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FOREST DEVELOPMENT IN NORTH AMERICA FOLLOWING MAJOR DISTURBANCES

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ABSTRACT


Large-scale, man-created or natural disturbances play a major role in determining forest structure and species composition in many areas of North America and probably other temperate and tropical forests. Trees begin growth by a variety of mechanisms — each of which can respond to disturbances of a different severity. Studies suggest: a single group of species is not predestined to inhabit an area; forest physiognomic appearances assumed to imply all-aged succession often occur in single-age class stands; and recruitment of new stems into a forest often follows a disturbance rather than being a constant occurrence. After disturbances, forests develop through general physiognomic stages: “stand initiation”, “stem exclusion”, “understory reinitiation”, and “old growth”. Disturbance severity determines which species will dominate the forest afterward. The frequency of disturbances is also important in determining the general forest type over a large area, because species dominance and stand physiognomy change with time following disturbance.

INTRODUCTION

The understanding of forest development and its relation to large-scale disturbances — one aspect of forest succession — has improved in recent years. Increased knowledge has resulted from the attention given in North America to forest regrowth following clearcutting: past studies have been reviewed (Drury and Nisbet, 1973; Connell and Slatyer, 1977; Harper, 1977), attention has recently been given to the theoretical significance of disturbances to plant communities (Horn, 1974; Levin and Paine, 1974; Pickett, 1976; Whittaker and Levin, 1977; Caswell, 1978; Connell, 1978; White, 1979), and new studies have been made using stem analysis and other aging techniques (Heinselman, 1973; Swain, 1973; Henry and Swan, 1974; Oliver and Stephens, 1977; Oliver, 1978; Franklin and Waring, 1979).

An early review of forest development by Jones (1945) and a more recent review by Drury and Nisbet (1973) have described a variety of development patterns. Forests have been reported as developing in an even-aged condition,
or with an even-aged component; as having several age classes; or as being all-aged.

Major disturbances to forests are quite common (Raup, 1964; Heinselman, 1970; White, 1979). Their frequency relative to the natural life span of many tree species and stem aging studies in old growth forests (review by Jones, 1945; Hough and Forbes, 1943; Oliver and Stephens, 1977; Franklin and Waring, 1979; Agee and Huff, 1980) suggests that forests in many regions have species compositions and age structures which are largely the results of previous disturbances.

This paper suggests a pattern of forest development following major disturbances and builds on many of the ideas of Jones (1945), Hough and Forbes (1943), Drury and Nisbet (1973) and Harper (1977). It is not an exhaustive review of past studies; rather it is an attempt to suggest a generalized pattern. Development after major disturbances is described because undoubtedly there are forests in certain parts of the world and in protected conditions which are rarely subjected to such major disturbances (Lorimer, 1977), even here the general pattern suggested in this paper should give a basis for understanding their growth.

“Major” disturbances are here defined as those which knock over or kill all living tree stems in an area large enough to ensure that most trees beginning growth after the disturbance do not encounter competition from surrounding, undisturbed trees. Examples of such major disturbances include crown fires, hurricanes, tornadoes and other severe windstorms, snow avalanches, landslides, mudflows and other severe soil erosion or deposition, and forest clear-cutting. For brevity, the role of less extensive disturbances (Oliver and Stephens, 1977; Hubbell, 1979; Means, 1980) has been omitted. With certain variations, stages described in this paper can occur in affected parts of stands where only partial disturbances occur (Oliver and Stephens, 1977). Also, minor disturbances or perturbations may affect the duration of developmental stages. Minor disturbances or perturbations would include surface fires, windthrow of some overstory forest trees, lightning strikes, insects, and diseases where only individual overstory trees are killed, and partial forest cuttings and thinnings.

This paper will cover three major themes during the description of forest development:

(1) The single-age class (or several age classes) pattern of forest succession is more common than has often been assumed. It is now clear that a forest with a narrow range of tree ages can display the vertical species stratification and broad diameter distribution normally associated with all-age forests (Smith, 1962; Oliver, 1978; Stubblefield and Oliver, 1978; Harper, 1977).

