Chapter 2

Disturbance Regimes in Temperate Forests

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I. INTRODUCTION

Different forest types can be characterized by the mortality patterns of their canopy trees. This chapter will begin by defining the parameters necessary to characterize the pattern of death of dominant individuals (canopy trees) in a community, also referred to as that community's ''disturbance regime.'' ''Disturbance'' is defined here as a force that kills at least one canopy tree. The disturbance regimes of two particular forest types will then be described. Finally, descriptions of natural disturbance regimes will be compared with the results of manipulative studies or artificial disturbance regimes. Special attention will be given to the relative importance of large-scale versus small-scale disturbance.

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II. COMPONENTS OF A DISTURBANCE REGIME FOR FORESTS

A. Average Disturbance Rates

The average rate at which trees die can have important consequences for the species composition and structure of a forest. High disturbance rates should select for fast-growing species that reproduce early and are short-lived (Grime, 1974, 1977). If disturbance rates are too high, the tree lifeform is no longer viable and community dominance switches to shrub or herb lifeforms. Natural disturbance rates for forests also have theoretical minimum values set by the maximum age and size limits of tree species. As a tree ages and increases in size, its efficiency in transporting water, nutrients, and photosynthate usually decreases (Spurr and Barnes, 1973; Oldeman, 1978). Its roots must support a proportionally greater aboveground biomass (Borchert, 1976), and its photosynthetic tissues must support a proportionally greater mass of nonphotosynthetic tissue (Harper, 1977). These factors, plus the tendency of the tree to develop a more massive crown, render it increasingly susceptible to smaller and more common disturbances. This relationship between the external environment (frequency of disturbances, e.g., wind speeds of a certain magnitude) and the plant itself (the rate at which aging increases its susceptibility to disturbances of smaller magnitude) diminishes the usefulness of terms such as ''allogenic'' or ''autogenic'' in connection with natural disturbances.

As a result of the above factors, forest disturbance rates seem to be constrained to a fairly small range of potential values. As one consequence, forest dominants in most parts of the world have a range of life spans of 100–1000 years (Budowski, 1965; Fowells, 1965; Ashton, 1969). For temperate deciduous forests the normal range is even smaller: 300 years is the age often reached by dominants with few individuals living more than 500 years (Jones, 1945).

The average rate of forest disturbance also shows fairly little variation, despite wide differences in vegetation and types of disturbance. Northern conifer forests affected primarily by fire (Heinselman, 1973; Zackrisson, 1977) and temperate and tropical forests affected primarily by the death of scattered individuals (Leigh, 1975; Abrell and Jackson, 1977; Hartshorn, 1978; Naka, 1982; Runkle, 1982) all show average rates of disturbance of $\approx 1\%$/year (ranging from ≈ 0.5 to ≈ 2.0/year in large samples). Although these forests are different from each other in many ways, they are similar in that most canopy individuals die due to the one mechanism studied—fire or wind throw. Disturbance rates for some specific agents of tree death (e.g., 0.02–0.16%/year for tropical landslides; Garwood *et al.*, 1979) may be lower than $\approx 1\%$ because many trees die due to factors other than the one studied.

Disturbance rates of 0.5–2.0%/year give natural return intervals (average time between disturbances for a given site) of 50–200 years. These values can be reconciled with 300- to 500-year average tree longevities for the following reasons. First, certain trees live longer than average due to their presence in more protected locations or to chance deviations from normal weather conditions. Second, many important forest dominants often persist for many years under a closed canopy, growing very slowly. For instance, using age–size (diameter at breast height, dbh) regressions, trees in mesic sites in the Great Smoky Mountains National Park averaged about 91 years to reach 25 cm dbh, the approximate minimum size at which they reach the canopy (Runkle, 1982). The average time spent by individuals in the canopy, again using age–size regressions, was 127 years, in good agreement with the natural rotation periods noted above.

The somewhat surprising conclusion is that different mesic forests probably do not show very great differences in their average rates of disturbance. Therefore, important differences among the disturbance regimes of different forests are more likely to occur in the distribution of tree deaths in time and space and in the severity of the disturbance.

B. Distribution of Disturbance in Space

Over a broad geographic area, a given level of disturbance can affect either many adjacent individuals, creating a few large disturbed patches, or many scattered individuals, creating many small disturbed patches. Because patch size affects the nature of the vegetation's response to the disturbance, these two alternatives should yield different results (see Section II,B,2).

Before proceeding, one note on terminology is useful. The term ''gap'' was used by Watt (1947) to refer to a site at which a canopy individual had died and at which active recruitment of new individuals into the canopy was occurring. The emphasis was on relatively small within-community disturbance patches. This emphasis has generally been maintained in later usages of the term (see, e.g., Bray, 1956; Williamson, 1975; Whitmore, 1978; Ehrenfeld, 1980; Barden, 1981; Runkle, 1981, 1982; Shugart and West, 1981; Nakashizuka and Numata, 1982a,b). This chapter will retain this usage, although clearly a gradient exists between disturbances affecting a single tree and those affecting many square kilometers of forest.

