Forest Dynamics

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Introduction

Forest stand dynamics (stand dynamics, forest development, forest succession) integrates plant community and population ecology, silvics, physiology, morphology, and knowledge about biotic and abiotic disturbance events and regimes. Forest stand dynamics informs silviculture since it allows predictions of the pathways along which forests could develop given initial conditions, growth, silvicultural operations, natural disturbances, regeneration, and other natural and human influences on the system. Practicing foresters and applied ecologists require a thorough understanding of stand dynamics to predict how stands will change, to determine what values they will provide and when, and to manipulate them as appropriate to ensure they provide the desired flow of values over time. Forest stand dynamics lays the groundwork for landscape management, in which the changes to many stands are coordinated across the landscape and through time.

The defining scale of forest stand dynamics is the individual stand – a relatively homogeneous area of vegetation, soils, climate, and disturbance history that can be easily discerned from an aerial photograph. The primary foci at this scale are the interactions that occur among individual plants and between plants and abiotic factors. Explicit in the term is that these interactions occur in time; forests are dynamic and can be expected to change, albeit in predictable ways. Despite the variety of climates, soils, and evolutionary backgrounds of forests in different parts of the world, they follow remarkably similar patterns of stand dynamics in those temperate, boreal, and tropical forests where stand dynamics have been studied. These similarities probably arise because their physiological similarities leads trees to follow a 'uniformity of processes' in their interactions.

Stand Structures and Development (Silvicultural) Pathways

A useful conceptualization of forest stand dynamics is that, over time, the structure of a stand changes (**Figure 1**). Stand structure refers to the spatial attributes of the living and dead plants and plant components in the stand: the species, sizes, and spatial distributions of living and dead trees and other plants and their components. These structures are helpful in identifying the suitability of the forest for different values – such as habitats for different species, timber quality, and recreation. Stand structure also contributes to risks of fires, insects, and windstorms. The sequence of structures that a particular stand moves among is described as its 'development pathway' or 'silvicultural pathway' (**Figure 2**). The pathway followed by a stand is determined by a number of factors; stands are not predestined to follow a single, specific pathway. Furthermore, pathways are not unidirectional and do not culminate in a fixed endpoint, although a now outdated ecological paradigm previously described forest succession as a fixed, unidirectional pathway towards a stable condition termed the 'climax' forest.

While it is possible – and perhaps sometimes useful – to differentiate many stand structures for a particular forest type, a relatively small number are sufficient to provide a structural overview of a majority of the world's forests. This article refers to five structures commonly encountered as forests develop. Some structures may not occur in some forest types, and more detailed structural classification systems may better explain certain objectives. The five structures used in this article are termed open, dense, understory, complex, and savanna (**Figure 1**). Subsets of these structures can be used to depict the different pathways a stand can follow. As an example of one pathway, a stand initiating after a major (stand-replacing) disturbance and with abundant regeneration would develop from an open structure to one characterized by density-dependent mortality (dense structure). Eventually the stand might develop an understory. Then, a partial disturbance might leave only a few large trees (savanna). As younger trees establish and grow beneath the sparse overstory, the complex structure could result.

One area of expertise that distinguishes professional foresters, especially silviculturists, is the ability to determine the pathway a stand is currently following, predict alternate pathways the stand could follow given various natural disturbances or silvicultural operations, and prescribe silvicultural operations that direct the stand along a desired pathway. The pathways and structural stages are most easily predicted and managed by first understanding the causes of changes in structures along the different pathways.

Ecological Processes Underlying Stand Dynamics

Stands contain a variety of organisms that happen to occur together at the time of observation. Paleoecological research indicates that different trees and