(2) Most stems that exist in a forest initiate during a relatively short period following a disturbance (Hough and Forbes, 1943; Raup, 1964; Heinselman, 1973; Henry and Swan, 1974; Long, 1976; Connell and Slatyer 1977; Oliver and Stephens, 1977; Oliver, 1978; Stubblefield and Oliver, 1978; Wierman
and Oliver, 1979; Larson and Oliver, 1979). Species that appear prevalent as the forest ages are generally present from the start but are not obvious at first, often because of their small size and infrequency relative to the early dominants. This is in contrast to the often used description of forest development in which species entering an area soon after a disturbance are gradually replaced by species invading later (Hough, 1932; Meyer and Stevenson, 1943; Braun, 1950; Worley and Meyer, 1951; Eyre and Zillgitt, 1953; Phillips, 1959; Puissi, 1966; Daubenmire, 1968).

(3) There is accumulating evidence that several different forest communities could potentially inhabit the same area for an indefinite period (Connell and Slatyer, 1977; White, 1979). This is contrary to the idea that a single species or group of species is predestined to dominate an area as “climax” vegetation in a steady state equilibrium.

This paper describes a general pattern of forest development following major disturbances, and discusses a mechanism by which the same area could be dominated potentially for extended periods by entirely different forest communities. Evidence presented is based on studies and observations in the north eastern and north western United States. Personal observations, discussions and reports of others in other parts of the United States (Loucks, 1970; Ohmann and Ream, 1971; Heinselman and Wright, 1973; Swain, 1973; Wright, 1974; Peet and Loucks, 1977) and elsewhere in temperate and tropical regions suggest that the patterns described are quite general. More theoretical aspects of forest development have been reviewed by others (Horn, 1974; Connell and Slatyer, 1977; Whittaker and Levin, 1977). Although they are important to a conceptual understanding of community development, they are not as immediately applicable to forest management and will not be discussed in detail here.

Influences of soil and climate are also beyond the scope of this paper. It is important to note, however, that these factors often control the frequency and intensity of natural disturbances (Heinselman, 1973; Wright, 1974).

GENERAL PATTERN OF STAND DEVELOPMENT

Forest development can be divided for convenience into four broad stages: stand initiation, stem exclusion, understory reinitiation, and old growth. Fig. 1 shows these schematically, and the stages are discussed below with examples from various studies.

Stand initiation stage

After a major disturbance, plant species can reoccupy an area by developing stems from pre-existing stumps and roots, buried or newly dispersed seeds, and advance regeneration — small individuals growing negligibly in the forest understory but adapted to accelerate growth when released (Mertz and Boyce, 1956; Beck, 1970; Sander, 1972; Marks, 1974). These advance regeneration
Fig. 1. Schematic diagram of stages of stand development following major disturbances. All trees comprising the forest start soon after the disturbance; however, dominant tree type changes as stem number decreases and vertical stratification of species progresses. Height attained and time lapsed during each stage would vary with species, disturbances and site. Barring intervening disturbances, the "old growth" stage may be reached in mixed alder–conifer stands in the Pacific Northwest in less than 200 years; in mixed oak–maple–birch stands in New England it may take several hundred years; in Douglas fir–hemlock–red cedar stands in the Pacific Northwest, it may take well over 500 years. (Letters designating different species refer to discussion in text.)

stems may be old in years; however, they behave ecologically as young seedlings (according to their size, rather than their age). Generally, tree age has been date from time of release of advance regeneration and new stem initiations from stumps, root sprouts and stem sprouts (Morris, 1948; Sprugel, 1974; Oliver and Stephens, 1977; Oliver, 1978) rather than from time of germination of the plant.

The developing individuals enlarge and utilize available growing space until one or more environmental factors become limiting (Holt, 1972; Connell
Species gaining competitive advantages are those which grow quickly following the preceding disturbance. Even tolerant species, such as eastern hemlock (*Tsuga canadensis* [L.] Corr.) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), were found to develop as forest components primarily during the periods immediately following large disturbances (Oliver and Stephens, 1977; Stubblefield and Oliver, 1978).

