stand would no longer be a single cohort after the forest floor stratum develops; and the development of the forest floor vegetation could be interpreted as "relay floristics" (Chapter 5). In practice, however, a stand is still considered to have a single cohort until younger trees from the forest floor grow much larger.

Barring intervening disturbances, the understory reinitiation stage can conclude within the first 100 years of the stand on highly stressed sites or can end when the stand is more than 500 years old if the overstory is shade-tolerant and vigorous.

The understory reinitiation stage generally contains more animal species than does the stem exclusion stage, but fewer than the stand initiation stage. Understory plants generally contain less starch nutrition for animals than those growing in full sunlight. Many resident animals are particularly adapted to growing in this stage and in the subsequent old growth stage, during which they utilize rotting wood and hollow trees for food and shelter. A large animal population can prolong the time before the understory reinitiation stage appears by browsing forest floor vegetation while it is very small.

Old growth stage

Older stands are often destroyed by periodic catastrophic disturbances. Where such disturbances do not occur, the overstory trees die from various agents (Peet, 1981; Peet and Christensen, 1987), such as winds or the accumulated effects of pathogens, droughts, or insects, which become more influential as trees age. The maximum life span of stand-grown trees can vary from less than 100 years for black willows to over 1,000 years for Douglas-firs and over 1,500 years for coastal redwoods. As overstory trees die, trees from the forest floor stratum of the understory reinitiation stage grow slowly into the overstory. Death of overstory trees and growing of understory trees are not caused by external factors. The autogenic process achieved when the trees regenerate and grow without the influence of external disturbances is referred to as the *old growth condition* (Thomas, 1979; Oliver, 1981; Runkle, 1981). This definition of old growth describes a process occurring by a unique development sequence. When the trees which invaded immediately after the disturbance have all died, the stand enters a *true old growth* stage. Young trees at first grow into the overstory, while some relic trees from a previous allogenic disturbance remain alive. Stands in this condition are referred to as *transition old growth* in this book.

As occurs in the transitions between other stages, the change from the understory reinitiation to the old growth stage may be gradual and spatially varied. Some areas may maintain distinct upper canopy and forest floor strata, while nearby areas where overstory trees have died can have a gradation of trees of different heights and diameters. The result is often a large variety of structures within a stand (Peet and Christensen, 1987).

The death of dominant trees in very old stands can be viewed as either allogenic or autogenic. Death of one or a few overstory trees acts like a small minor disturbance and permits a small, single-cohort stand to grow from advance regeneration and other regeneration mechanisms. Development of a forest by such minor disturbances has been referred to as *gap phase development* (Watt, 1947; Veblen and Stewart, 1982*a*; Pickett and White, 1985).

When part of the overstory begins to die during the transition from understory reinitiation to old growth stages, other overstory trees may weaken and the residual overstory may not last many more decades. Eventually, no trees are left alive which are relics of past disturbances other than minor disturbances caused by the deaths of individual overstory trees. At that time, all existing stems have begun from autogenic origins. Such a condition—a true old growth stand, in which the tree species live a long time—has very rarely been reached, because the probability of a large disturbance increases as the stand becomes older. Very old stands in the cold climates of Alaska and northern Canada may develop into organic bogs (muskegs) if they persist without a disturbance. Gradually, the trees die as forest floor organic matter increases, tying up nutrients, moisture, and oxygen (Heilman, 1966, 1968; Reiners et al., 1971; Vitousek and Reiners, 1975; Ugolini and Mann, 1979; Strang and Johnson, 1981). Such conditions may require over 1,000 years without a disturbance. In warmer climates with more rapid decomposition of organic matter, old growth stands maintain a variety of tolerant and intolerant tree species.