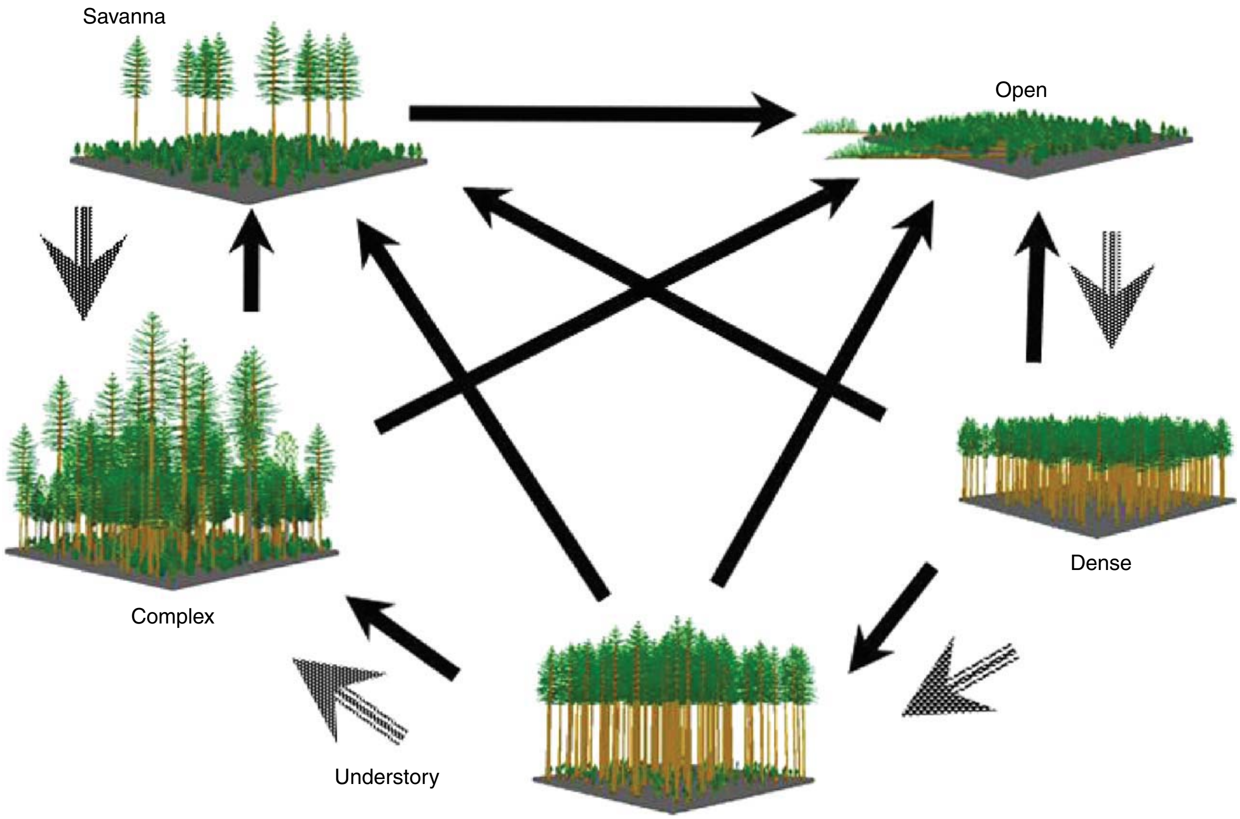

Figure 1 Stands change in structure over time with growth (large, striped arrows) and disturbances (solid black arrows). A robust classification suitable for many forests and purposes are the five structures shown here; however, different structure classifications may be better for certain purposes. © Professor Chadwick Oliver.

other organisms have lived together for only a few hundred or thousand years, have migrated from different locations at different rates, and in many instances are continuing to migrate to new locations. Different organisms evolve at a variety of timescales, with new generations occurring several times each year in insects but only every hundred years or more in trees. Because evolution in trees occurs over very long timescales, trees are slow to evolve mutualistic relationships with their associated species. Most evidence suggests that the dominant interactions among trees are best explained in terms of competition. Trees and other green plants require the same basic factors for survival and growth – light, moisture, nutrients, and warmth. In general, all tree species generally grow best when they receive these factors in the same, relatively narrow ranges of concentration, rather than having diversified into growing best at different ranges. For example, nearly all tree species grow best in full sunlight, under similar soil moisture regimes, and at approximately the same temperatures. A primary difference among species is that various tree species have evolved different abilities to tolerate (survive at) low levels of one or more of these factors. Species that tolerate a wide range of conditions are termed site insensitive and are considered to have wide ecological amplitudes. Species that have a low tolerance for growth factor limitations are termed site sensitive. In general, relative tolerance or intolerance is specified with respect to a particular growth factor, and tolerances such as shade or drought tolerance or intolerance in species are commonly described (**Figure 3**).

Different growth factors, or resources, needed by trees are frequently limited in the natural environment. Trees compete for these limited resources, with different individuals and species gaining a competitive advantage depending on whether they were first to access the growth factors and on whether they can efficiently use the specific range of growth factors found on the site at a given time. Different growth factors become limiting at different times of the day, month, year, and stand development stage. Sometimes it is the interaction of growth factors that determines whether growth is limiting. It is convenient to refer to the net presence of the factors required for growth as the available 'growing space' within a stand. Growing space fluctuates with seasonal variations in rainfall, temperature, and other factors. Growing space is referred to as 'occupied'