As an example, over 85 percent of the stems alive at 60 years had initiated within 20 years of the original clearcut in several mixed species stands in New England (Oliver, 1978). Here stems had not all invaded immediately after the disturbance, but had reoccupied the site and excluded later stem recruitment after a relatively short time. Also, an extensive fire (several thousand acres) burned a cutover area in the Cascade Mountains of Western Washington 50 years ago. Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock, western red cedar (*Thuja plicata* Donn.), and red alder (*Alnus rubra* Bong.) stems reinvaded only during the following 20 years (Stubblefield and Oliver, 1978). In drier forest types in eastern Washington, Douglas-fir and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) were found to invade during a long interval (about 60 years) after a major fire of 90 years ago. After this, trees did not invade (Larson and Oliver, 1979).

The period during which new seedlings actively invade or (in the case of sprouting stems or advance regeneration) begin growth following a disturbance is here referred to as the "stand initiation stage". Duration of the initiation stage of a given stand varies widely (Oliver, 1978; Stubblefield and Oliver, 1978; Franklin and Waring, 1979; Larson and Oliver, 1979) and depends on several factors, such as (1) intensity of disturbance; (2) area of disturbance; (3) growth rates of invading species; (4) regeneration mechanisms of invading species; (5) coincidences of disturbance, seed crop and weather; and (6) density and multiplication rate of seed predators or competing shrubs.

(1) **Disturbance intensity.** A very intense disturbance can destroy part of the soil profile and reduce potential growing space in the soil. As plant roots reinvade the soil and expand the soil's ability to support more roots, other individuals may later invade to fill the newly created growing space.

(2) **Area of disturbance.** If the area covered by a disturbance is large and the regeneration mechanism favored is incoming seeds, a long time may elapse before enough seeds are dispersed into the area to allow complete growing space reoccupation (Spring et al., 1974).

(3) **Stem growth rate.** New individuals continue to invade an area until existing plants have usurped all available growing space. If growth conditions are favorable, the first invading plants grow rapidly and leave no growing space available for later arrivals. In less favorable sites with less rapid plant growth, late arrivers continue to find unoccupied growing space for an extended period.
(4) *Regeneration mechanisms of invading species.* As will be discussed later, trees can regenerate by a variety of sexual and asexual mechanisms. Certain mechanisms (which respond to certain disturbance types) allow the trees to be present sooner than other mechanisms do, and/or to grow more rapidly at first, thus refilling the growing space quickly and excluding later arriving stems.

(5) *Coincidence of disturbance, seed crops and weather.* In places where the tree species produce abundant seed crops only periodically, a disturbed area can be refilled quickly and the establishment time of the new stand will be short if the disturbance occurs just before a plentiful seed year and is followed by favorable weather conditions for germination and growth. If these do not occur together, the time required to refill the growing space may be quite extended.

(6) *Density and multiplication rates of seed predators or competing shrubs.* Predators and competitors which eliminate, set back or kill regenerating trees prolong the time before the growing space is refilled with trees. Late arriving trees can continue to invade the site under these conditions, thus creating a broad age range.

*Stem exclusion stage*

After a major disturbance new stems expand to fill the growing space until one or more growth factor becomes limiting — such as light after crown closure (Assmann, 1970). A stage in stand development then occurs during which even younger stems cannot become established.

This stage was demonstrated in a stand in the central Cascade Mountains of western Washington. Alder, hemlock, Douglas-fir, and red cedar had regenerated over a 20-year period beginning after a post-logging fire 50 years previously. No stems were found which began more than 30 years after the fire (Stubblefield and Oliver, 1978). Also, Long (1976) studied several stands that had started between 10 and over 500 years ago at higher elevations in the same region. These stands contained western hemlock, Douglas-fir and Pacific silver fir (*Abies amabilis* [Dougl.] Forbes). Long also deduced here the existence of a period in which no new stems had begun after the initial period of regeneration.

In eight mixed stands studied by Oliver (1978) and Oliver and Stephens (1977) in central New England, little recruitment of new stems occurred except immediately following disturbances. Moreover, small disturbances caused by removing a few trees from these mixed stands did not allow a new age class to develop, but simply allowed pre-existing stems to enlarge to refill the available growing space.