The term "old growth" has also been used to describe stands of specific structural characteristics, regardless of the autogenic or allogenic processes which led to these structures, as discussed later. Structural features include large, living old trees; large, dead standing trees; massive fallen logs; relatively open canopies with foliage in many layers; and diverse understories. Such structures are achieved by a variety of major and/or minor disturbance patterns in single- or mixed-species stands; therefore, they do not represent a unique stage of forest development

The old growth structure probably has the greatest horizontal and vertical variation in structure, with both large and small trees growing in separate and intermixed patches (Alaback, 1982*a,b*). The number of plant and animal species found is generally more than in most other structures (Manuwal and Huff, 1987) but less than in the open structure of the stand initiation stage. Some plants and animals are dependent on the rotting wood or other conditions found exclusively in these old growth forests for their survival. The spotted owl in the Pacific northwestern United States and the red-cockaded woodpecker in the Southeast, for example, seem to exist predominantly in forests with old growth structures.

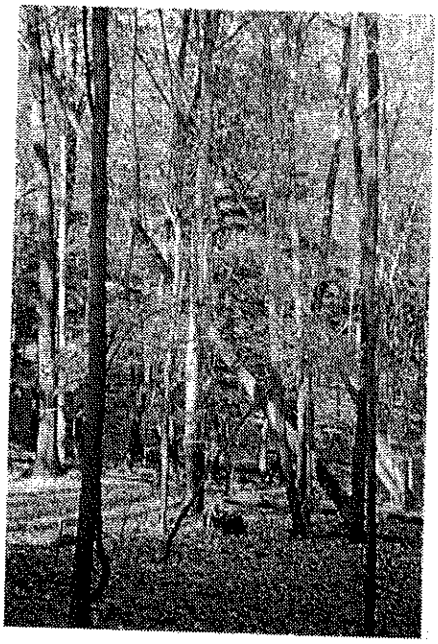
Development Patterns following Minor Disturbances

Overview

Minor disturbances that injure or kill some of the trees in a stand can occur between or instead of major disturbances. Like major disturbances, their type and frequency are determined by both allogenic and autogenic factors. Minor disturbances may reduce the frequency of major disturbances. For example, understory fires which reduce litter buildup prevent large conflagrations which kill all trees in a stand (Agee, 1981).

Windstorms which blow over some trees allow residual ones to grow more windfirm and hence more resistant to winds (Wiley, 1965).

(A)



(B)

Figure 5.4 Minor disturbances can create (A) multicohort stands of various structures or may even result in (B) a single-cohort stand. (A) This multicohort stand began after repeated, small disturbances—primarily cuttings—in northern Idaho. (B) This stand in northern Connecticut began in 1897, but a hurricane in 1938 blew down some trees and tilted others, releasing growing space (photo taken in 1972). The minor impact of the hurricane and the vigor of residual trees allowed the residual trees to grow and reoccupy the growing space, excluding a new cohort.

Minor disturbances create multicohort stands when new trees regenerate following the disturbance. A single-cohort stand can be maintained if a single-cohort stand was disturbed but the residual trees reoccupied the released growing space and excluded a new cohort from initiating or surviving (Fig. 5.4B). A minor disturbance can create a multicohort stand where the surviving trees are not vigorous or the disturbance is too severe to exclude a new cohort from entering (Fig. 5.4A).

Response of a stand to a minor disturbance depends on several factors: type of disturbance—fire, windstorm, human cutting, animal damage, or other; severity of the disturbance; location of damage in the stand—in the upper (A- and B-) strata, middle strata, or forest floor stratum; and vigor of the residual trees—their ability to grow after the disturbance. These factors are partly the result of stand development patterns and partly the result of influences external to the stand.

Species vary in ability to endure different disturbances and in ability to regenerate soon afterward. The different types of disturbances act as "environmental sieves," determining which species continue to constitute the stand. A light fire in an eastern mixed hardwood stand eliminates thin-barked species and thus increases the predominance of oaks and pines; in mixed conifer stands in the western United States, a light fire kills thin-barked spruces, firs, and hemlocks but allows Douglas-firs and pines to grow. Insect and disease outbreaks are selective for certain species; e.g., spruce budworm kills fir species (Blais, 1954); the chestnut blight killed chestnuts; and the white pine blister rust attacks white pine species (Hepting, 1971).

Disturbances lead to changes in a stand's structure, species composition, and tree shapes depending on which trees are left. Minor disturbances kill trees in the upper (A- and B-) strata, the middle strata, or the forest floor stratum. Surface fires kill forest floor trees and, when more intense, kill trees in higher strata (Viers, 1980*a,b*, 1982; Means, 1982). Lightning often kills the tallest trees—in the A- and B-strata. Insects and diseases which attack weakened trees often kill intermediate and suppressed trees in upper strata and more dominant crown classes in lower strata.