1. Relation of the Environment to the Size of the Disturbed Area

The physical environment within a small open area surrounded by forest differs from that under the canopy or in a large open area. In a small opening, temperatures fluctuate more and light and soil moisture are both more abundant than under a closed canopy. As the opening size decreases, humidity increases, wind speed decreases, and temperatures remain more constant (Geiger, 1965). Opening size is frequently quantified as the D/H, ratio, where D is the diameter of the open area and H is the mean height of the surrounding stand (Geiger, 1965). Several studies (Jackson, 1959; Minckler, 1961; Berry, 1964; Minckler and Woerheide, 1965; Minckler *et al.*, 1973) have shown light to increase with increased opening size, reaching a maximum when $D/H \approx 2$. March and Skeen (1976) found that differences in light between a small opening and a closed forest persist throughout the growing season. Minckler *et al.* (1973) found the opening size to determine the number of years the increase in soil moisture persists, although not the size of the initial difference. Tomanek (1960) found that the shape and orientation of openings, as well as their size, can be important in determining their microclimate.

2. *Relation of Species Composition to the Size of the Disturbed Area*

Many forestry studies and general reviews state that the selective cutting of individual trees will favor shade-tolerant species such as American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*) (see, e.g., U.S. Forest Service, 1973; McCauley and Trimble, 1975; Leak and Filip, 1977; Tubbs, 1977). However, openings as small as 400 m^2 have been found to be sufficient for tuliptree (*Liriodendron tulipifera*) and yellow birch (*Betula alleghaniensis*) to maintain themselves in a forest (Merz and Boyce, 1958; Tubbs, 1969; Trimble, 1970; Schlesinger, 1976; Beck and Della-Bianca, 1981). Tryon and Trimble (1969) found a 1000-m^2 opening sufficient to regenerate several intolerant species, with relatively few adverse affects of border trees on the growth of saplings near the edge of the opening. Runkle (1982, 1984) found significant differences in the response of potential canopy species to differences in gap size for naturally formed gaps ≤ 1000 m^2 and generally ≤ 400 m^2. Williamson (1975) found evidence that gaps 50–250 m^2 were sufficient to regenerate tuliptree and white ash (*Fraxinus americana*).

C. Distribution of Disturbance in Time

A given average annual disturbance rate can be achieved by a low level of disturbance occurring in most years or by occasional years of very high disturbance followed by many years of few or no disturbances. Forests at either extreme are known. On a local level, differences in the periodicity of disturbance often parallel differences in the spatial distribution of disturbance. If most tree mortality is concentrated in a few years, then probably much tree mortality is concentrated in large openings. Therefore, species composition at sites where disturbance is concentrated in time should resemble species composition at sites where disturbance is concentrated in space. The temporal distribution of disturbance is more important on a landscape level than on a local level because it determines the synchrony of the regeneration processes occurring over a broad area. The level of synchrony of regrowth is important because of the close relationship between tree population dynamics and ecosystem changes in biomass and production (Peet and Christensen, 1980; Peet, 1981).

D. Severity of Disturbance

In addition to varying in temporal and spatial distributions, disturbances can vary in their severity. "Severity" measures the degree to which the predisturbance vegetation has been damaged and ecosystem properties have been disrupted. It is equivalent to the term "magnitude" used by White (1979). The vegetation of a site will develop more slowly after a severe disturbance than after a mild disturbance. The size and severity of a disturbance are two different properties. It is possible to have a small, severe disturbance or a large, mild one.

Several compilations of species regeneration strategies have been made (e.g., Bormann and Likens, 1979; Oliver, 1981; Canham and Marks, Chapter 11, this volume). In general, individuals growing after disturbance are present at the time of disturbance as suppressed seedlings and saplings, as seeds buried in the soil, or as seeds newly dispersed into the area. The severity of disturbance determines which of these strategies is most likely to succeed. A mild disturbance, e.g., windthrow of just the canopy trees, probably favors the suppressed sapling strategy. A more severe disturbance may eliminate suppressed saplings but leave the soil intact and favor species such as pin cherry (*Prunus pensylvanica*), which are well represented in the seed pool (Marks, 1974). A disturbance that is both very severe, e.g., long-term agriculture (eliminating saplings and the seed pool) and is conducted over a large area (greatly diminishing the potential seed rain) can result in a very protracted recovery time.

Some types of disturbances can enhance the success of certain regeneration strategies through the creation of special microhabitats. Uprooting of trees creates pits and mounds that differ in several properties from soils that have not been overturned (Lyford and MacLean, 1966; Armson and Fessenden, 1973; Stone, 1975). In particular, pits have more litter and standing water and mounds have less than do other soils. Some species differ in the part of the pit and mound surface on which they grow (Hutnik, 1952). Decomposing logs also provide a specialized habitat on which some species, such as yellow birch and eastern hemlock, reproduce (Fowells, 1965). Other examples in which the type of disturbance determines the pattern of species replacement are given by Grubb (1977).

The severity of disturbance can also be measured as the effect on ecosystem functioning. The primary influence is on soil properties and long-term nutrient dynamics. A severe disturbance results in substantial erosion and nutrient losses, which may take decades for the ecosystem to replace (Bormann and Likens, 1979). For example, low-intensity fires may have no long-term effect on ecosystem properties, but intense fires can volatilize much nitrogen, cause severe erosion, and greatly diminish future productivity at the site (Wells *et al.*, 1979).