Sprugel (1974, 1976) also observed a stage of stem exclusion in balsam fir forests (*Abies balsamea* [L.] Mill.) which were periodically destroyed by winter desiccation at high elevations in the Adirondack Mountains of
New York. He also found that trees, shrubs and herbaceous vegetation were excluded for a period after stand initiation.

In addition to the exclusion of new stems there is also intense competition between existing stems (Fig. 1). The various species have different early growth rates and tolerances to shade. Species with relatively fast early growth rates first appear as dominants and are referred to as "pioneers" (species A and C of Fig. 1). Other species, although present at this time, may not assert themselves in early competition (species B and D of Fig. 1). After a time of intense competition (referred to as the "brushy stage" by Gingrich, 1971), there is a vertical "sorting out" — or stratification — of trees, whereby one or several species become dominant and suppress other species' growth. In Fig. 1, species B is the eventual dominant (one species in this case).

As can be seen in Fig. 1, the eventual dominant is not necessarily the species that was largest or most numerous in the beginning. Other species may appear dominant at first and then be overtaken (A and C of Fig. 1). If those overtopped are intolerant of shade, they die (species A); if not, they remain alive but grow slowly as long as there is overstory shade (species C and D). Species with infrequent individuals which do not appear dominant at first (such as B in Fig. 1) may be overlooked until they begin to overtop their more numerous competitors, as was noted by Egler (1954) and Drury and Nisbet (1973). When they are finally observed overtopping and suppressing the early pioneers, the pioneers can then be mistaken for younger trees invading beneath an older overstory.

The predictable vertical sorting out of species — or vertical stratification — in essentially even-aged stands has been found in a variety of species in several parts of North America, as the following examples show.

On upland till soils in central New England, disturbances favoring deciduous species and hemlock resulted in even-aged forests with a vertical stratification which changed in time (Oliver, 1978). All species initiated together; but black birch (Betula lenta L.), gray birch (Betula populifolia Marsh.), and red maple (Acer rubrum L.) and sugar maple (Acer saccharum Marsh.) dominated at first. Red oak (Quercus rubra L.), although with fewer initial numbers, eventually outgrew and dominated the others. Unlike gray birch, the black birch and maples did not die upon being overtopped but were relegated to the understory where they existed with tolerant hemlock trees. Also in central New England, when severe disturbances caused development of gray birch—white pine (Pinus strobus L.) stands, gray birch dominated during the first 20 to 25 years (Tarbot and Reed, 1924; Cline and Lockard, 1925; McKinnon et al., 1935; Harvard Forest, 1941). After this the birches died and even-aged pine stands remained.

Similar stratification has been observed in stands on certain sites in western Washington where Douglas-fir predictably dominates contemporary western hemlock in mixed stands of these two species (Wierman and Oliver, 1979). Also, red alder stratified above western red cedar and usually western hemlock in extensive mixed stands in western Washington; this occurred even though alder was several years younger (Stubblefield and Oliver, 1978).
Understory reinitiation stage

The overstory forest eventually appears to "lose its grip" on the site. Understory herbaceous and woody plants, including tree species that can exist as advance regeneration, begin to grow in favorable environments in the understory (Fig. 1). The length of time before this understory reinitiation begins seems to depend on the tolerance of the overstory as well as on the frequency of minor perturbations. Note in Fig. 1 that species present as shade tolerant advance regeneration are often the same as those in the lower, shade tolerant strata of the overstory. If size distribution is assumed to represent age distribution as well, this leads to the mistaken idea that these species invade continuously.

As an example, advance regeneration of deciduous species appeared to enter old field white pine stands in central New England about 50 years after stand initiation. Pine stands that were clearcut at less than 50 years old reseeded to white pine, whereas stands cut later became deciduous forests (McKinnon et al., 1935).

Also, in the Adirondack Mountains of New York, subalpine balsam fir stands that were periodically desiccated by wind developed understory herbaceous plants and balsam fir seedlings approximately 35 years after stand initiation — after a period of only 20 years of stem exclusion. The overstory canopy fell apart completely at about 60 years (Sprugel, 1974).