A disturbance's severity and the vigor of the surviving trees determine how many and what trees are killed, and thus how much growing space becomes available (Fig. 5.5). If a light, minor disturbance releases very little growing space, vigorous residual trees can refill it rapidly and prevent a new cohort from becoming established (Fig. 5.4B; Woods and Shanks, 1959; Hibbs, 1982). Such disturbances only stimulate a change in the growth rates of trees which survived. A slightly more severe minor disturbance may create a new cohort which soon becomes so suppressed that the trees remain in the forest floor stratum as advance regeneration. More severe minor disturbances release more growing space, allowing a new cohort of trees to grow as a major component of the stand. Vigor of surviving trees determines how rapidly they expand into released growing space. If they expand rapidly, the invasion or survival of a new cohort is prevented. Vigor is dependent on the trees' ages, their canopy strata and crown classes, their crowding, and the site conditions (Awaya et al., 1981).

In young stands in the early stem exclusion stage, most residual stems are vigorous enough to grow rapidly after a minor disturbance and reoccupy released growing space completely, maintaining a single-cohort stand. A partial disturbance in the stand initiation stage prolongs the time of plant invasion (Oliver and Stephens, 1977; Franklin and Hemstrom, 1981); however, it is difficult to determine which stems invade because of the second disturbance, and a second cohort is generally not recognized here. Dominant and codominant trees in any stratum generally respond more rapidly to minor disturbances than trees in lower crown classes do (Oliver and Murray, 1983). Consequently, ground fires or silvicultural thinnings from below tend not to create a new cohort, whereas "high-grade" logging, which eliminates the more dominant trees, favors establishment of a new cohort.

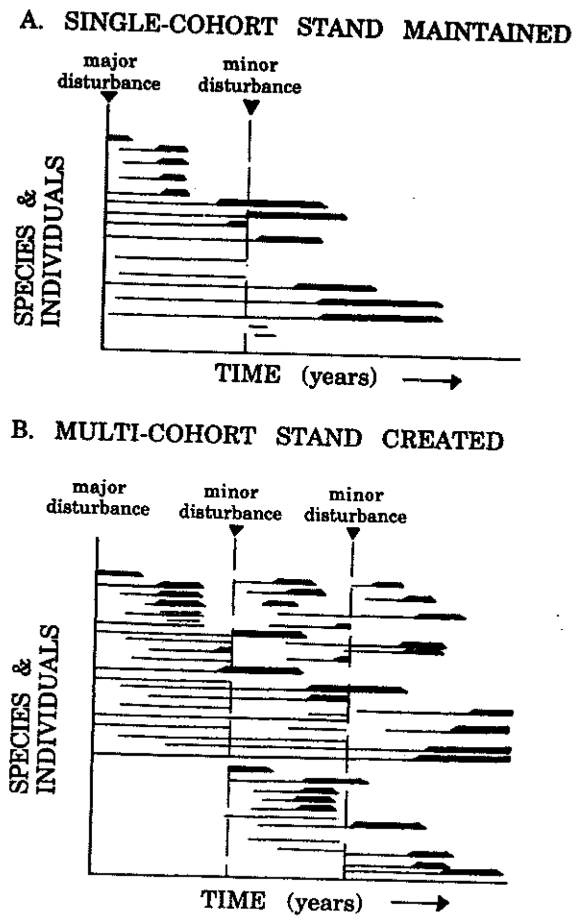


Figure 5.5 Minor disturbances (which do not kill all trees above the forest floor) may (A) allow any remaining trees to grow larger as they reoccupy the released growing space or (B) create new cohorts. New individuals enter primarily following disturbances, similarly to the initial floristics pattern of Fig. 5.1.

