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# **Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains\***

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## **Abstract**

In constructing models of species and community distributions along environmental gradients in the Great Smoky Mountains, R. H. Whittaker (1956) focused on old-aged, apparently stable, natural communities. More recent studies indicate that disturbance gradients potentially influence and are influenced by the complex environmental gradients of Whittaker's original models. Using primarily fire and exotic species invasion as examples, this paper shows: 1) disturbance parameters vary along the topographic, elevation and moisture gradients in the Great Smoky Mountains in much the same way as temperature, moisture and solar radiation change; 2) species composition at different locations along the major environmental gradients is partially determined by the disturbance parameters; 3) species characteristics such as mode of reproduction are often correlated with specific disturbance parameters; 4) functional aspects of ecosystem response to disturbance vary along environmental gradients; and 5) man-caused disturbance may vary along environmental or biotic gradients. Since disturbance gradients may parallel physical environmental gradients, the two may be difficult to distinguish. Modification of disturbance frequencies along major environmental gradients may result in slow shifts in the distribution of both individual species and whole communities.

## **Introduction**

R. H. Whittaker's classic study of vegetation of the Great Smoky Mountains (Whittaker, 1956) documented population and community distributions along major environmental gradients. In this work, Whittaker presented an enduring model of the vegetation-landscape relations of this diverse region and provided central paradigms for the field of plant ecology. As a simplification, Whittaker focused his work on old-aged, apparently stable, natural communities and avoided sites obviously influenced by recent disturbances such as fire, logging, and windfall. In the last decade, however, plant ecologists have intensified work on the role of natural disturbance in community structure and

dynamics (see e.g. White, 1979; Pickett & Thompson, 1978). Biologists in such preserves as Great Smoky Mountains National Park have also become concerned with the influence of direct and indirect human disturbance (White & Bratton, 1980).

Whittaker's original study sites are protected within the second largest eastern North American National Park (Great Smoky Mountains National Park; hereafter, GRSM). However, as is the case for most preserves worldwide, preservation does not connote stasis (Bratton & White, 1980). Natural and anthropogenic disturbances overlay Whittaker's original model of the Great Smokies coenoplane. Our purpose in this paper is to show how these disturbance gradients potentially influence and are influenced by the complex environmental gradients of Whittaker's original model. We devel-

\* Botanical nomenclature follows Radford *et al.* (1968).

op this theme using several of the better documented disturbance regimes in this landscape.

### Characteristics of disturbance gradients

In this paper we present five characteristics of disturbance-vegetation interaction along gradients.

First, disturbance parameters vary along the topographic, elevation and moisture gradients in GRSM in much the same way as temperature, moisture and solar radiation change (White, 1979; Bratton *et al.*, 1981). These disturbance parameters include

- a) *Frequency* – average number of disturbance events per time period within a given area (most commonly used as point frequency, the number of events per time period at one locus in the landscape).
- b) *Predictability* – inversely related to variation around mean frequency.
- c) *Area* – average area disturbed per event.
- d) *Cycle* – time interval required to disturb an area equivalent to the arbitrarily defined area of interest (i.e., the study area, see Heinselman, 1973). This does not assume each site was disturbed once during the cycle; some sites may not have been disturbed while others may have been disturbed several times.
- e) *Severity and intensity* – these two are distinguished as follows: severity represents the impact of the disturbance on the community, thus, severity is defined in terms of change in community properties such as basal area, density, species composition and biomass; intensity refers to properties of the disturbance itself. In the case of fire, intensity equals heat released per length of fireline per time, whereas, in the case of rainstorms, intensity equals volume or depth of precipitation per time period.

Second, the species composition at different locations along the major environmental gradients is partially determined by the disturbance parameters. In other words, to fully understand the distribution of species along environmental gradients one must often consider disturbance effects. For example, with widespread burning, *Pinus* covers a broad portion of the moisture gradient, but with little fire it occurs only on the most xeric sites

(Barden & Woods, 1976; Barden, 1977). Disturbances such as severe windstorms and fires, may influence both local (within stand) species composition and the position of large areas of successional vegetation along topographic, moisture and elevation gradients.