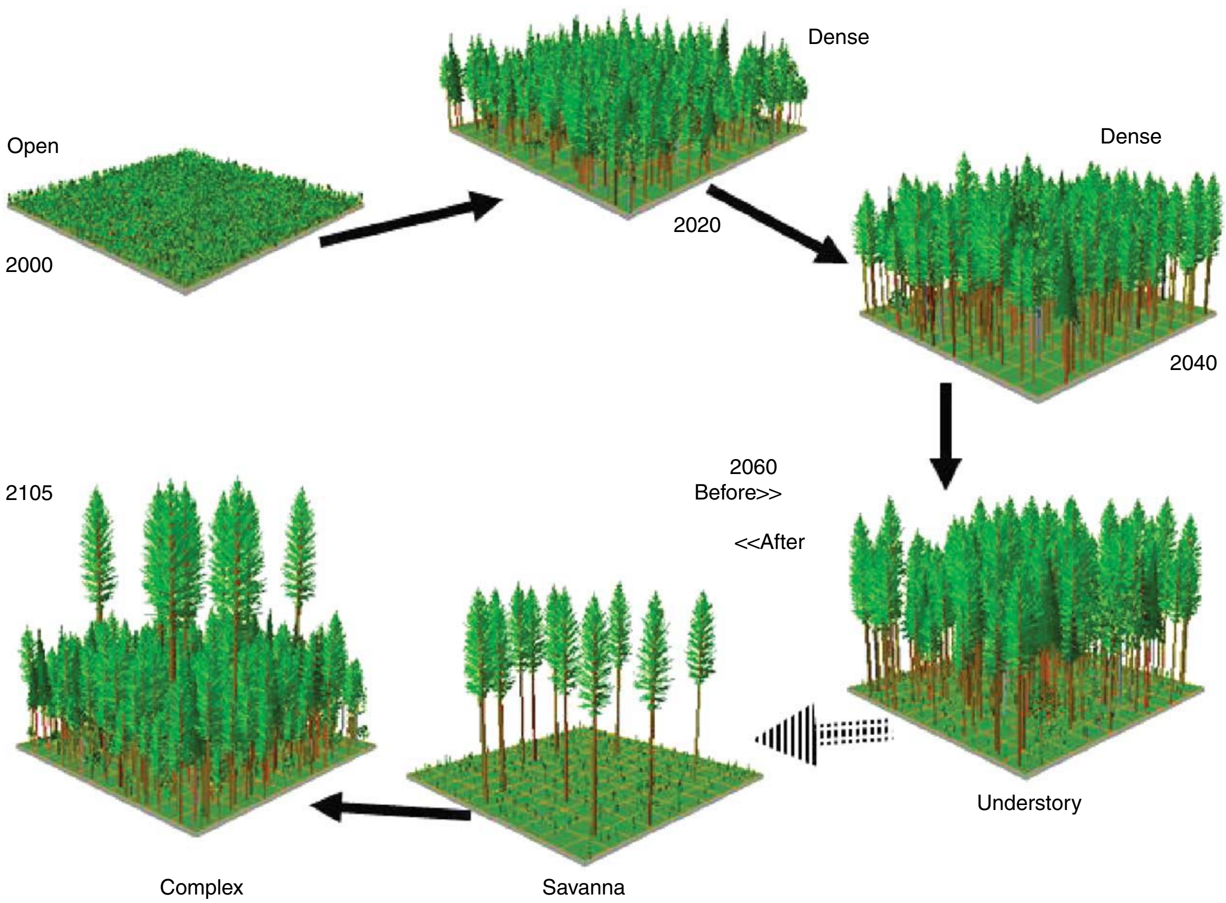

Figure 2 The change in a stand over time caused by growth, natural disturbances, and silvicultural operations is its development pathway or silvicultural pathway. The pathway is depicted here by the stand's changes in structures. This stand modeled here began after a stand-replacing disturbance in 1995, and was shelterwood treated in 2080. A stand can potentially follow many different pathways. © Professor Chadwick Oliver.

when a tree or other plant's roots or leaves are utilizing the moisture or light growing space and excluding other plants from utilizing it. Growing space is available when it is not occupied, such as immediately after a disturbance or during early spring in a field previously occupied by annual plants.

Trees compete with each other over available growing space. The ability to compete successfully is a result of the ability of an individual tree to capture this growing space. Trees that compete successfully become the dominant trees in the stand. Trees that lose the competition for growing space are eliminated or relegated to subordinate positions if they can tolerant less-than-optimal ranges of the growing space. The latter instance is more commonly found where competition for growing space occurs among trees of different species. Competitive ability under a given circumstance integrates species' physiological traits, such as rapid juvenile growth or early germination, with the environment.

Stand dynamics is also concerned with the impacts of natural and human disturbances on the ecological processes, pathways, and structural characteristics of stands. All forests are impacted by disturbances, with different regions of the world characterized by different disturbance regimes. A disturbance regime refers to the integration of the typical kinds, magnitudes, frequencies, and sizes of disturbances impacting a region. In general, disturbances that occur frequently are of less magnitude than disturbances that rarely occur. On one end of the disturbance spectrum are infrequent events such as volcanic eruptions or continental glacial expansions. Other disturbances include hurricanes, landslides, avalanches, fires, ice storms, and insect outbreaks. Some frequent disturbances (at least in some locations) include thunderstorms, windstorms, livestock grazing, and endemic insect and pathogen activity.

Disturbances affect forests by physically deforming or killing trees and other plants and by improving or degrading the soils, depending on specific characteristics of the disturbance. Growing space becomes available when trees are killed; following a disturbance residual and newly initiating trees

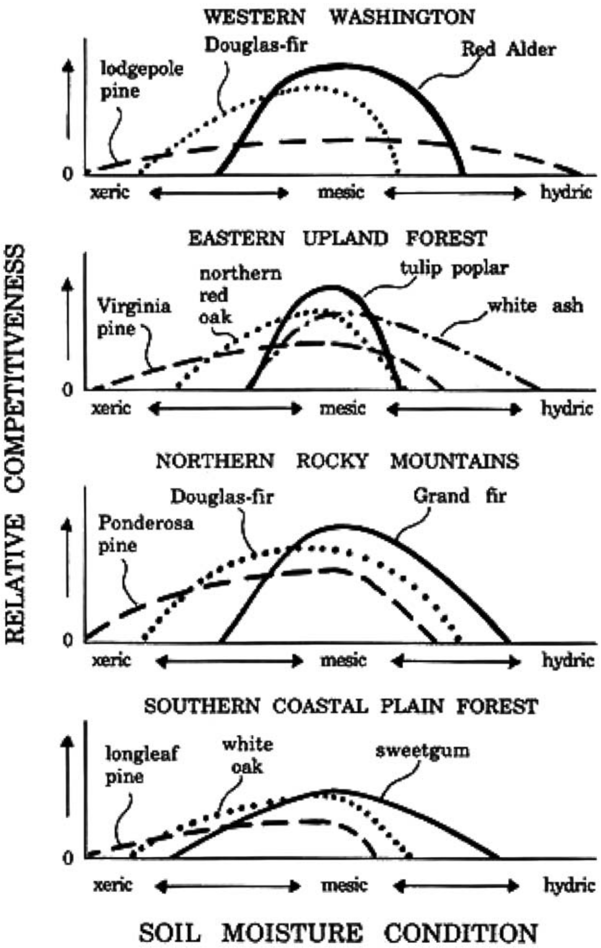

Figure 3 Schematic of relative growth (and competitiveness) of selected species growing together in four forest types found in the USA. All species grow most vigorously under optimum (mesic) conditions, but each species is found where it can outcompete other species, or where other species, cannot grow at all. Reprinted from Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn, Copyright © John Wiley & Sons Inc. Reprinted by permission of John Wiley & Sons Inc.

reoccupy this growing space. The forest that develops following the disturbance could have a similar or very different structure than the preceding one.