Individual trees may remain in the understory for a very long time. The oldest Pacific silver fir found in the understory of a 550-year-old hemlock—Douglas-fir—Pacific silver fir stand in the Cascade Mountains was 138 years old but only 3.8 m tall (Long, 1976). Pacific silver fir trees less than 1 m tall and between 55 and 130 years old have been commonly observed by this writer beneath 350-year-old hemlock—Douglas-fir—Pacific silver fir stands in the same area.

Old-growth stage

Eventual fates of the understory and overstory in the absence of a major disturbance are unclear. Since stands can become more susceptible to disturbances as they age (White, 1979), as a rule old stands would be less frequent than younger ones. The probability that a stand will be subjected to natural catastrophes increases with time. For example, the overstory becomes more susceptible to windthrow as trees grow larger and more exposed to the wind, and the understory becomes more susceptible to fire with fuel buildup (Heinselman, 1973).

If the overstory is destroyed, by windthrow for example, understory advance regeneration can be released and form the dominant trees of the next forest. If a fire or a landslide occurs, the understory (as well as the overstory) will simply be destroyed (or possibly set back in the case of sprouting species). If the overstory breaks up slowly by individual trees dying (Fig. 1), under-
story advance regeneration can be locally released and move into the canopy, forming the uneven-age mosaic pattern of succession. This was found occasionally in hemlock—Douglas-fir—Pacific silver fir forests by Long (1976) in the Cascade Mountains of western Washington. The prevalence of all-age stands would vary by region, depending on the frequency of major disturbances and the maximum age attainable by the dominant species.

**POTENTIAL FOREST DOMINATION BY ANY OF SEVERAL COMMUNITIES**

An area can be dominated by any of several relatively stable forest communities, as will be discussed below. First, it is important to realize that some of the species invading after a major disturbance dominate the stand for a very long time — usually until the next major disturbance. Different types of major disturbances can give different species the initial advantage and hence the dominant position in the resulting stand.

*Disturbance-initiated species domination*

The dominant trees in most forests probably began only after major disturbance; the potential life span of dominant species is generally greater than the time between major disturbances for most forests in North America.

Forests have often been assumed to proceed rapidly after disturbance to an all-aged condition. Supposedly “younger”, more tolerant stems are assumed to be the eventual dominants of “climax forests”. Such “climax” forests have not been often observed, however. Stems which are often mistaken as younger and more “climax” can actually initiate after the same disturbance as the overstory. These stems grow more slowly and, being more shade tolerant, are able to exist in the understory. Very often the single-age class stratification pattern of the “stem exclusion stage” and “understory reinitiation stage” of Fig. 1 is assumed to be the all-aged pattern approached by the “old-growth stage”. This has been shown for mixed deciduous forests in central New England (Oliver, 1978) and for mixed Douglas fir—hemlock (Wierman and Oliver, 1979) and mixed alder—conifer (Stubblefield and Oliver, 1978) stands in western Washington.

Major disturbances are often neglected as important factors in succession because they generally occur at intervals longer than the life span of the average person. Even if a major disturbance occurs only every 250 years or more, it can nevertheless have a profound effect on the species composition and physiognomy of the intervening forest (Henry and Swan, 1974).

Long-term records of disturbances in relation to forest composition are rare. Stand reconstruction can document several hundred years (Stephens, 1956; Heinselman, 1973; Henry and Swan, 1974; Oliver and Stephens, 1977; Oliver, 1978; Hemstrom, 1979; Franklin and Waring, 1979; Means, 1980). Longer records of over 1,000 years have been obtained by examination of annual laminated (varved) lake sediments (Swain, 1973; McAndrews, 1976).
The species that potentially comprise the forest for a very extended period are those which are able to invade after a major disturbance and occupy the available growing space, thereby excluding or dominating later arriving species.

Several-age class forests (Oliver and Stephens, 1977) often behave similarly, which each large partial disturbance creating its own characteristic wave of new stems.