Third, species characteristics such as mode of reproduction, are often correlated with specific disturbance parameters. The distribution of such characteristics will likely be the result of a combined response to environmental factors such as moisture availability and disturbance events such as fires.

Fourth, functional aspects of ecosystem response to disturbance vary along environmental gradients. This is particularly true of soil recovery and decay of dead organic matter.

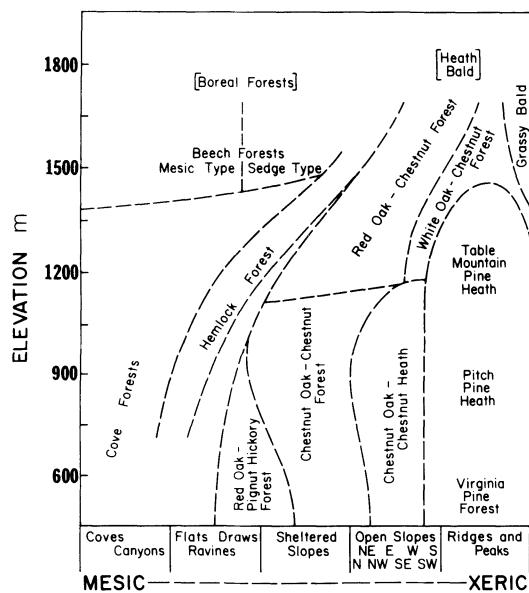
Fifth, man-caused disturbances, including those which have appeared since the establishment of the National Park may vary along environmental or biotic gradients, and gradient analyses, such as those of Whittaker, may be used to predict the frequency, intensity, and severity, of these unnatural disturbances on a landscape basis. The differentiation of man-caused and natural disturbance is fundamental in U.S. National Park Service management philosophy in that the former are, at least in a theoretical sense, to be excluded, while the latter are, ideally, to be allowed. In reality, however, some man-caused disturbances have permeated National Park borders (e.g., chestnut blight), while some natural disturbances (e.g., lightning fire) have often been suppressed. Some man-caused disturbances closely resemble natural disturbances (e.g., fire in GRSM, at least in some kinds of pine stands), whereas other man-caused disturbances have no close analog among natural disturbances (e.g., rarely are natural pathogens as dramatic in effect as chestnut blight).

Natural disturbances occur as a result of an interaction of climate, topography, geology and biota. In GRSM, windstorms, ice storms, floods, droughts, late frosts, debris slides, erosional processes, karst processes and the activities of both vertebrates and invertebrates have caused, at various times, major disruptions of community structure or ecosystem function. We analyze some of the better documented disturbances, including both man-caused and lightning-caused fire and exotic species invasion to illustrate the five above-mentioned points.

## Study area

The 208 000 ha GRSM National Park, located at N 35°37', W 83°31' in the southern Appalachian Mountains, has had only minor boundary revisions since R. H. Whittaker first studied the area in 1947. Elevations are among the highest in the southeastern United States, ranging from 256 to 2 025 m. However, the mountains are not high enough for a climatic tree line. The climate is continental warm temperate. Rainfall is high, ranging from 1 500 mm at 445 m to 2 500 mm at 1 520 m (Stephens, 1969). The bedrock is largely metamorphosed sandstones and shales of Precambrian age. Ordovician limestone is exposed in 'windows' through the Precambrian overthrust in the western part of the park (King *et al.*, 1968). Whittaker (1956) did not investigate stands below about 500 m elevation and did not consider the diverse, and largely successional communities on limestone.