E. Rates of Recovery from Disturbance

The rate at which a community recovers from disturbance depends upon the characteristics of the disturbance discussed above. For small and mild disturbances, recovery is determined primarily by the rates at which bordering canopy trees expand into the opened area and seedlings and saplings grow into the canopy. For larger and more severe disturbances, a more varied and elaborate process of vegetation development occurs.

In general, the latter process has been studied as ecological succession, while the former has been considered as characterizing gap dynamics. The division between the two processes is arbitrary, with "succession" being used primarily when whole communities change and "gap dynamics" when the disturbances occur within a single community. "Community" here refers to a site of sufficient size to be studied by itself. Dynamics within a gap caused by a single treefall are usually studied in relation to the surrounding forest, whereas recovery of a large area in which trees were blown down by a large storm or burned in a fire is often studied without mention of the surrounding areas.

This section will concentrate on the recovery processes most important in gap dynamics, as defined above, that is, lateral growth of canopy trees bordering the gap and height growth of seedlings and saplings within the gap.

1. Lateral Extension Growth

Several studies differing in location, species, and technique have measured reasonably similar rates of branch growth by trees bordering openings (Trimble and Tryon, 1966; Phares and Williams, 1971; Erdmann *et al.*, 1975; Hibbs, 1982; Runkle, 1982). Average rates generally range from 4 to 14 cm/year. Some trees expand at rates of up to 20 to 26 cm/year. The impact of these branch growth rates on gap regeneration depends upon the rate of sapling height growth and the size of the gap. Smaller gaps have a large ratio of edge to interior. Therefore, lateral extension growth should be proportionally more important in small gaps than in big ones.

2. Sapling Height Growth

The rate at which a gap closes due to the height growth of saplings depends on both the rate of height growth of saplings and the heights of the saplings at the time the gap was formed.

Many species from different areas in the eastern deciduous forest show average growth rates of 0.5–1.0 m/year following cutting or in naturally created (usually large) openings (e.g., Kramer, 1943; Downs, 1946; Kozlowski and Ward, 1957; Tryon and Trimble, 1969; Marks, 1975). Minckler *et al.* (1973) found species height growth to range from 9 to 73 cm/year near the centers of gaps of different sizes (less than or equal to two times the height of surrounding trees). Hibbs (1982) measured sapling height growth (the average of the three largest stems) in a hemlock–hardwood stand in Massachusetts. In small gaps ($\leq$5-m radius), saplings of different species grew 10–50 cm/year; in open field conditions, species grew 25–50 cm/year. Hibbs (1982) related the rates of sapling growth to the rates of canopy branch growth calculated for the same woods and concluded that few or no tree seedlings will reach the canopy in openings with a radius of $<$5 m. Some seedlings may reach the canopy in larger gaps because of the increased time until canopy closure occurs via branch growth.

Small gaps may still close primarily due to sapling height growth if sufficiently large, suppressed saplings are present in the gap when it is formed. Good descriptions of the height distribution of saplings in gaps immediately after formation are not available. However, many forests contain large numbers of suppressed saplings. If the disturbance is mild, then one of these saplings may grow to become the next canopy tree in less time than it would take for a new seedling to reach the canopy, especially if taller individuals grow faster than small ones, as at least occasionally occurs (Laufersweiler, 1955; Burton *et al.*, 1969; Tubbs, 1977).

To include the effects of both initial sapling size distribution and growth rates, Runkle (1982) compared the rate at which the total gap area disappeared for small gaps (average, 100 m^2) with the rate expected if branch growth by canopy trees were the only mechanism of gap closure. After the fifth year, height growth was the primary mechanism of gap closure. Even small gaps can result in successful tree regeneration if they include a large, formerly suppressed individual.

F. Importance of Multiple-Gap Episodes

One last component of a forest disturbance regime is the extent to which a tree may be affected by two or more different gaps in the course of its growth into the canopy. Such multiple gap effects should be more common after mild disturbances than after severe ones, which might kill the regenerating individual. Such multiple episodes are also more important when disturbances are small and scattered rather than clustered. Small, scattered disturbances have the greatest ratio of edge (areas affected but not injured) to internal area.

Such multiple gap episodes may be fairly common. Individuals of several species, notably hemlock, often show multiple release and suppression of ring widths, implying several episodes of gap formation and closure (Henry and Swan, 1974; Oliver and Stephens, 1977). Also, if, as mentioned earlier, average tree mortality rates are approximately 1%/year, repeated disturbances should be fairly common. For example, 36 gaps examined in Hueston Woods State Park, Ohio (Runkle, 1981, 1982) had 257 border trees, or 7.1 border trees per gap. Given those values (1%/year, mortality; 7.1 border trees per gap), about half of the gaps should be affected by a new disturbance (death of at least one border tree) within 10 years of initial gap formation. The Hueston Woods gaps were revisited 4 years after their original census (Runkle, 1984); 11 border trees had died or become moribund during that time, a value close to the 10 predicted from average rates of disturbance. Therefore, for this forest, return rates of disturbance may be common and generated primarily by deaths not influenced by the proximity of a previous tree death. In other forests, e.g., high-elevation forests of balsam fir (*Abies balsamea*) (Sprugel and Bormann, 1981), repeated disturbances are even more common because the environment next to a disturbed area is more severe than elsewhere, and so new tree deaths occur primarily among border trees.

That such multiple-gap episodes are common for at least some forest types may be very important for forest regeneration and species evolution. Species may be able to reach the canopy fairly often by using a series of small gaps rather than a single large one.