Processes, Stand Development, and Development Stages

As a stand develops, many interactions, or processes, occur among trees and between trees and the environment, with different processes becoming more dominant influences as stands change. It is useful, therefore, to divide the processes of stand dynamics into development stages that reflect the dominance of different processes. Not surprisingly, these development stages are similar to, but not identical with, the stand structures. Four development stages are commonly recognized, but like the stand structures can, if required, be further subdivided. These development stages are shown in **Figure 4** and are discussed below.

Stand initiation Following a stand-replacing (top left, **Figure 4**) or partial (bottom left, **Figure 4**) disturbance, growing space becomes available. Newly initiating trees, other plants, and surviving residual trees can expand to capture this growing space. Where surviving trees are absent, weak, or infrequent, the growing space is primarily occupied by newly initiating plants. Plants, including trees, have a variety of regeneration mechanisms that confer a competitive advantage depending on disturbance type and magnitude. For example, toppling of mature trees by a windstorm can release small advance regeneration of shade-tolerant species growing in the understory. Because this advance regeneration is already established and has a developed root system, species with this regeneration mechanism have a competitive advantage over species that must regenerate from seeds. Fires consume organic matter (and frequently, advance regeneration) on the forest floor, leaving a nutrient-enriched seedbed that favors species with light, windblown seeds or species that can resprout from the root collar or other underground structure. The different regeneration mechanisms can be listed in a gradient according to their relative advantage following disturbances of different magnitudes. This gradient, and examples of species with different regeneration mechanisms, is shown in **Figure 5**. Ages of newly sprouting trees or advance regeneration released by a disturbance are conventionally considered from the time of release (when the stem begins to grow beyond the forest floor level) rather than from the date of germination. Trees that initiate following a specific disturbance are considered a 'cohort,' regardless of whether they initiated from seed germination, sprouts, advance regeneration, or other mechanisms. On very poor sites, or on sites where seedling establishment is slow, there can be a wide range of ages within a single cohort.

Trees and other plants continue to invade during the stand initiation stage until the growing space is refilled with perennial trees, shrubs, and/or herbs. Refilling the growing space can take many decades where the site (soils and climate) is poor and the only regeneration mechanism is primarily from seeds having a distant source. Alternatively, it can take less than 5 years where the site allows rapid growth and preexisting advance regeneration or sprouts are present at the time of the disturbance. During stand initiation, trees compete for growing space with annual and perennial herbs and shrubs, creating a great diversity of potential interactions.

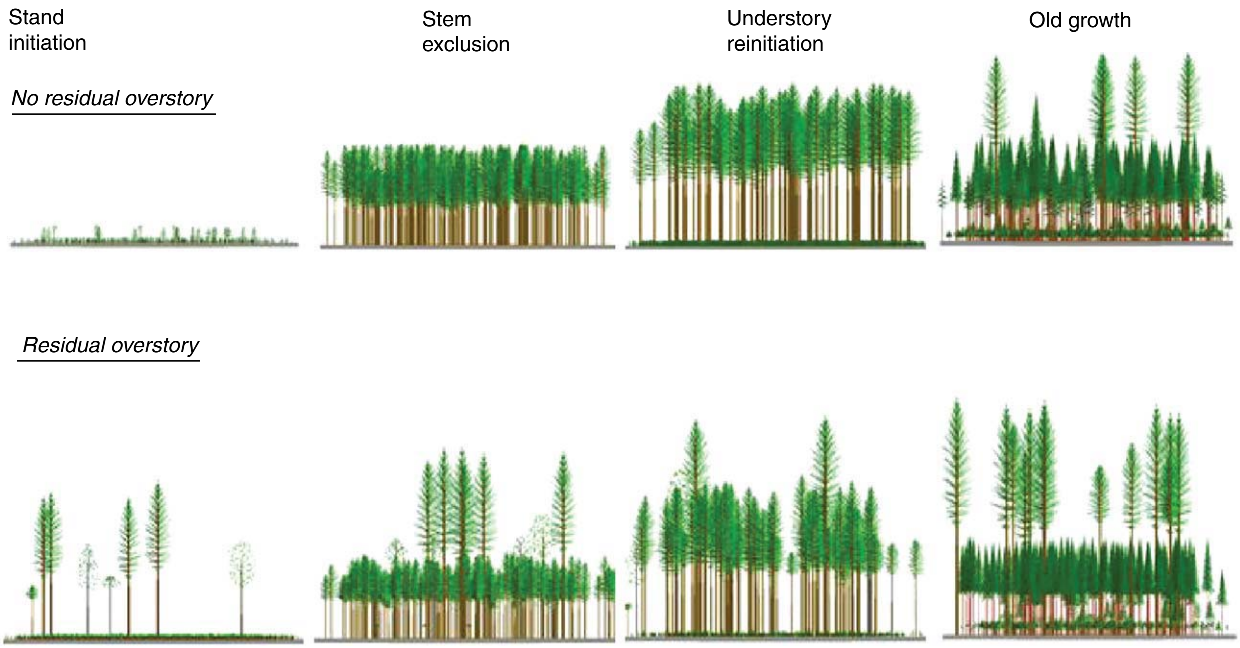

Figure 4 Stages of forest development over time (left to right) when no disturbances occur following the initial one (occurring just before stage at far left). Different ecological processes are dominant during the different stages. Top: the stages when no residual trees were left following the initial disturbance. Bottom: the stages when some residual trees are left following the initial disturbance. © Professor Chadwick Oliver.