Development of multicohort stands

Development of multicohort stands is determined by the behavior of stand components following each minor disturbance. Following a minor disturbance, surviving trees expand and newly initiating ones invade and expand. There is a period of "free growth" during which both new and old plants grow into unoccupied growing space. Eventually, all growing space is reoccupied by existing stems and newly invading ones, even newer stems are excluded, and some existing stems are eliminated or severely suppressed through competition. In this way, there are also "stand initiation" and "stem exclusion" stages following minor disturbances.

Growth of new stems. After a minor disturbance, new stems begin growth from advance regeneration, stump and root sprouts, and buried and invading seeds, depending on the type of disturbance. Many shade-tolerant and -intolerant species initiate growth by utilizing stored energy in the seeds, roots, or stems of germinating, sprouting, or releasing trees.

As these new plants grow, they and the surviving older plants reoccupy the available growing space and begin competing. High shade from older trees slows height growth of the understory trees (Minckler and Woerheide, 1965). Shade cast by the overstory gives a competitive advantage to those species capable of surviving and growing most rapidly under partial, high shade (Toumey and Kienholz, 1931; Lutz, 1945; Bray 1956; Franklin and DeBell, 1973; Veblen et al., 1980).

Where numerous large trees survive the disturbance, regenerating species capable of living under deep high shade survive and have the growth advantage. The shade cast and the root competition increase as the overstory trees reoccupy newly available growing space. The understory trees first continue to slow in height growth. Then they begin to lose epinastic control and become flat-topped (Fig. 3.7). Less shade-tolerant species are soon eliminated from a new cohort when the residual overstory casts much shade. These intolerants generally do not survive the low light intensity even though they were able to begin growth. Finally, all understory trees die if the overstory excludes too much sunlight.

Response of the understory strata. Older trees in the lower (C- and D-) strata generally have flat-topped crowns characteristic of trees living in high shade (Fig. 3.7). After release, the terminal reasserts its dominance, producing a branching pattern characteristic of suppression and release—a cluster of branches, a crook, or a fork (Trimble, 1968*a*). Growth after release varies by species and depends on the tree's ability to withstand exposure and on the size of its crown (Marquis, 1981*a,b*). Dominant and codominant trees in lower strata often grow rapidly, since they have large living crowns capable of rapidly increasing their foliage. More suppressed trees continue growing slowly for a long time, until their photosynthetic surface area becomes large.

Growth of overstory trees. There is little visible effect on the upper strata if a minor disturbance injures or kills trees in the lower or forest floor strata, since the disturbance does not provide extra room for crown expansion. There is generally some increase in growth of these trees, since soil growing space becomes available.

A disturbance to some overstory trees can cause water sprouts and sun scalding on the remaining ones. Soon after release, foliage increases throughout the crowns of dominant and codominant trees. Diameter and height growth are also rapid. Intermediate and suppressed trees in all strata increase foliage and height and diameter growth relatively little, since most photosynthate is used for maintenance respiration.

The limbs of species with weak epinastic control rapidly grow outward into sunlight if a neighboring tree dies. Species with strong epinastic control maintain symmetric crowns, and branch growth does not increase. Even when overstory branch growth does not increase after a disturbance, light reaching lower strata dramatically declines as foliage increases within the overstory crowns. In temperate forests sunlight never comes from directly overhead, and long, dense crowns reduce light to the understory even when adjacent crowns are not touching.

The understory can reduce the vigor of overstory trees when a minor disturbance allows a vigorous understory to develop beneath a scattered overstory. The vigorous understory often outcompetes the overstory for root growing space—moisture and nutrients. This mechanism may be responsible for the susceptibility of loblolly pines to the southern pine beetle (*Dendroctonus frontalis*) on clay soils in the southeastern United States as hardwoods grow in the understory. Similarly, large areas of mixed conifers are dying from *Armellea obscura* in mixed conifer forests in the eastern Cascades of Washington. *Armellea* attacks weakened trees. Exclusion of ground fires in recent decades has allowed grand firs to grow into the understories of these stands and possibly weaken the overstory trees.

Overview of Forest Development Patterns

Forests are frequently subjected to disturbances. Trees in young, vigorous stands can respond to light, minor disturbances by rapidly expanding into available growing space and thus maintain a single-cohort stand. Stands resembling the understory reinitiation stage may begin after a minor disturbance if the existing trees are too old to exclude the new stems but vigorous enough to prevent them from growing large. Trees in the old growth stage behave like those responding to minor disturbances.