Species specializing in this mode of reproduction should be able to take advantage of temporary openings in the canopy and then should suffer only slightly after the canopy closes, thereby increasing the chance that they will still be able to respond while awaiting a new gap in the vicinity. High rates of multiple gap occurrence can also imply that individuals of tolerant species will usually be exposed to one or more gaps at some stage before reaching the canopy.

The question of whether understory-tolerant species can occasionally reach the canopy without benefiting from gaps is not resolved. To my knowledge, no species under a closed canopy has been shown to have a steady increase in height to reach canopy status. Several lines of evidence suggest that this phenomenon will rarely if ever occur. Seedlings and saplings in complete shade grow very slowly. For example, Morey (1936) found that on average it took beech 12 years and hemlock 29 years to reach a height of 1.2 m. Sugar maple and beech seedlings in Ontario grew only 2–4 cm/year both under shaded conditions and in a 200-m^2 gap (Cypher and Boucher, 1982). In small gaps (10–50 m^2), Hibbs (1982) found hemlock to grow only 10–20 cm/year. Presumably growth under a closed canopy would be even less. As a result of these very slow growth rates, these species would take ≥200–300 years to reach the canopy without occasional spurts of faster growth. This time interval is at the outer limit of the lifespan for most of these species (Fowells, 1965). Similar conclusions can be reached for diameter growth. Many tolerant trees show little or no diameter growth under shaded conditions. For example, one study in Pennsylvania found a 9-cm dbh beech missing rings for 46 of the previous 70 years and a hemlock missing rings for 39 of the previous 70 years (Turberville and Hough, 1939). Given the rates of disturbance that occur in these forests, however, the probability that a gap will affect one spot at least once within a 100- to 300-year period is extremely high.

III. NATURAL DISTURBANCE REGIMES FOR SPECIFIC TEMPERATE FORESTS

Workers in the eastern deciduous forest of North America have had several advantages in the determination of natural disturbance regimes. Although the majority of the original forest has been logged or severely disturbed, several remnants do remain on which the formerly widespread processes of forest regeneration can be studied. Historical records of other primeval forests and natural disturbances exist. Some of these historical records are remarkably quantitative, such as those of the General Land Office Survey (Bourdo, 1956). Also, North American plant ecologists have long been interested in the processes of forest disturbance and succession, and so much information is available in the literature.

This section will describe the disturbance regime associated with two different forest types and locations. The cove forests of the southern Appalachians are affected almost entirely by small-scale, mild disturbances. The forests of the Allegheny Plateau, in Pennsylvania, are affected by both small-scale and large-scale, usually mild, disturbances. The description of the Allegheny forests will also include the distribution of disturbances over the landscape, including the effect of topographic position on both disturbance regime and vegetation.

A third type of disturbance regime exists in the white pine (*Pinus strobus*)–northern hardwoods section of northern Minnesota and adjacent Canada. For these forests, fire is the primary source of large-scale forest disturbance (Frissell, 1973; Heinselman, 1973) and has been important for 10,000 years (Swain, 1973). Heinselman (1973) found average rates of burning of ≈1%/year before widespread fire suppression was adopted. Disturbance was clumped in time and space, with most of the area burned in one of only a few major fire years. All present stands within the 415,782-ha Boundary Waters Canoe Area owe their origin to fire. Therefore, small-scale disturbances seem to be relatively unimportant. Because this disturbance regime has been adequately summarized elsewhere (Heinselman, 1973, 1981a), it will not be discussed further here.

A. Cove Forests of the Southern Appalachians

Cove forests occur in sheltered areas near creeks at middle elevations throughout much of the southern Appalachian mountains (Braun, 1950; Whittaker, 1956; Golden, 1981). They are dominated by differing combinations of mesophytic tree species, particularly sugar maple, yellow buckeye (*Aesculus octandra*), yellow birch, American beech, silverbell (*Halesia carolina*), white basswood (*Tilia heterophylla*), and eastern hemlock.

The disturbance regime for the cove forests is determined by their regional and local topographic positions. Fire occurrence rates on a county basis are very low to moderate for most of the mountainous counties of eastern Tennessee and western North Carolina, in contrast to higher rates nearer the coast (Nelson and Zillgitt, 1969). Within the mountains, fires are uncommon, occurring primarily on south-facing slopes near ridge tops, especially on lower ridges (Barden and Woods, 1976; Harmon, 1982). North-facing lower slopes and sheltered ravines have the lowest incidence of fire (Harmon, 1982).

Wind-related disturbance tends to be dominated by small-scale events. Glaze storms are more common than large-scale, damaging tropical storms (Nelson and Zillgitt, 1969). Tornadoes are not as common or severe as they are in most of the rest of the eastern deciduous forest (Fujita, 1976). Occasional tornadoes do occur, however.

Human disturbance of most sites once dominated by mixed mesophytic species has been extensive. Therefore, most work on the long-term dynamics of mixed mesophytic forests has been done in one of the remaining old-growth remnants, either the Great Smoky Mountains National Park (GSMNP) of Tennessee and North Carolina or unlogged coves in one of the nearby national forests. These areas were protected from extensive logging by their regional inaccessibility until about 1900 and by the formation of the GSMNP in 1940. Between 1900 and 1940, however, virgin timber was removed by commercial loggers from most of the present-day park. Also, substantial areas of the GSMNP had been cleared and selectively cut by local people (Frome, 1966). Despite these human influences, enough undisturbed forest remains at middle and high elevations to allow a meaningful characterization of the natural disturbance regime.