**Vegetation of Great Smoky Mountains Pattern of Eastern Forest System**



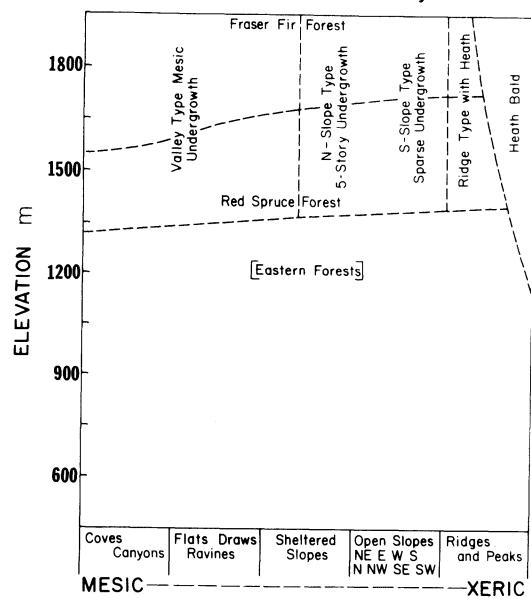
*Fig. 1a.* The original gradient analytic model of Whittaker (1956). Major vegetation types are shown relative to their topographic and elevation positions. Vegetation in the eastern and western halves of the Great Smoky Mountains is dissimilar in that spruce-fir forest dominates the high ridges in the east but hardwood types dominate in the west. On the abscissa, the diagram shows the shift from sheltered valley (coves) with low evapotranspiration to drier exposed ridges. The ordinate shows changes with increasing elevation.

Whittaker (1956) listed 14 major mature vegetation types (Figs. 1a and 1b).

As indicated by Whittaker's community type names, chestnut (*Castanea dentata*) was formerly a co-dominant in four communities. It has been eliminated as a canopy tree due to chestnut blight (Woods & Shanks, 1959).

Whittaker's basic gradient model of vegetation types is shown in Figures 1a and 1b. In this paper, we assume that Whittaker's model is largely correct, but the five points we have proposed concerning disturbance are not dependent on Whittaker's data *per se*. Recent work by Baron & Matthews (1977) showed that Whittaker's scheme applied to the generally more xeric North Carolina side of the park (where Whittaker did little sampling), but that communities are displaced somewhat in regard to topographic position. For example, mesic communities such as hemlock forests tended to be limited to stream valleys whereas oak forests extend onto the valley floors. Data of Eager (1978) and Johnson (1977) indicate a higher elevation range for red spruce than that reported by Whittaker

**Vegetation of Great Smoky Mountains Pattern of Boreal Forest System**



*Fig. 1b.* The original gradient analytic model of Whittaker (1956). Major vegetation types are shown relative to their topographic and elevation positions. The diagram is separated from Figure 1a, because hardwood types dominate between 4 500 and 5 800 feet in the western half of the park.

(1956). The grassy balds appear to be anthropogenic communities, and should be removed from the topographic analysis (Lindsay & Bratton, 1979a; 1979b; 1980). Stratton & White (1982) indicate that heath balds occur on less than 50% of the seemingly appropriate sites as defined by elevation and topography. Disturbance is probably a key element in their occurrence although soil depth and moisture availability are doubtless also critical. Our observations indicate there are flood plain communities at low elevations, which were not described by Whittaker, and therefore his data do not cover a full range of edaphic conditions in the National Park.

## Methods

The results presented in this study have been derived from several sources. First, the fire history statistics and the distribution of fires along environmental gradients are derived from U.S. National Park Service records collected from 1940–1979 and analyzed by Harmon (1981). These records include the date, the probable point of ignition, the probable source of ignition and the maximum extent of an individual fire. Topographic and forest type information in the park records was verified by plotting on topographic maps, and in some cases, by visiting the site of the fire. The data were supplemented by fire frequency estimates obtained by removing wedges of wood from the trunks of fire-scarred trees and reading tree rings to date fire scars going back to about 1850 (Harmon, 1982a). The diagrams of species response to disturbance were constructed using Whittaker's (1956) models of individual tree species distribution. Species were classified as sprouters or non-sprouters and then densities for individual species were summed to give totals for the response classes.

The discussion of recovery after fire adapts Olson's (1963) model for prediction of forest floor recovery rate which is based on relationships between production, decay rate and the time required to reach a steady-state litter biomass. In the simplest case, Olson assumed that litter production was not affected by the presence of fire and that 100% of the original litter layer was removed. In this case the time required to reach 95% of the steady-state biomass  $t_{0.95} = \frac{3}{k}$  where  $k$  is the exponential decay rate.