Both initial and relay floristics patterns occur at various times in forest development. The shifting dominance among species during the stem initiation, exclusion, and reinitiation stages is not the result of relay floristics. Rather, the initial floristics pattern occurs after a disturbance, with all species and individuals invading during a relatively short interval. Once established, they exclude plants arriving later. Later development of shade-tolerant species in the understory during understory reinitiation follows the relay floristics pattern. This invasion could be interpreted as directional development of a stand toward specific species compositions, since trees invading during understory reinitiation are generally shade-tolerant and only a limited number of such species exist in each region. Actually, the patterns are the casual result of competitive interactions rather than any grand design or external force on forest development.

Structural vs Process Approaches to Stand Classification

Much of this book describes the processes of change. For ease of discussion, the processes have been classified into discrete development stages where different interactions are dominant. The processes can lead to various stand structural features.

Various stand structures have also been observed and classified as discrete conditions—or structures—independent of the processes leading to the structures. Because each structure is generally, but not always, the result of processes occurring in each development stage, the same terms have been used to classify both processes and stand structures (e.g., Oliver, 1992*a,b,c*).

Confusion has arisen because each of the various stand structure classes are wrongly assumed to be *uniquely* achieved in a single development stage; and the confusion is especially strong when development stages and structures have the same names. Specific, defined stand structures can often be achieved by several processes and in several development stages; and in some cases, a stand structure with a given name can not be achieved in a developmental stage with the same name. For example, "old growth" is defined both as a process (Oliver, 1981) and a development stage (Franklin et al., 1981, 1986; Hunter, 1990). As a development stage, it defines a stand's condition when disturbances have been absent for so long that none of the trees which invaded during the "stand initiation" stage following the disturbance are still alive. As a structure, "old growth" has different definitions and usually describes large trees, multiple species, and some component of rotting wood, snags, and logs. In many cases, the "old growth" *structure* would not exist in stands in the "old growth" *development stage.* For example, "old growth" longleaf pine stands (structural definition) suitable for the red cockaded woodpecker habitat are generally found in stands in the "understory reinitiation" development stage or in stands impacted by minor disturbances. If longleaf stands were allowed to grow to the "old growth" development stage, they would probably not be suitable habitat for the red cockaded woodpecker. Similarly, most stands with the "old growth" *structure* in the Pacific Northwest (Franklin et al., 1986) are not in the "old growth" *development stage*; rather, they are the result of minor disturbances or specific growth patterns in much younger stands (Newton and Cole, 1987; McComb et al. 1993; Oliver et al. 1994*b*).

This book will follow the general practice of referring to such terms as "stand initiation," "stem exclusion," "understory reinitiation," and "old growth" as both structures and development stages. It is important to realize that the two are not the same, and this book will distinguish between the two wherever there appears to be ambiguity. Other structural classifications have also been used, usually with more structures defined. Which and how many structures are defined depends on the objectives of management.

Forests generally are suited for various commodity and non-commodity values based on their structural condition, rather than the development stage they are in. For example, large trees with knot-free wood are valuable regardless of whether they are found in stands in the "stem exclusion," "understory reinitiation," or "old growth" development stage or in a multicohort stand. Certain animal species are found where there is a large vertical distribution of foliage, which can be found in stratified, mixed species stands in the stem exclusion development stage, as well as in older stages.

Disturbance Frequency and General Forest Type

Disturbances generally do not occur randomly within a region. Instead, they often occur in waves during times of unusual weather conditions, insect outbreaks, fuel buildups, or economic pressures (in cases of human disturbances). Within a region, each severe past disturbance has created many stands or cohorts (within multicohort stands) which grow and become predisposed to later disturbances (Fig. 4.1) of a given magnitude at approximately the same time. When a later regional disturbance occurs, the stands or cohorts create another wave of one cohort distributed throughout many single and multicohort stands. Consequently, ages of stands or cohorts are often not randomly or uniformly distributed throughout a region. Rather, stands and cohorts are often of characteristic ages dating from regionwide disturbances.