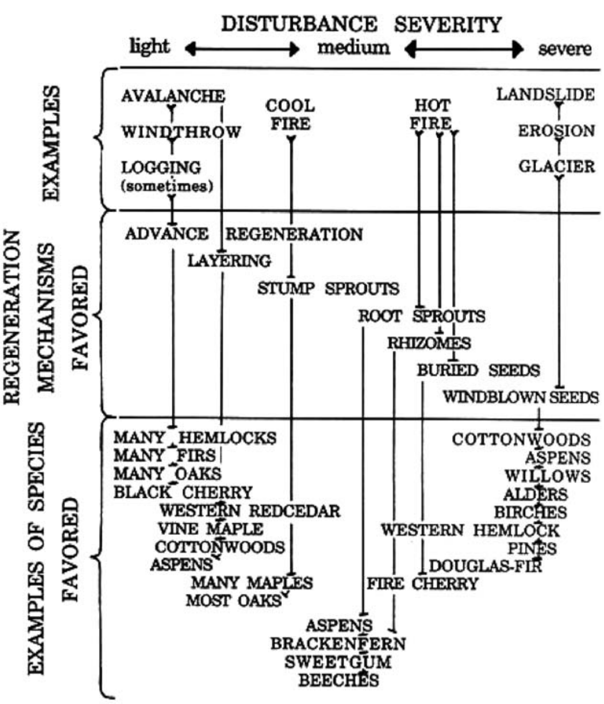

Figure 5 Disturbance 'severity' is here listed as a gradient according to how much of the understory, forest floor, and soil is destroyed. Different forms of sexual and/or asexual regeneration have competitive advantages depending on the severity of the disturbance. Species listed occur in different forest types in the USA. Reprinted from Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn, Copyright © John Wiley & Sons Inc. Reprinted by permission of John Wiley & Sons Inc.

The species, or groups of species, that gain the competitive advantage during stand initiation can dominate the growing space during the subsequent stem exclusion and understory reinitiation stages, which can last several hundred years. Consequently, a stand can be dominated by a different suite of species than those that previously occupied the site, depending on which species gain a competitive advantage because of regeneration strategies, disturbance type, or stochastic factors such as good seed years.

When no residual trees are present, the stand initiation stage reflects the open structure (**Figure 1**). Because many herbaceous species also initiate following a disturbance, this stage usually contains a high diversity of plants, which attracts a high diversity of animals – butterflies, insects, deer, rabbits, and their predators.

When a partial disturbance leaves residual trees from older cohorts, these trees compete with new regeneration for the released growing space. The influence of the residual trees depends on their vigor and number. If residual trees are numerous and vigorous they can completely reoccupy the growing space, preventing a new cohort from establishing, or outcompeting and eliminating any newly initiating trees. The stand then quickly returns to a dense structure. If a new cohort does establish but is so suppressed that it remains as advance regeneration, the understory structure develops. If the residual trees are few and widely spaced, the savanna structure develops. As in the open structure, the savanna structure contains a great diversity of herbaceous plants and accompanying animals. The savanna structure can also provide habitat for woodpeckers, raptors, and other birds that utilize the relatively isolated trees. In some instances, presence of these trees attracts birds that disseminate the heavy seeds of species that would otherwise have a difficult time moving into open areas.

Partial disturbances during the stand initiation stage can reduce the competitive advantage of established plants, allowing other species to capture and hold growing space. For example, burning newly regenerating conifer forests in arid parts of the United States can convert them to semipermanent brushfields. Frequent surface fires or grazing can maintain a savanna structure by killing new cohorts of trees and promoting the growth of grasses in the growing space between large trees.

Stem exclusion Once growing space is fully occupied, intense competition occurs among existing trees, generally excluding new cohorts. This stage is referred to as the stem exclusion stage and can last between about 40 years for shade-intolerant pine species to over 100 years in mixed species stands that include shade-tolerant species.

Some natural stands and most plantations occur as monocultures of trees that regenerate within relatively short time-frames. Because conspecific trees require an identical set of growth factors, development pathways and resulting structures in monocultures are somewhat limited. Unless moisture or nutrients are limiting, trees will grow vigorously during the stand initiation and early stem exclusion stages until their crowns touch and sunlight becomes limiting. In a uniformly spaced stand with trees of nearly identical ages, the period of vigorous growth will be similar for all trees. In a stand with more irregular spacing and age, some trees will continue to grow vigorously while others will be less competitive, develop small crowns, decline in vigor, and become relegated to subordinant positions. The more vigorous trees in single species stands are generally those that have a competitive advantage because of microsite, age, spacing, and/or genetic makeup. In general, trees in single species stands do not grow well after being relegated to a subordinant position in the stand. Species that are more shade tolerant can sometimes persist, albeit in a condition of low vigor. In a single species, single cohort stand, the canopy will remain as a single layer, with crown differentiation into dominant, codominant, intermediate, and overtopped trees (**Figure 6**).

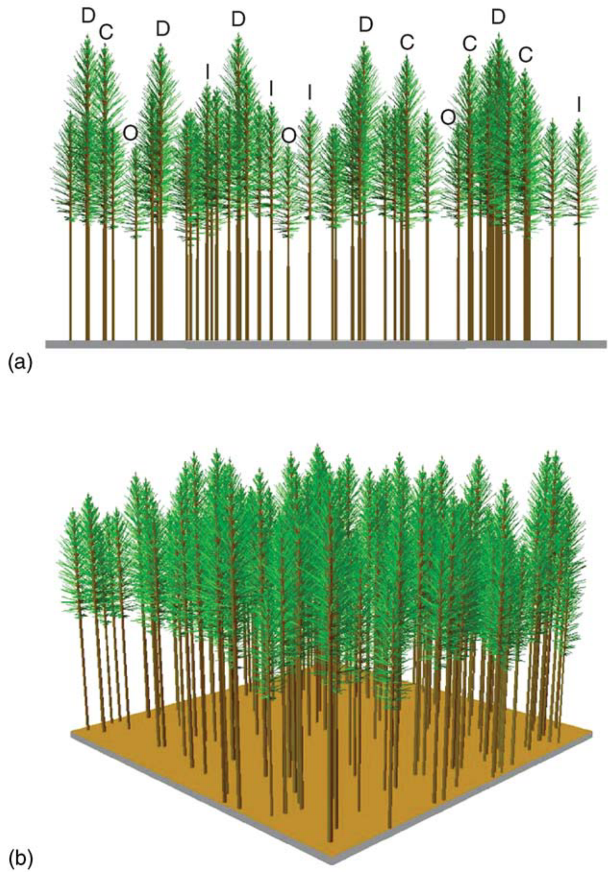

Figure 6 (a) Single species, single cohort stands usually develop in a single stratum; the trees differentiate into crown classes within this stratum. D, dominant; C, codominant; I, intermediate; O, overtopped. (b) The same stand as above, from perspective view. © Professor Chadwick Oliver.