The amount of biomass accumulated at steady-state is equal to  $\frac{I}{k}$  where  $I$  is the input or production rate. Although few fires would meet the assumptions of this simple model, these relationships represent a relative index by which ecosystems can be compared. Figure 7 was prepared by estimating the  $t_{0.95}$  for the species shown in Whittaker's (1956) species nomograms. Data from Shanks & Olson (1961) and Singh & Gupta (1977) were used to estimate  $t_{0.95}$  for specific species. Since our knowledge of species decay rates is very rudimentary we grouped  $t_{0.95}$  into 5-year intervals. The mosaic charts were then used to calculate a weighted average  $t_{0.95}$ . That is, each species contributed litter relative to its density. We have made two simplifications in presenting this model: we have assumed 1) that biomass is proportional to stem density, and 2) that decay rates can be represented as a single value per species (more realistically they vary with environment).

The diagrams of the spread of the exotic chestnut blight and balsam woolly aphid impact were obtained directly from Whittaker's (1956) data on the host species distributions. The pattern of wild boar (*Sus scrofa*) impact was derived from an indirect gradient analysis using data from 60 50 m × 20 m vegetation plots placed at representative positions across the major elevational and topographic gradients. The ordination was completed using the Cornell Ecology Programs package (Gauch, 1973) for principal components analysis of the total basal area, by species, for all woody stems 1 cm in diameter or greater, 1.4 m above the ground. The percentage of hog rooting was estimated for the entire surface area of the plots in 1977 and 1978 (see Bratton *et al.*, 1982 for details).

## Results and discussion

### *Fire as a cause of disturbance*

Our first two characteristics of vegetation-disturbance gradients (that disturbance parameters vary along gradients and species composition along gradients is partially determined by disturbance) are well illustrated in GRSM by fire pattern and history. Fire in GRSM has been both natural and anthropogenic. The pattern and impact of fires has

changed dramatically over the history of GRSM and much of this change has been associated with the management practices of man. Recent records of fire occurrence, size and cause are very complete when compared to disturbances such as wind or frost damage. However, records predating the establishment of GRSM are incomplete and mostly qualitative in nature. Man has inhabited the southern Appalachians for at least 12 000 years (Dickens, 1976) and has probably been a major cause of fires during this time. When Euro-American man first contacted the Cherokee tribes, man-set fire was probably an important landscape influence (Goodwin, 1977). Euro-American settlers inhabited GRSM between 1790 and 1930 and frequently burned submesic and xeric forests below 1 500 m elevation (Ayres & Ashe, 1905; Lambert, 1958). Harmon (1982a) found that *Pinus*-dominated forests in the western portion of GRSM were burned with a mean frequency of once every 12 year during the period ca 1850–1930. The fire interval frequency for Harmon's entire study area, which included many mesic forest types, was estimated to be 25 yr. Many of the fires set by man during this period were light surface fires (Ayres & Ashe, 1905). This contrasts strongly with the period of logging fires between 1910 and 1930 (Lambert, 1958) when large quantities of logging slash combined with dry weather conditions led to severe and widespread fires. Since 1930 much of GRSM has been protected from fire. The characteristics of all GRSM fires between 1940 and 1979 were studied by Harmon (1981). Man caused the majority of fires during this period both in terms of number (87%) and area burned (97%). This pattern reflects the overall trend in the southern Appalachians as a whole (Barden & Woods, 1974). At present the GRSM fire cycle is very long: 840 yr for man-caused and over 30 000 yr for lightning-caused fires. Clearly, fire suppression activities of park management have all but eliminated fire as a disturbance.

The distribution of fires over the landscape is not even and varies with the cause (Figs. 2 and 3). For both natural and man-caused fires, occurrence decreases as elevation increases, but most lightning fires occur on xeric sites while most man-caused fires start on mesic sites. The decrease in fire frequency with elevation is probably associated with many factors including decreasing temperatures, decreasing evapotranspiration, increasing precipi-