The exact locations of the sites to be discussed below were further constrained by two additional factors. Most sampling was done far enough away from streams or near small enough streams so that *Rhododendron maximum* was nearly or entirely absent. The presence of a dense shrub layer of rhododendron influences regeneration by greatly diminishing the success of an advance sapling regeneration strategy. As a consequence, cove forests with rhododendron have more red maple (*Acer rubrum*) and more hemlock and *Betula* spp., which regenerate on fallen logs, and less sugar maple, yellow buckeye, beech, silverbell, and basswood, all of which depend on advance sapling growth than do cove forests without abundant rhododendron (Oosting and Bourdeau, 1955; Barden, 1979, 1980; Lorimer, 1980). The second local restriction in sampling was to avoid slope communities in which American chestnut (*Castanea dentata*) had been important before its demise (Woods and Shanks, 1959).

The disturbance regimes of the cove forests are thus influenced by their regional and local positions. Deaths of canopy trees occur primarily as scattered small-scale disturbances affecting only one or a few trees at a time in any one location. Likely causes of tree mortality are glaze storms, lightning strikes, or occasional very high winds. Disturbances are not very severe. Surrounding vegetation diminishes the loss of nutrients from the site, so that long-term ecosystem functioning should not be harmed. Many saplings and other advance regeneration are present, so vegetation recovery should proceed rapidly.

The following data on the disturbance regime parameters for cove forests are summarized primarily from Runkle (1982), unless otherwise stated.

Overall, in the cove forests, 0.5–2.0% of the land surface area in individual sites was converted from forest to new treefall gaps per year. The average for all sites studied was 1.2–1.3%/year, in agreement with figures from other forest types, as discussed above. Romme and Martin (1982) found lower disturbance rates (0.25–1.0%/year, depending on the method of calculation) for an old-growth mixed mesophytic forest in Kentucky. They did not include very small gaps created by parts of still living canopy trees, so the two results are not strictly comparable.

Gap areas followed a lognormal distribution, with many small and a few large gaps. The average size of a canopy opening was ~31 m^2 if the very small gaps caused by the fall of large branches or small canopy trees were included. Canopy opening sizes ranged up to 1490 m^2, with ≈1% of the total land area in gaps of >400 m^2. Most gaps were created by the death of single trees, but multiple treefalls accounted for most of the larger gaps. Similar values for gap size in these forests are given in Barden (1981). Similar values for gap size were also found in a climax stand of Japanese beech (*Fagus crenata*) and other mixed mesophytic species in Japan (Nakashizuka and Numata, 1982a,b). Because the gaps were fairly small, with diameter/canopy height ratios <1, the difference in environmental conditions between the gap and the forest understory is smaller than for a forest dominated by large-scale disturbances. However, small gaps have greater edge/area ratios than do larger openings. Therefore, cove forests should contain very large fractions of land area partly affected by disturbance.

Yearly fluctuations in the rate at which gaps are formed occur but are minor. For example, for 10 different sites in the southern Appalachians and for 15 years per site, the maximum fraction of land area per year in gaps was only 7.4%. Every year, several storms in the general area down enough trees to cause notable economic damage (Environmental Data Service, 1975). The rugged topography results in different areas having different peak years of disturbance, with no sign of regional synchrony in gap formation.

A disturbance regime characterized by many small gaps with a large ratio of edge to area might be expected to show high rates of repeat disturbance. New gaps should often form close enough to old gaps to maintain the changed environmental conditions associated with gaps and to slow the processes of gap closure. In one study designed to test this hypothesis (Runkle, unpublished data), high rates of repeat disturbance were found. For 273 gaps revisited 6–7 years after originally being sampled, one or more canopy trees surrounding the gap had died or been severely injured in 114 gaps, a former large stump from the tree creating the gap had fallen in 62 gaps, and new gaps were created near but not immediately adjacent to the original gap 35 times. In only 112 gaps did none of these new disturbances occur. Canopy trees surrounding gaps died at about the same rate as canopy trees in general. Multiplying the number of original surrounding canopy trees by a 1%/year disturbance rate by 6 or 7 years gives a predicted number of deaths of 151 trees versus 164 deaths or severe injuries actually recorded. For these forests, therefore, repeat disturbances are common and are a property of the size and age distributions of gaps. The evolutionarily important consequence of this result is that tree species should be favored whose saplings are able to alternate between periods of moderate to rapid growth while in gaps and periods of slow growth during the times between gaps.

Gaps close both by the branch extension growth of trees surrounding the gap and by the height growth of saplings in the gap. For these small gaps, both processes are important in gap closure. Small gaps close primarily by lateral extension growth, except where large, previously suppressed saplings are present. Large gaps close primarily by sapling height growth.

Species responses to gap size form a gradient. At one extreme are tolerant species, whose life cycle usually includes a lengthy suppressed sapling stage. These species, e.g., sugar maple, yellow buckeye, beech, and hemlock, are adapted to alternating periods of growth and suppression, and therefore seem especially able to benefit from small but repeated disturbances. They can also grow well in some larger gaps. At the other extreme are intolerant species, e.g., tuliptree, which can grow very rapidly in large gaps but cannot grow in small gaps and cannot withstand suppression. These species are therefore restricted to gaps large enough to preclude closure by lateral extension growth or by previously suppressed saplings.