Different structural features are commonly found across a landscape in certain topographic positions (Camp, 1995) because of the effects of topography on disturbance patterns and growth rates. Variation in disturbance impacts across the landscape has generally created a variety of stand structures following each disturbance. Some areas were sheltered for topographic or edaphic reasons and were subject to a minor disturbance, if disturbed at all; other areas were frequently subjected to stand-replacing disturbances. Following the disturbance, there was a variety of stand development patterns occurring as different areas grew to single and multicohort stands (Yamamoto, 1992, 1993; Cao, 1995; Mizunaga, 1995), . The variety of structures became more diverse with time because stands grew differently on soils with different productivities, even if the disturbance had left them with initially similar structures.

The types of disturbances are also somewhat characteristic of each region, favoring particular regeneration mechanisms and certain forest species compositions within each soil and climatic area. The common species compositions and ages of stands and cohorts over regions give them similar physiognomies which change slowly with time. Before recent, rapid communication and accumulation of historical records proved otherwise, forest types were assumed to be permanent and stable on an area, because changes occur so slowly.

Figure 5.6 shows how types and frequencies of large disturbances can determine the stand patterns over broad forest regions of similar soil and climate. Figure 5.2 shows the relative time after a major disturbance during which each species (or group of species) is dominant. Figure 5.6A shows the pattern of dominance of each species in an area where major disturbances occurred at equal time intervals. If the disturbance was of a given severity (shown as "X" in Fig. 5.6), the species shown in Fig. 5.2 would be favored. If a more severe or less severe disturbance occurred ("Y" in Fig. 5.6), different species would be favored and the forest composition would be different until the next disturbance. If disturbances were more frequent (Fig. 5.6B), the predominant forest types would shift to species which dominated when the stands were younger. The probability of finding a particular forest type in a large area, and hence the dominant type of the area, is therefore directly related to both frequency and type of disturbance. Minor disturbances would similarly influence the pattern, depending on their type and severity, except not all trees would be eliminated at each disturbance. Consequently, each cohort would be characteristic of the type and frequency of the disturbance, as well as its magnitude.

Figure 5.6 also shows how different stands can achieve a targeted structure at different times and in different development stages. If stands with a large vertical distribution of canopy strata were desired, the structure can be achieved quite readily during the stem exclusion development stage and maintained thereafter in stands containing species "A" through "D." On the other hand stands containing species "E" and "F" may have only one stratum and may remain in the "stem exclusion" and "understory reinitiation" development stages for much longer; consequently, the targeted stand structure would not be achieved in these stands for a very long time--if at all.

Where disturbances are randomly scattered in space over a large area, travel across the region can be substituted for time in determining the probability of occurrence of a given forest type. Pulselike patterns have also been suggested by others (Odum, 1969; Loucks, 1970; Heinselman, 1973; Wright, 1974; Whittaker, 1975; Connell, 1978; Oliver et al., 1985).

Applications to Management

Management of stands does not alter a "natural direction" of forest development, since no single obligatory direction occurs. Repeatable patterns which emerge from similar disturbance regimes on similar sites are consequences of plant interactions, not driving forces.

Most commodity and non-commodity management objectives are better expressed in target structures, rather than in processes. For example, if an "old growth" structure is desired, this *structure* is better explicitly stated, rather than stating a desire to follow the *process* of avoiding all disturbances to a stand—thus achieving (or trying to achieve) the old growth developmental stage. As discussed above, following the process of avoiding disturbances may not achieve the old growth structure—and usually not as rapidly as through other means. Understanding the processes of development, the development stages, and how different processes can lead to different structures will allow the silviculturist to design management activities which will achieve the desired structures as efficiently as possible.

Silvicultural operations are tied to the stages of stand development. Applying operations during an inappropriate stage makes them much more difficult and costly or virtually impossible to implement successfully. Some operations may not be necessary if the natural stages of development are known and anticipated. For example, since advance regeneration becomes established during the understory reinitiation stage, planning on this form of regeneration of a desirable species can avoid costly planting of seedlings (e.g., Seymour, 1992).