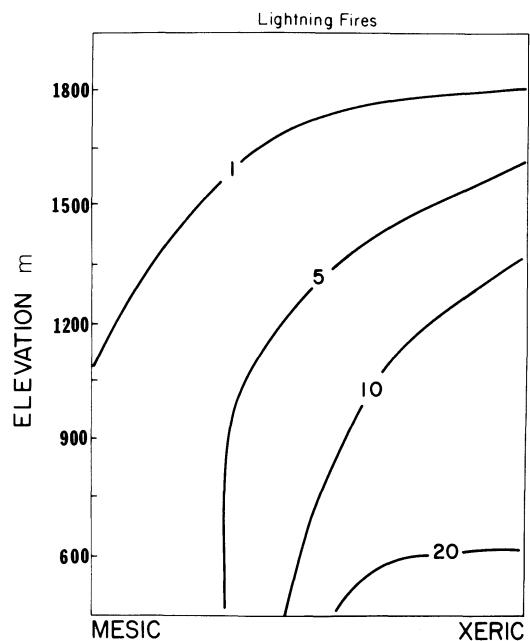


Fig. 2. Distribution of lightning fire ignitions based on data from Harmon (1981). The isolines represent the relative abundance of total lightning-caused fires observed between 1940 and 1979.

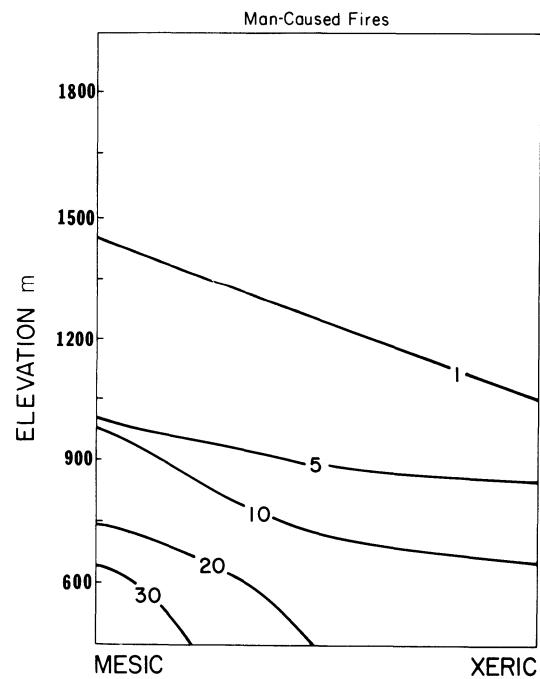


Fig. 3. The distribution of man-caused fire ignitions based on data from Harmon (1981). The isolines represent the relative abundance of total man-caused fires observed between 1940 and 1979.

tation, and increasing period of snow cover. Lightning tends to strike topographic high points which also are drier and thus more flammable whereas many man-caused fires start along roads which tend to run through valleys and not along ridges.

Calculated fire return cycles for the sites of highest fire occurrence are 180 and 9 400 yr respectively for man-caused and lightning fires. Before the establishment of the park many forests were exposed to more frequent fires and these fires influenced community composition and tree population age structure. Lightning fires would have to increase in size 1 000 times to become equivalent to the pre-park frequency of largely man-set fires. Since an increase of this magnitude is unlikely, simply allowing lightning fires to burn will still lead to major changes in composition as the forest equilibrates to reflect the new frequency. Moreover, because the severity of lightning fires tends to be lower than man-caused fires (Barden & Woods, 1974), the importance of shade intolerant species will probably decrease even on sites burned by lightning fires.

We infer from this discussion that the species composition of pine and oak forests as sampled by Whittaker (1956), was influenced by disturbances prior to park establishment in 1934. Without fire, pine forests are likely to be replaced by oaks and other hardwoods on all but the most xeric and exposed sites (Barden, 1974). Vegetation types will shift through time relative to their positions in Figure 1. It is also worth noting that Figure 3 represents the pattern of man-caused fires during the park era only. In earlier, post-colonial times (1790–1930), pine and oak forests were purposefully burned to encourage fruit crops, such as blueberries, and to improve forage for cattle (Lindsay, 1976). Prior to the establishment of the park man-caused ignitions were probably: 1) more frequent, and 2) extended to higher and more xeric slopes. Thus, the gradient positions for pine and oak forest reported by Whittaker (1956) may not represent 'natural' in the sense of pre-European settlement conditions. A change in park policy to allow lightning fires to burn would be unlikely to be sufficient to maintain the vegetation patterns present in the 1940's.