**Disturbance type and species composition**

Major disturbances vary in intensity from light — such as tornadoes, hurricanes and snow avalanches, which remove the standing trees but often do not remove the soil profile or advance regeneration — to very severe — such as landslides, which remove the soil profile as well (White, 1979). Disturbance intensity can be regarded as an environmental gradient and therefore a dimension of the n-dimensional niche hypervolume described by Hutchinson (1957), as are temperature and soil moisture (Franklin and Dyrness, 1973). Different species vary in competitive advantage gained by each type of disturbance.

Each species has one or several adaptive mechanisms for development after disturbance (Harper, 1977). Below are listed five mechanisms of sexual and vegetative reproduction. (There may well be more, as well as gradations, among these.)

The mechanisms are listed in a gradation of those which would give a competitive advantage from after the most severe disturbance to after the least severe disturbance. Most severe disturbances would remove overstory trees, understory trees, root systems and soil profiles. Examples of these are soil erosion, mudflows and alluvial deposition, and glacial advancement and retreat. Least severe disturbances would remove the overstory but leave the short understory (less than about 2 m in height) intact. Examples of these are windthrows and avalanche runout zones.

1. germinating from seeds entering the area after a disturbance;
2. germinating from dormant seeds in the soil predating the disturbance (Marks, 1974); either:
   (a) seeds with limited longevity which predate the disturbance only one or several years, or
   (b) seeds with prolonged longevity which stay resident in the soil for many decades;
3. sprouting of new stems
   (a) from lateral roots (Kozlowski, 1971),
   (b) from root collars if old stems are broken off but not uprooted (Wilson, 1968; Marks, 1974), or
   (c) from the stems of fallen trees (here new roots can also sprout in some species);
4. layering, a process by which a branch touches soil, establishes roots and begins growth of a new tree; or
(5) accelerating growth from existing advance regeneration.

A species has a competitive advantage if a major disturbance favors a developmental mechanism to which it can quickly respond. On one extreme, if a tornado destroyed standing tree stems it would favor species able to sprout from the root collar since these sprouts are generally able to grow more rapidly with pre-established root systems than plants initiating from seeds. On the other extreme, if a landslide removed root systems as well as stems on the same area, light-seeded species capable of invading mineral soil would be favored.

For example, forested uplands of central New England have supported either white pine forests or hardwood forests. White pine forests predominated when initiating disturbances were either very hot fires (Henry and Swan, 1974) or plowing (and grazing and then field abandonment) (Cline and Lockard, 1925; McKinnon et al., 1935; Harvard Forest, 1941); both of these eliminated the stumps and root systems from which competitive hardwood trees could have sprouted. Hardwood forests dominated the same areas after hurricane windthrows (Henry and Swan, 1974; Oliver, 1978) or forest clearcutting (Cline and Lockard, 1925; McKinnon et al., 1935; Harvard Forest, 1941; Oliver, 1978) which did not destroy root collars or advance regeneration hardwoods.

Also, red alder stands now often exist in the Cascade Mountains of western Washington where stumps of mixed Douglas-fir—hemlock—red cedar still witness a different previous forest type in the same area. Here, too, changing disturbance patterns favored alders rather than conifer species.

In some former pine forests of the south eastern United States, changing the type, severity and frequency of disturbances from frequent surface fires to clearcutting and suppression of fire has promoted deciduous forests (Croker, 1968).

Major disturbances (as well as climate, soils and other factors) determine species composition for an area. If the type of major disturbance is altered, eventual species composition is altered for a quite lengthy period — usually until the next major disturbance occurs. For this reason there is no single set of "climax" species predetermined to occupy an area. Instead, there are several types, each capable of responding for a long time to the preceding disturbance.

DISTURBANCE FREQUENCY AND GENERAL FOREST TYPE

Frequency of large disturbances can also determine the relative dominance of each species over a broad area. As an example, the upper part of Fig. 1 shows the relative time after a major disturbance during which each species (or group of species) is dominant. Fig. 2A 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. 2), species shown in Fig. 1 would be favored. If more severe or less severe disturbance occurred ("Y" in Fig. 2), different species would be favored and
A. Disturbances at Long Intervals ("Old Growth" stage reached)

![Diagram showing forest composition at long intervals with dominant species A, B, C, D, E, F, and changes in tree height over time with disturbance type X.]