Within limits, however, the time a stand appears in any stage can be prolonged or shortened with appropriate management. Single cohort stands can be moved rapidly through the initiation stage by planting trees and controlling weeds to stimulate tree growth, and this stage can be prolonged by removing some trees. The stem exclusion stage can be prolonged with judicious, light thinnings of intermediate and suppressed overstory trees, and shortened by heavy thinnings which allow an understory to develop.

The understory reinitiation stage can also be prolonged by light thinnings which stabilize the overstory, or shortened by heavy thinnings which allow the advance regeneration to grow upward, creating a structure resembling old growth.

Operations such as weeding and planting or interplanting to alter the species composition of the new stand are most efficient during the stand initiation stage. Trying to adjust the species composition by adding species during the stem exclusion stage is nearly impossible. If the desired species stratifies above the undesired one, thinning operations which adjust to the species composition which occurs naturally during the stem exclusion stage may not be necessary.

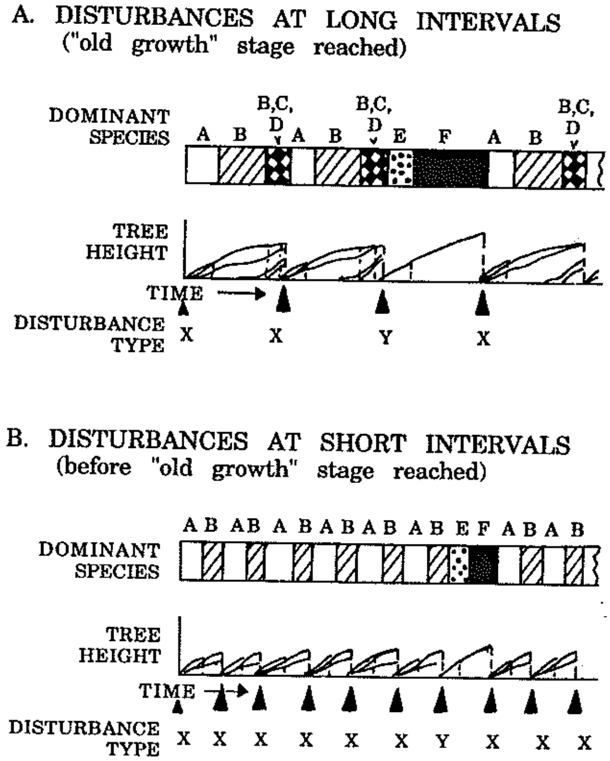


Figure 5.6 Changes in forest composition over many centuries, based on development patterns in Fig. 5.2 and following periodic disturbances of type X. Sloping lines represent tree height growth patterns shown in Fig. 5.2. (A) The forest is dominated with species B (pure or mixed with C and D) if disturbances are infrequent enough to allow all four development stages. The forest shifts to being dominated by species E and F after a different disturbance (type Y) favors other species. (B) The forest is equally dominated by species A and B when disturbances of type X occur more frequently. Again, a type Y disturbance is followed by a predominance of species E and F. (*Oliver, 1981.*) (See "source notes.")

Stand structures reached at different development stages are susceptible to certain disturbances. The forester can anticipate dangerous conditions at each stage of development. Both fires and insect attacks tend to occur during the stem exclusion stage; activities such as thinning can reduce or increase the risk of fires or insects. Thinning which is planned for a time early in the stem exclusion stage may need to incorporate extra slash disposal measures which may not be necessary later in the development of the stand. Progressively older stands become more susceptible to windthrow as the trees grow taller.

Each structure generally has both commodity and non-commodity values (Oliver 1992*a*). For example, mushrooms and berries can be plentiful in the stand initiation structure; rapid tree volume growth (per hectare) occurs in the stem exclusion structure; advance regeneration, mushrooms, floral greens, some medicinal plants, and high quality timber are often found in the "old growth" structure. In addition, each forest structure is necessary for some species to survive. Some structures are more or less aesthetically pleasing and affect the recreational value of the stand.