#### *Species responses to disturbances*

Turning to the third disturbance-vegetation

characteristic, that reproductive patterns are related to the major environmental and disturbance gradients, we consider sprouting ability in the GRSM landscape. In GRSM, such disturbances as fire, insect outbreaks, wind, frost, logging, or pathogen epidemics often cause top-kill or defoliation. Given disturbances of equal intensity, a community rich in sprouting species would be expected to respond differently than one with few sprouters. For example, in GRSM, mortality of trees is lower in communities rich in sprouters. Vigorous sprouting also can inhibit seed reproduction in the post-disturbance stand.

The ability to sprout or form new foliage is a complex function that varies with species and individual stem age and size (Kramer & Kozlowski, 1979). For the purposes of this paper we will assume sprouting is an all-or-nothing response. We will also assume that conifers cannot sprout although some *Pinus* (e.g. *Pinus rigida* and *P. echinata* in GRSM) can form sprouts (Stone & Stone, 1954). In our experience epicormic sprouting in *Pinus rigida* and *P. echinata* may result in refoliation after crown scorch but large individuals of these two species do not recover after more severe disturbance such as stem girdling. Most important hardwoods found in GRSM have the ability to sprout. Such sprouting can produce dense patches of hardwood saplings two to four years after moderate disturbance.

Using stem density data presented in Whittaker's (1956) analysis of GRSM vegetation, we have plotted the percentage of stems capable of sprouting as a function of position within the Whittaker mosaic chart (Figs. 4 and 5). Underlying these figures is the fact that stands with high percentages of conifers do not respond to moderate fire disturbance in the same way that hardwood stands respond. Because dense sprout saplings outcompete seedling reproduction (which often depends on exposure of mineral soil as well), the two recovery modes (sprouts and via seedlings) are non-randomly distributed within the mosaic diagram. In eastern GRSM the proportion of stems in a stand capable of sprouting peaks in submesic, oak-dominated stands and decreases to xeric stands. An exception is the relatively low importance of sprouting in mesic stands at mid elevations, corresponding to peak *Tsuga* density. Potential sprouting also decreases from low to high elevations. Sprouting patterns are the same in

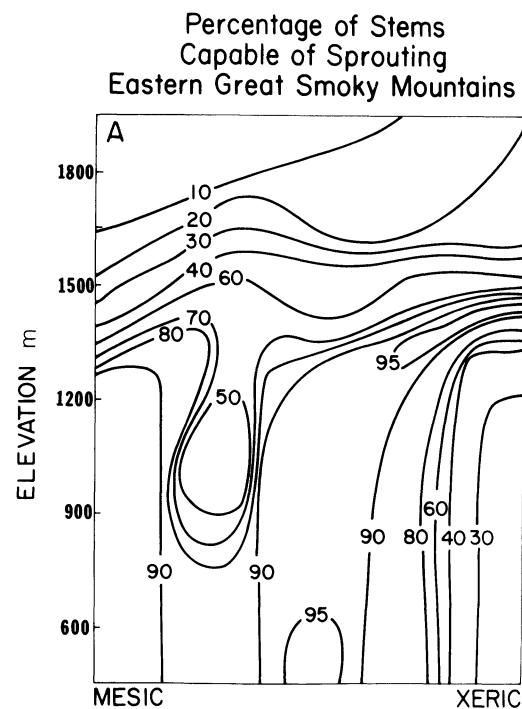


Fig. 4. The percentage of stems for all species capable of sprouting after top-kill or total defoliation for GRSM east of Double Springs Gap. Species incapable of sprouting are *Abies fraseri*, *Picea rubens*, *Pinus pungens*, *P. rigida*, *P. virginiana* and *Tsuga canadensis*. In the eastern Great Smokies, conifers dominate the high elevations.

the western GRSM except that there is no decrease with elevation since upper elevations are oak and beech dominated.