Given these species differences, are processes presently occurring in the range of gap sizes studied sufficient to account for the canopy composition of the stands studied? Is there evidence that episodic large-scale disturbance events need to be involved to generate the species composition present? Runkle (1981) and Barden (1981) both found very good matches between the species composition of saplings in gaps and the species composition of the canopy in several different cove forests. Therefore, small-scale disturbance does seem adequate to perpetuate these forests. The distribution of gap sizes results in forests dominated by tolerant species, with intolerants persisting at low densities.

This analysis suggests that the relative abundance of tuliptree may be a good indicator of the disturbance regime present in a stand. Its importance should be related to the frequency of gaps >400 m^2 or so. Support for this suggestion comes from the fact that of the sites studied by Runkle (1981), Joyce Kilmer had both the largest gaps and the highest importance of tuliptree. Lorimer (1980), in a more intensive study of Joyce Kilmer, found average rates of disturbance (3.8–14.0% of total land area/decade) similar to those of other cove forests but concluded that tuliptree originated primarily after occasional large windthrows. The widespread distribution of tuliptree in climax forests of the Piedmont (Skeen *et al.*, 1980) implies that such intermediate-size disturbances (say, 400 m^2 to 1 ha) are fairly common there. The virtual absence of tuliptree in most cove forests studied in the GSMNP implies that disturbances >400 m^2 are relatively rare there.

B. Forests of the Allegheny Plateau, Pennsylvania

The forests of the Allegheny Plateau in northwestern Pennsylvania differ from the cove forests of the southern Appalachians in their disturbance regime. The Allegheny forests are affected more often by large-scale disturbances. However, small-scale disturbances also occur and are important. Thus, the Allegheny forests represent a disturbance regime intermediate between the cove forests and forests whose dynamics are dominated almost completely by occasional large disturbances, such as the pine-dominated forests of northern Minnesota. Also, the literature on the Allegheny forests relates more clearly how topographic position and soil structure influence the disturbance regime and the vegetation.

The Allegheny Plateau contains broad, level uplands interspersed with narrow river valleys (Hough and Forbes, 1943). The uplands are 600–750 m above sea level south of the glacial border and held up by the hard sandstones of the Pottsville and Pocono series. The valleys are V-shaped, narrow, and winding, with a relief of $\geq$120–240 m. Slopes are usually steep and rocky. A mantle of surficial materials of varying thickness completely covers the bedrock of almost the whole region, becoming generally thicker on lower slopes (Goodlett, 1954).

Differences in soils and topography are reflected by differences in vegetation. Of several types of presettlement forests that occurred in this area, two will be examined here. Stands dominated by white pine occurred on sandy river flats and terraces and on lower slopes where the soil was loose and sandy, particularly on south-facing slopes (Hough, 1936; Hough and Forbes, 1943; Marquis, 1975b). American chestnut, red maple, northern red oak (*Quercus rubra*), and white oak (*Q. alba*) were confined mainly to these stands. A second major vegetation type was dominated by eastern hemlock and American beech. This vegetation type was the most widespread climax type, occupying most north-facing slopes and poorly drained upland sites (Hough, 1936; Hough and Forbes, 1943; Marquis, 1975b; Bjorkbom and Larson, 1977). Common associates of hemlock and beech in these stands were sugar maple, black cherry (*Prunus serotina*), and yellow birch.

These two different vegetation types were characterized by substantially different disturbance regimes, which interacted with the soils and topographic positions to determine the vegetation. White pine was associated with disturbances such as fires and windthrows large enough to allow light to reach the forest floor and severe enough to expose mineral soil. Fire frequency in the region is greater than in the Appalachian mountains, although less than in the forests of northern Minnesota (Bormann and Likens, 1979). In sites near Heart's Content, Lutz (1930b) found fire scars on 86 trees, accounting for 41 different years in the interval 1727–1927. Five fire years were noted on six or more trees each. Such fires are thought to have given rise to white pine stands in Heart's Content and Cook Forest, two of the only extant pine stands in the region (Lutz, 1930b; Hough and Forbes, 1943). In other places, white pine originated primarily after windthrows uprooted trees and exposed mineral soil on treefall mounds (Goodlett, 1954). Large white pine stumps are still abundant on treefall mounds in various stages of settling (Goodlett, 1954). This mechanism of establishment also helps explain the existence of white pine in several areas as scattered individuals rather than as a pure stand originating after one large-scale disturbance (Lutz and McComb, 1935; Goodlett, 1954).

The disturbance regime of the moister uplands varied considerably from that of the pine-dominated stands. Fires were rare or absent due to the moist forest floor and lack of inflammable undergrowth (Lutz, 1930a; Hough, 1936; Goodlett, 1954; Bjorkbom and Larson, 1977). Even at Heart's Content, the section without pines, which was cooler and moister than the section with pines, contained no evidence of fires (Lutz, 1930b). Occasional large-scale windthrows do occur (Hough, 1936; Goodlett, 1954). For instance, large storms in 1808 and 1870 uprooted trees in areas many hectares in extent in the Tionesta tracts (Bjorkbom and Larson, 1977). Areas affected by such large-scale disturbances regenerate into stands dominated by species with intermediate tolerance and long-lasting dormant seeds, such as red maple, black cherry, black birch (*Betula lenta*), and yellow birch. Surviving saplings of hemlock, beech, and sugar maple may also be present.