Other stand structures have value by their contribution to the habitat of certain wildlife species. Different wildlife species require different stand structures, so different species are more abundant in each development stage. Some wildlife require a group of stands in different stages, and some development stages may or may not be desirable depending on the structure of surrounding stands in the forest. Because there is no single structure which will provide all values at all times, the various values can be maintained by coordinating stands across a landscape so that a proportion of the landscape is maintained in each desired structure at all times (Boyce, 1985, 1995; Oliver, 1992*a,b,c*; Oliver et al. 1992). Maintaining the various structures requires a coordination of silvicultural activities among stands and through time as the structures change through growth and disturbances. Several technical tools have been developed to allow this coordination to occur (Boyce, 1985, 1995; Sessions and Sessions, 1992; Oliver and McCarter, 1995), and various incentives (Lippke and Oliver, 1993) and portfolio approaches to management (Oliver, 1994*a,b*) have been developed to make landscape management as efficient as possible.

Managing landscapes to provide and maintain all structures using silvicultural activities will generally cause less extreme shifts in structures and species populations than would occur if large areas were set aside as reserves and excluded from human activities (discussed in Chapter 4).

Forests can develop in only certain patterns, depending on their present conditions. A stand in the stem exclusion structure may take many decades to appear as an old growth structure, even with appropriate silvicultural manipulations; a single-cohort stand in the stem exclusion stage takes many decades to develop as a stand with three or more cohorts; and a stand with several cohorts takes many years to revert to a single-cohort stand in the stem exclusion structure.

Various studies have proposed efficient ways to achieve desired structures (Newton and Cole, 1987; McComb et al., 1993; Oliver 1994d; Oliver et al., 1994a). The silviculturist can take advantage of different growth rates on different sites to achieve the desired structures as rapidly as possible.

Thinning, pruning, harvest, prescribed fire, or other silvicultural activities often detract from the stand's appearance for several years afterward, until the responding growth begins creating the desired structure. Because of the commonly unattractive early appearance, the silviculturist needs discipline and diagnostic tools to help ensure that the correct actions have been done to achieve the results. Some of these tools are described in Chapter 15.

Stand structures can be defined in many ways, depending on the objectives, the region, and other biological and non-biological factors. They have been defined several ways:
—tree size classes (e.g., seedling-sapling, pole, small sawtimber, large sawtimber);
—modifications and variations of the development stages of Figure 5.2;
—other definitions (e.g., "savanna," "open," "ancient," and others).
Other classifications are currently being developed as more emhasis is being placed on managing for a variety of objectives. It is premature and probably inappropriate to set standard structures for universal use. Eventually, coventional classification systems may become accepted for various regions, objectives, and/or management organizations.

Because structures often take time to develop, silvicultural practices often focus on actively encouraging stands to develop toward those structures in short supply, recognizing that the stands will become increasingly more valuable as they accumulate attributes of the desired structure.

The precise target amount of the various structures across the landscape is often not an immediate concern. Historical records and some understanding of the structure needs to provide the different values can give a preliminary indication of *which* structures are to be maintained. Where there is too little of one stand structure, there will be too much of other structures; and most forested landscapes in the world have quite disproportionate areas in the different stand structures. For several decades, silvicultural activities can focus on converting the stand structures which are extremely plentiful to those in extremely short supply; during this time, more detailed studies and adaptive management approaches (see "Applications to Management," Chapter 15) can determine more precisely the target amounts of each structure needed. Fractal geometry and other geometric tools may prove useful in managing different spatial patterns at different scales (Lorimer et al., 1994; McQuillan, 1995).

Disturbances such as wind or agricultural land abandonment often cover large areas, creating many stands (or cohorts within stands) in very similar stages of stand development, with similar structures, and with similar species compositions. Where stands are similar over large areas, returns from the forests and the silvicultural operations needed are limited by the little variation in development stages. There is a danger that silvicultural innovation can become stifled because the development of these similar stands occurs over a long time. As a result, foresters tend to do what has been done in the past and what has worked in the past. As stands reach more advanced stages of development or are harvested and stands with new development patterns emerge, new silvicultural problems and opportunities will exist. Foresters must adapt to the changes and devise prescriptions which reflect the changes in stand development.

CHADWICK D. OLIVER
BRUCE C. LARSON

FOREST STAND DYNAMICS

UPDATE EDITION