A comparison of the sprouting gradients to the occurrence of fires reveals some interesting relationships. Lightning fires are frequent in the chestnut oak-heath and the pine communities. The former community has many sprouting species while the latter has few. Present-day man-caused fires tend to occur in communities (mesic and sub-mesic hardwoods) where the proportion of sprouting species is high.

The sprouting response gradients also have some important implications for man-caused disturbances such as logging and agricultural clearing. Logging in areas low in sprouters, such as the hemlock and spruce-fir communities, should lead to an abundance of seed reproduction by shade-intolerant species. In contrast, logging in the chestnut oak-chestnut community should lead to heavy

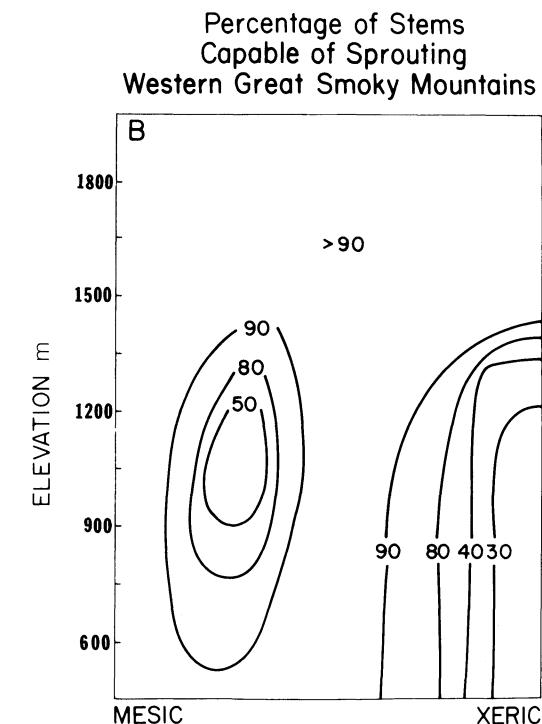


Fig. 5. The percentage of stems capable of sprouting after top-kill or total defoliation in GRSM west of Double Springs Gap. The high elevations in this section of the park are dominated by hardwoods.

dominance by sprout reproduction. Agricultural clearing, which removes sprouters as well as non-sprouters, should lead to an increase in reproduction of intolerants from seed.

Comparison of the pattern of sprouting to the distribution of vagile, early successional tree species that colonize by seedling establishment (some of which also reproduce by sprouts), reveals that four major groups are collectively able to occupy all major positions on the environmental gradients: 1) *Prunus pensylvanica*, 2) *Liriodendron tulipifera*, 3) *Betula* spp. and 4) *Pinus* spp. (Fig. 6). *Pinus* predominates on lower, more xeric slopes, *Liriodendron* is dominant on the lowest stream flats and in mesic positions in logged over sites, and is replaced by *Betula lutea* at the middle elevations. *Prunus pensylvanica* and *Betula lutea* dominate cut over sites well into the high elevation spruce-fir zone.

#### Forest floor recovery rate

Our fourth point, that functional aspects of eco-

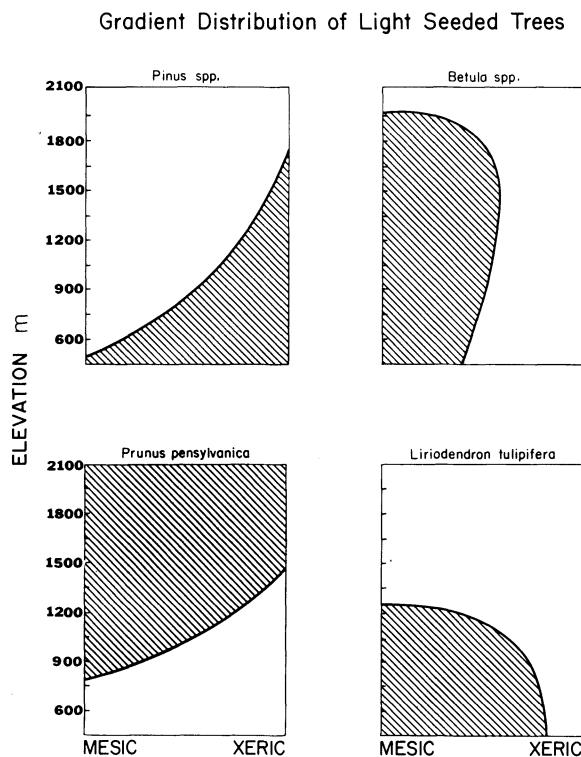


Fig. 6. The distributions of important, light seeded tree species in GRSM.

system resources are related to environmental gradients, is illustrated by fire effects. Fire differs from many other disturbances in that it removes dead organic matter (fuel) when it kills live portions of the canopy (windfall by contrast increases dead organic matter).