Despite the existence of these large-scale disturbances, "a widespread blowdown during a single intense storm is probably less common than the loss of a single tree here and there throughout the stand over a long period" (Hough 1936, p. 19). Many of the major sources of regional disturbances affect trees singly or in small clumps. Prolonged periodic droughts occur and result in heavy mortality of shallow-rooted trees species such as hemlock and yellow birch (Hough and Forbes, 1943; Bjorkbom and Larson, 1977). However, the effects of such droughts might be expected to be restricted to scattered individuals that are already weakened or located on unfavorable microsites. Similarly, ice or glaze storms occur but cause loss primarily of branches or scattered trees, particularly because the dominant species are fairly resistant to ice damage (Bjorkbom and Larson, 1977).

The regime of small-scale disturbances or gaps presently occurring in protected old-growth hemlock–beech stands is very similar to the one described earlier for the southern Appalachian cove forests (Runkle, 1981, 1982). Gaps were smaller on average than in the cove forests and rates of disturbance were only 0.5% of land surface area per year, near the low end for eastern forests although close to measurements from some parts of the southern Appalachians (Runkle, 1982). This low rate of disturbance is perhaps related to the more complete dominance in the Tionesta sites of two of the longest-lived species, beech and hemlock. Also, occasional cutting or large-scale disturbances may have decreased the number of old trees likely to form gaps. Beech dominated the gap regeneration for all gap sizes, but there was some tendency for hemlock to reach its maximum abundance in small gaps and sugar maple to reach its maximum abundance in intermediate-sized gaps. Overall, the species composition of saplings in gaps was very similar to the species composition of the canopy (Runkle, 1981). Therefore, a disturbance regime characterized by small-scale disturbances seems sufficient to maintain the beech–hemlock forests.

The effect of non-Indian settlement on the area was to disrupt the natural disturbance regime, with major direct and indirect consequences for the vegetation. These disruptions were not uniform, but affected some areas and some species much more than others.

The white pine-dominated areas were the most severely affected. White pine was the most prized timber species and was eliminated from the canopy almost completely by 1900 (Goodlett, 1954; Marquis, 1975b). Extensive fires from the logging slash eliminated the seedling pines (Marquis, 1975b). As a result, white pine is virtually absent from the forests today and is unlikely to return in the foreseeable future. A second important species, American chestnut, has been almost completely eliminated due to an introduced disease. As a result of these two species eliminations, the drier sites today are dominated by various species of oak (Goodlett, 1954).

The effects of human settlement on the upland forests have been less striking and more indirect, but still important. Hemlock remains important but less so than in the primeval forests, due partly to extensive logging for its tannin-rich bark. Hardwoods have increased in relative density due to their ability to sprout or survive as buried seeds following logging and fires (Marquis, 1975b). A large deer herd has become established due both to increased protection from hunting and to abundant forest growth following cutting, resulting in much available browse (Marquis, 1975b). Deer populations are now high enough to impede the growth of seedlings and saplings following natural or human-caused disturbances (Hough, 1965; Jordan, 1967; Marquis, 1974, 1981; Bjorkbom and Larson, 1977; Marquis and Brenneman, 1981). The net impact of deer browsing has been to favor beech at the expense of hemlock and other hardwoods. Because beech is one of the dominant species, the effect on the vegetation overall may be small. However, the elimination of many small hemlock stems is a concern and may result in sharp decreases in hemlock density in the future. On the other hand, hemlock regeneration in much of the region occurs irregularly, so the species may be able to survive a prolonged period of very little regeneration (Hough and Forbes, 1943).

Another change in disturbance regime affected by human use has been the elimination of large stems and therefore a decrease in the rate of gap formation. Forests characterized by small-scale disturbances have a sizeable fraction of their total area in or near gaps. Repeat disturbances are common. Therefore, saplings of many species are able to become established and be ready to respond to new openings. A second growth stand does not possess as many opportunities for saplings to become established. Unfortunately, especially given high deer-browsing pressure, the success of all cutting methods in establishing a favorable new stand requires that an abundance of seedlings already be established beneath the canopy of the existing overstory (Marquis and Brenneman, 1981). The most effective response of foresters is to mimic the primeval disturbance regime through shelterwood cutting, in which the canopy is removed in stages, gradually increasing light to the understory and increasing the number of saplings available to grow when the last of the old canopy is removed (Marquis and Brenneman, 1981).

In summary, the forest composition of the Allegheny Plateau is determined by the interaction of the natural disturbance regime, topography, and soils. South-facing slopes and sandy soils are affected by fires and blowdowns that uproot trees, both of which disturbances favor white pine and associated relatively shade-intolerant species. Upland moist sites are affected primarily by small-scale disturbances that favor shade-tolerant species. Large-scale blowdowns on these sites favor species of intermediate shade tolerance. Human influences on the area have disrupted the natural disturbance regimes, producing several changes in the species composition of the area.