During the stem exclusion stage, dominant trees continue to grow in height and diameter. Subordinant trees continue to grow in height, but diameter growth as well as insect and disease resistance decline considerably. There is less tendency for trees to differentiate in stands that are uniformly spaced, on poor soils, and/or have limited genetic variability. Trees in such stands simultaneously can decline in diameter growth and insect and disease resistance, with the result that entire stands become highly susceptible to wind damage, ice breakage, and insect attacks. In differentiating stands, the number of trees in the stand decreases over time as the average size of the tree (measured in diameter or total volume) increases. The relationships among tree sizes, numbers, and other measures have been quantified and studied.

Multiple tree species regenerating after a disturbance follow a similar pattern of intense competition during the stem exclusion stage. The primary difference between mixed and single species stands is that the different species in mixed stand have different tolerances for growing under conditions where resources are becoming limited. A slower growing species with greater tolerance for light-limited conditions may survive if overtopped by a faster-growing species. Because of these differences among species, the canopy of a mixed species stand can segregate into different strata representing the variety of species' tolerances for growing in shade (**Figure 7**). Trees in lower strata grow very slowly because of the reduced light environment, and eventually are much smaller than upper stratum trees in the same cohort. Small trees in lower strata have been mistakenly assumed to be younger, with the stand considered the result of an uneven or all-age pattern of development. Mixed species, single cohort stands often produce trees of higher timber quality more economically than in pure species or multiple-cohort (uneven-aged) stands. Trees that are eventually relegated to lower strata surround the trees that will eventually form the B-stratum when the stand is young, acting as 'trainers' and keeping the B-stratum crop trees pruned. The B-stratum tree crowns eventually expand above the trainers avoiding the need for a costly thinning.

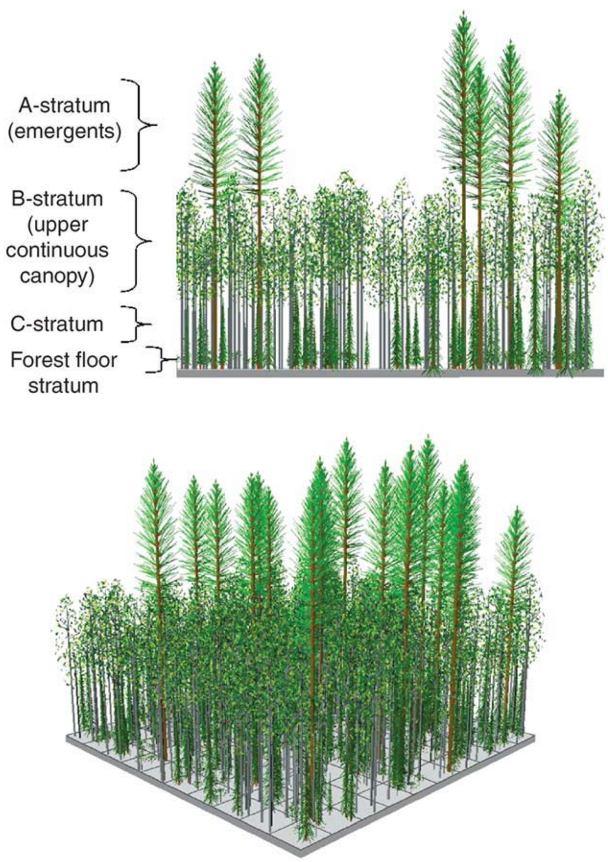

Figure 7 Mixed species, single cohort stands can develop into strata. Nomenclature shown here is common. (a) Within each stratum, the trees can differentiate into crown classes, similar to those in Figure 6. (Multiple cohort stands can develop into similar strata.) (b) The same stand as above, from perspective view. © Professor Chadwick Oliver.

Mixed species stands also differentiate into dominance classes within each canopy stratum. Trees in lower strata will express dominance in essentially the same manner as trees in the upper stratum by retaining a full, deep crown of photosynthetically active tissue (leaves or needles). Dominant trees in lower strata usually do not grow rapidly until released. Upon release these lower stratum dominants are likely to grow more rapidly than the less dominant trees in any stratum, providing they can survive the initial 'shock' of release. While it is possible to have shade-tolerant species in all strata in a stratified, mixed species stand, shade-intolerant species will be found only as emergents (the A-stratum) or in the continuous upper canopy (the B-stratum).

Especially in stands of coniferous species, the forest floor is devoid of vegetation during the stem exclusion stage because most herbaceous plants are eliminated by the vigorous occupation of growing space by the trees. In stands dominated by deciduous trees, shrubs and herbaceous plants that can take advantage of trees' dormant season sometimes are able to persist. Single species stands in the stem exclusion structure commonly create the dense structure. There are generally fewer species of plants and animals in the dense structure than in other structures. Mixed species stands in the stem exclusion stage can assume the dense structure, but are sometimes classified as having the complex structure because of the vertical distribution of their canopies. Mixed and pure species stands in the stem exclusion stage that contain some older, residual trees can be classified as having the complex structure. Such stands may be suitable to more wildlife species than single species, stem exclusion stands lacking residual overstory trees.