B. Disturbances at Short Intervals (before "Old Growth" stage reached)

![Diagram showing forest composition at short intervals with dominant species A, B, C, D, E, F, and changes in tree height over time with disturbance type X.]

Fig. 2. Changes in forest composition over many centuries, based on stratification pattern of Fig. 1 and following periodic disturbances of type "X". Sloping lines represent tree height growth patterns shown in Fig. 1. Note all stems did not initiate at exact time of removal of previous forest. 2A: Forest is predominately dominated with species B (pure or mixed with C and D) if disturbances are infrequent enough to allow all four stages (Fig. 1) to be achieved. Forest shifts to being dominated by species E and F after a different disturbance type ("Y") favors other species (C and D) to gain initial advantage. 2B: Forest is equally dominated by species A and B when disturbances of type "X" occurs more frequently. Again, type "Y" disturbance was followed by species E and F.

Forest composition would be different until the next disturbance. If disturbances were more frequent (Fig. 2B) predominant forest types would shift to earlier successional stages. 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. In some instances disturbances are randomly scattered in space on adjacent areas. In these cases travel across the region can be substituted for time in the probability of a given forest type occurring. Pulse-like patterns have also been suggested by others (Odum, 1969; Loucks, 1970; Whittaker, 1970; Heinselman, 1973; Wright, 1974; Connell, 1978).

Disturbance is, and has been, one determinant of species composition of North America forests. It is oversimplified here for several reasons: site and weather variations are not considered; distinction between advance regeneration and a new age class may be arbitrary at times; and intermediate disturbances may create more complex age structures within a stand than described here (Oliver and Stephens, 1977).
SUMMARY

Large-scale disturbances play a major role in determining forest structure and species composition in many areas of North America. Past and recent studies suggest that: (1) forest physiognomic appearances often assumed to imply all-age succession can in fact be indicative of disturbance-initiated, single-age class succession (Oliver, 1978; Stubblefield and Oliver, 1978); (2) recruitment of new stems into a forest often follows a disturbance (Egler, 1954; Drury and Nisbet, 1973; Oliver, 1978; Stubblefield and Oliver, 1978), rather than being a constant occurrence which would result in an all-age forest; and (3) a single group of species is not predestined to inhabit an area. Rather, several different communities could potentially inhabit an area indefinitely (Connell and Slatyer, 1977).

Following disturbances, forests from many areas develop through the same four general physiognomic stages:

1. "stand initiation", when trees from the new stand invade the released soil and light growing space;
2. "stem exclusion", usually upon canopy closure, when new stems are excluded from initiating and there is a vertical stratification by species in the existing stems;
3. "understory reinitiation", when brush and advanced regeneration reinvade the understory as the overstory becomes very mature;
4. "old growth", when the overstory gradually dies and the understory slowly fills in to replace it.

Evidence for the patterns can be found in many forests in eastern and western North America. The "stem exclusion" stage has often been mistaken as an all-age successional stage because the smaller stems are assumed to be younger than their actually contemporary dominants. The advance regeneration of the "understory reinitiation" stage is also incorrectly assumed to be a successional continuation of an all-age pattern. The "old growth" stage is often never achieved because of the long time required to reach this stage and because major disturbances often disrupt the forest before this.

The severity of disturbances determines which species will dominate the forest following the disturbance. This is important because species invading after a disturbance dominate the forest for a very long time. Tree species initiate growth by a variety of mechanisms, each of which can respond to disturbances of a different severity. Relatively non-severe large disturbances are those, such as windstorms, which blow over all overstory trees but do not destroy the forest floor; very severe large-scale disturbances are those, such as erosion, which remove the soil horizons as well as the overstory and forest floor. Some of the initiation mechanisms are (in order of increasing severity of disturbance they respond to): advance regeneration, layering, sprouts from a fallen stem, sprouts from root collars, sprouts from lateral roots, buried seeds, and seeds entering after a disturbance.

The frequency of disturbances is also important in determining the general forest type over a large area, because species dominance and stand physiognomy change with time following disturbance.
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