IV. ARTIFICIAL DISTURBANCE REGIMES

In the preceding section, forest type and disturbance regime were found to be somewhat correlated. The causal relationship is not clear. Do the species otherwise adapted to an area (due to soils, climate, etc.) determine the disturbance regime, or does the potential disturbance regime in an area determine the vegetation? Both factors may interact simultaneously and reciprocally, so that simple causation is impossible to detect. To identify the chain of causation, it would be useful to conduct field studies, varying the disturbance regime to determine whether the pattern of disturbance by itself can affect species composition and the forest as a whole. Fortunately, such studies have been done many times at many different locations by foresters concerned with maximizing the harvest while selecting for a certain species composition in the new growth following disturbance. In the forestry literature, artificial disturbance regimes are referred to as "silvicultural systems."

Many such systems have been proposed and tested for particular locations and particular species (see, e.g., Smith, 1962; U.S. Forest Service, 1973, 1978; Tubbs, 1977). Two examples follow.

Trimble (1965) compared the effects of two different cutting regimes on cove hardwood forests in West Virginia. Uncontrolled clear-cutting on good sites had produced stands that included a high proportion of shade-intolerant species. Tuliptree, northern red oak, and black cherry made up more than half of the stems in the overstory. In contrast, Trimble (1965) used selection cuttings on 40- to 50-year-old stands to harvest individual trees. The trees removed were either large and salable or of poor quality (culls). The result of this cutting regime after 10–15 years was to favor sugar maple, which eventually seemed likely to make up over half of the stand. American beech would also greatly increase, except that it is heavily culled by foresters. The three relatively intolerant species listed above would shrink in importance to ≤20% of the future stand.

Leak and Filip (1977) obtained similar results from a stand of northern hardwoods in New Hampshire subjected to group selection. Groups of trees were removed, leaving openings averaging about 2000 m^2. This disturbance regime was sufficient to allow intermediate and intolerant species to maintain their relative importance in the stand at 25–35%. In contrast, under single-tree selection cuts, tolerant species came to represent 92% of canopy individuals.

One of the general conclusions of these and similar studies is that to reproduce the original species composition of the northern hardwood forest region, it is necessary to use a mixture of selection cuts (of one or a few trees at a time) and larger patch cuts or clearcuts. Selection cuts favor tolerant species such as American beech, sugar maple, and eastern hemlock. Larger cuts favor relatively intolerant species such as yellow birch and tuliptree. This mixture of gap sizes is precisely the one that characterized much of the primeval forest. Another useful silvicultural system for this forest type is the shelterwood system, in which scattered trees remain after the first cut and are removed only when the sapling layer is established. The scattered trees help shade and protect the young saplings. This system seems similar to damage by mildly severe natural windstorms or to glaze storms in which scattered trees are left standing.

The responses of individual species to different silvicultural systems can also be used to estimate the natural disturbance regime of forests originally dominated by those species. For instance, because beech and sugar maple are favored by selection cutting, it seems reasonable to hypothesize that the beech–maple forest region (Braun, 1950) was characterized by a prevalence of small-scale gap disturbance. Also, because beech is very susceptible to damage by fire (Fowells, 1965), the small-scale disturbances most common to this forest region must have been due to wind or glaze storms.

V. SUMMARY

Temperate zone forests such as those discussed here differ in species composition and structure. However, some broad similarities in their disturbance regimes exist. Usually, these forests are affected by both large-scale and small-scale disturbance, with the relative importance and spatial distributions of each having great consequences for the regional vegetation (Whittaker and Levin, 1977; Pickett, 1980). The interplay of disturbances of different sizes is probably more important than the existence of a single intermediate type of disturbance (to oversimplify Connell, 1978) in determining species diversity and other community properties. Some forest types fit the generalization of Horn (1981a) and Oliver (1981) that large-scale (clumped in time and space and often severe) disturbances occur frequently enough so that most canopy individuals originate following such disturbances. However, small-scale gap disturbance is of primary importance for many areas and forest types. Most forests probably follow the pattern of cyclic development (succession) and steady state (climax) described by Loucks (1970), with great variations in the time and number of canopy tree generations between cycles, ranging from decades to millennia.

Further study is needed to clarify several aspects of the disturbance regimes of temperate zone forests. The primeval and therefore evolutionarily important disturbance regimes for many forest types need to be described in more detail. In North America, oak-dominated forests in particular require more study to determine the relative importance of fire, large- or small-scale windthrows, insect defoliation, and other factors. The effects of disturbance regimes greatly modified by human activity also need to be documented. The disturbance regimes associated with particular successional stages need to be clarified to determine at which successional stage a treefall provides sufficient resources for a sapling to reach the canopy instead of allowing solely for the crown expansion of its neighbors. It is also important to know the tolerance of different species of plants and animals to deviations in their primeval disturbance regimes so as to manage best their continued existence.

In summary, the concept of a disturbance regime has proved a useful way to summarize much information on the natural dynamics and regeneration of temperate zone forests. It also lends itself well to the continued development of a management theory for those forests.

RECOMMENDED READINGS

Bray, J. R. (1956). Gap phase replacement in a maple–basswood forest. *Ecology* **37,** 598–600.
Loucks, O. L. (1970). Evolution of diversity, efficiency, and community stability. *Am. Zool.* **10,** 17–25.
Watt, A. S. (1947). Pattern and process in the plant community. *J. Ecol.* **35,** 1–22.
White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* **45,** 229–299.