Upper and lower strata affect each other's growth in both single and multiple cohort stands. These effects are more pronounced in mixed species stands with more than one cohort. Trees growing immediately beneath an intact canopy experience a light regime that alternates between spots of full sunlight (sunflecks) and shade as the sun moves across the sky. With enough periods of full sunlight, trees in lower strata can retain a full crown and their terminals continue to grow upwards, retaining a single-stemmed form. A light environment that alternates between periods of full sun and shade is termed low shade. A high shade environment develops when trees in the upper canopy grow much taller than trees growing beneath them. Sunlight in this environment is extremely diffuse, with few, if any, sunflecks reaching the understory. Trees growing in high shade develop characteristically flatter tops as the ratio between terminal and lateral branches decreases. These trees die unless they are extremely tolerant of shade, and once released from the effects of this shade, trees may not retain a single terminal leader. Trees in lower strata trees can sometimes affect overstory trees. Especially on sites limited by moisture or nutrients, lower strata trees in the same or younger cohorts can deplete soil moisture and nutrients to such an extent that overstory trees are weakened and invaded by insects and/or pathogens.

Disturbances affect mixed species stands in more complex ways because species differ in their responses to various kinds of disturbances. A fire may selectively kill trees in lower strata because these trees are smaller, have thinner bark, and commonly consist of species more susceptible to fires. Windstorms will generally topple trees in the emergent or upper continuous canopy. Insects and diseases are usually host specific to varying degrees. In this way, disturbances have the potential of reducing the number of species initially present in a stand. Small disturbances in mixed species, single cohort stands can also result in the establishment of new cohorts.

Residual trees of older cohorts can suppress newly initiating cohorts during the stem exclusion stage, depending on the number and vigor of these residual trees. Extreme suppression can kill the younger cohort or relegate it to advance regeneration, as described earlier. Even less extreme suppression will reduce height growth or eventually kill younger trees, with shade-intolerant species killed first. Recent studies suggest that in some instances surprisingly little overstory shade is required to suppress or kill a younger cohort.

The physical appearance of a mixed species, single cohort stand is quite similar to a multiple cohort stand, and the same stratification classification (and crown classes within strata) of **Figure 7** is used in both stand types. Management of these stand types is also similar, recognizing that dominant trees in each stratum are the potentially more vigorous ones and that lower strata trees can become flat-topped, lose their vigor, and possibly die, especially if shade intolerant.

Understory reinitiation Eventually trees grow so large that the death of an individual tree releases enough growing space that adjacent trees cannot rapidly capture all of it, and a new cohort (often a different species that is more tolerant of shade) establishes. The establishment of a new cohort signals the onset of the understory reinitiation development stage. This stage can last for several hundred years because trees in the newly regenerating cohort are commonly so suppressed that they remain in a flat-topped condition near the forest floor as advance regeneration or die within a few years. They are then replaced by more newly germinating seedlings that also may die after a few years. Residual trees of an older cohort can suppress the intermediate cohort and any newly regenerating trees, prolonging their suppression.

The understory reinitiation stage can exhibit the understory structure, although in mixed species stands and in stands with residual older trees it more commonly reflects the complex structure. The understory structure can also result from partial disturbances in the stem exclusion stage that created a new cohort that became suppressed as the forest floor stratum.

Old growth The old growth development stage describes what would happen in the event that no external (autogenic) disturbance event impacted a stand during the lifespan of any of the original initiating trees. The old growth development stage is probably not particularly common in many parts of the world, as fire, wind, insect outbreaks, or other disturbances generally impact a stand before it attains this stage. The old growth stage occurs as overstory trees become increasingly weak and die intermittently, allowing the trees existing near the forest floor in the understory reinitiation stage to grow to the overstory, through a series of suppressions and releases. The resulting stand would consist of shade-tolerant trees in a variety of heights as individual gaps created by senescing overstory trees allowed the released trees to grow at different rates.

Because most tree species live for hundreds of years, a true old growth development stage would not occur until a stand was several hundred years old and had not been impacted by an intermediate disturbance. In some instances of shorter-lived species, this stage might occur much sooner.

The old growth stage would generally take on the attributes of the complex structure; however, most stands identified as having the complex structure are not in the old growth development stage. Instead, they are generally in the stem exclusion or understory reinitiation development stages. These stands are generally made complex by the presence of residual trees and multiple strata (bottom line of **Figure 5**).

These phases of stand development have been observed and documented by foresters and scientists in temperate and tropical forests in many parts of the world. The four phases of stand development are sometimes contrasted with ‘gap phase’ dynamics, which describes forest development as the ongoing process of recolonization of small openings in the forest that occur upon the death of individual or small groups of trees. The two systems differ mainly in terms of temporal and spatial scales. In some tropical and temperate forests, stand-replacing disturbances occur at longer timescales than the lifespans of individual trees. Senescence and death of individual canopy trees create gaps that are regenerated by seedlings or advance regeneration. As the trees in these gaps grow, they compete with each other for resources. The tree that eventually replaces the gap-forming tree is one that can successfully regenerate and compete in the gap environment. Depending on their geographical location, orientation, and size, gaps can have an abundance or dearth of resources required for tree growth. Trees that can capture resources and/or tolerate lower levels of resources will be favored.

Application of Stand Dynamics to Silviculture

By understanding the processes affecting each development stage and the structures created by the different processes, silviculturists can predict the development pathways that each stand could take and the values that each stand might provide at different times in the future. Moving stands along desired development pathways can be achieved using silvicultural operations as surrogates for natural processes such as disturbances and regeneration. An appropriate silvicultural operation can be prescribed by understanding how the stand will respond. Through understanding the dominant processes occurring within a stand at different development stages, silvicultural operations can be implemented when they will be most effective – at appropriate 'windows of opportunity.' Well-timed silvicultural operations will cause the stand to follow a planned development pathway – a silvicultural pathway.

When in each structure, a stand will provide some values, but not others. For example, an open structure will provide deer and butterfly habitat, but not habitat for 'late successional' species and no opportunity for obtaining timber revenue for a long time. Alternatively, an understory structure will provide some late successional habitat and opportunities for obtaining high-quality timber, but no 'early successional' habitats for deer and butterflies. The full spectrum of forest values can only be obtained when individual stands are managed in concert across a landscape.

Stand Dynamics and the Landscape Scale

Although the primary scalar focus of stand dynamics is the forest stand, knowledge of stand-level processes readily scale up to the landscape. Landscapes are mosaics of individual stands. Landscape vegetation patterns arise from the interactions between vegetation, soils, climate, and disturbances. At the landscape scale, disturbances vary with climate, geomorphology, topography, soils, and vegetation. Some portions of landscapes are very prone to disturbances such that stand development or silvicultural pathways are constrained. Other areas of the landscape are protected from disturbances such as wind and fire and act as 'disturbance refugia' where developmental pathways and structures may differ markedly from those found in the surrounding matrix. At the landscape level, each stand follows developmental pathways and exhibits characteristic structures that reflect its disturbance history and its structure at the time of the disturbance. Like individual stands, landscapes are dynamic, but landscapes still reflect the developmental pathways and forest structures that are possible given the climate, soils, vegetation, and inherent disturbance regimes of the region. Some landscapes are a mosaic of many different structures and development stages, reflecting a history of small disturbance sizes or an underlying patchwork of geological or soil conditions. Other landscapes are structurally and compositionally more homogeneous, indicating large-scale disturbances, homogeneous substrates, and few species; such landscapes typically exhibit a narrow range of structures and pathways.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Ecology**: Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Health and Protection**: Biochemical and Physiological Aspects; Diagnosis, Monitoring and Evaluation. **Landscape and Planning**: Landscape Ecology, the Concepts; Landscape Ecology, Use and Application in Forestry; Spatial Information. **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation. **Plantation Silviculture**: Forest Plantations; Multiple-use Silviculture in Temperate Plantation Forestry. **Silviculture**: Natural Stand Regeneration; Unevenaged Silviculture. **Soil Development and Properties**: The Forest Floor. **Tree Physiology**: A Whole Tree Perspective; Shoot Growth and Canopy Development.

Further Reading

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Natural Regeneration of Tropical Rain Forests

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Introduction

Natural regeneration is the process by which juvenile plants and coppice that have established naturally replace plants which have died or have been killed. Over time, following a disturbance, the growth of natural regeneration will reestablish canopy trees. This natural recovery process can be exploited in tropical forest management systems to create a new stand after canopy trees have been harvested. This article provides a review of the advantages and problems associated with natural regeneration. The effects of different silvicultural systems on natural regeneration are examined and the causes of success and failure discussed.

Advantages and Disadvantages of Natural Regeneration

Tropical rainforests are well-known for their extraordinarily high diversity of species, including trees. The use of natural regeneration in forest management helps to reduce logging impacts on biodiversity, since the objective is to ensure that exploited trees are replaced by juveniles of tree species characteristic of the natural forest. The diversity of natural regeneration will generally exceed the diversity of species that could be planted on a commercial scale. For example, in a recent large-scale forest rehabilitation project in Borneo many thousands of hectares of logged rainforest were replanted with only 33 commercial tree species. Some of these were not native to the region. Planting replacement trees in sites that are often remote and inaccessible is an expensive operation. Consequently there is little incentive to use species that are of low commercial value or that are relatively slow-growing. Such species are only likely to remain a component of a sustainably managed forest under a natural regeneration system.

Natural regeneration systems exploit existing seed and seedling banks and circumvent the problem of obtaining healthy planting stock. Seed production in many important tropical tree species is erratic and poorly documented and it is often difficult or impossible to obtain a regular supply. Planting stock cannot therefore be produced on demand. Where planting stock is available it is often collected from a narrow range of sites outside the local area and is likely to be of unknown but probably rather narrow genetic composition. Planted seedlings often suffer an initial period of poor growth and high mortality, termed planting shock. Poor initial growth will often put planted trees at a significant competitive disadvantage relative to the regeneration of other plants in disturbed forest sites. In contrast, natural regeneration will often show enhanced survival and vigorous growth in response to canopy disturbance.

In many parts of the world little is known about the ecology of commercially important tree species, including their tolerance of a range of site conditions or their requirements for successful establishment as seedlings. This can make artificial regeneration problematic. Where new trees have been planted extensively in tropical rainforest (typically, enrichment planting of forests with poor natural regeneration of commercially valuable species), seedling mortality has often been high and growth rates disappointing. This has been attributed to poor site–species matching, poor planting and maintenance techniques. The use of natural regeneration increases the chance that seedlings and saplings are of species capable of growing to maturity under local site conditions because they belong to species (and ecotypes) that are already growing in the immediate vicinity.

Under an appropriate silvicultural system the density of seedlings in a naturally regenerating tropical rainforest can be very high. Densities in excess of 75 000 seedlings ha^{-1} of commercial species have been recorded in forests in Borneo. This gives a broad base for the selection of the fastest-growing, best-formed individuals of the most desirable species. In contrast, the costs of replanting a forest are so great that the forester generally aims to make sure that a large proportion of all individuals survive and grow to maturity regardless of their quality. However, a