Litter accumulation response times range from 5 yr on mesic low elevation sites to over 60 yr on high elevation sites in eastern GRSM (Fig. 7). The time required to reach steady-state also increases from 5–30 yr as one progresses along the moisture gradient from mesic to xeric at low elevations. Man-caused fires occur on sites which recover rapidly from fuel removal, whereas lightning fires occur on sites with recovery times ranging from 20–40 yr. Man-caused fires occur on sites with low total fuel accumulations, lightning fires burn areas with moderate fuel accumulations, and the zones with the highest biomass accumulations rarely burn. Although considerably less is known about decay rates of wood, a similar diagram could be prepared for the time required for woody stems

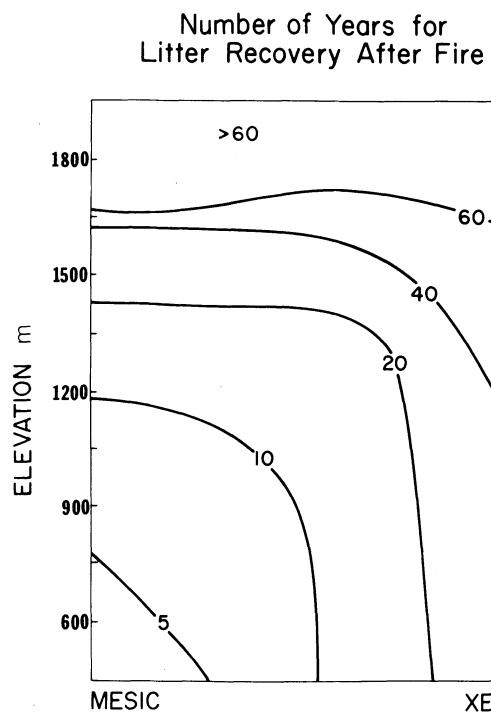


Fig. 7. Number of years estimated for the forest floor to recover from litter removal by ground fire which did not kill the canopy. The number of years to reach the steady-state represents a weighted average for the species in a portion of the mosaic chart.

killed by disturbance to disappear. The overall patterns would probably be similar to the litter accumulation gradients with increasing times as one proceeds from mesic to xeric sites and from low to high elevations. For example, in one study (Harmon, 1982b), logs were predicted to take less than 20 yr to disappear on low elevation sites whereas at a high elevation spruce-fir site was observed to have equivalent diameter logs remaining from a fire in 1910.

#### *Post-park disturbances*

Finally, to approach our fifth point, that recent, anthropogenic, disturbances vary along environmental and biotic gradients, we consider exotic species invasions. In the case of species-specific pathogens and parasites, the range of the new disturbances will be determined by existing biotic gradients. The chestnut blight, *Endotheca parasitica*, for example, was originally introduced to the United States in 1919 and by 1930 it had killed most

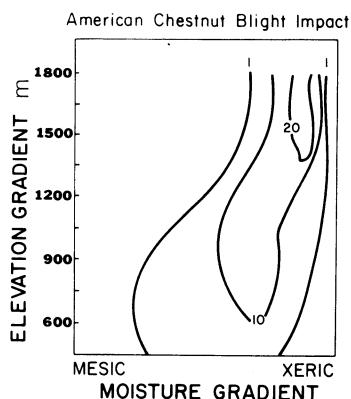


Fig. 8. The impact of the chestnut blight on the forest canopy, in percentage of stems removed from stand.

of the mature individuals of *Castanea dentata* in eastern North America including the study area. At that time there were about 75 000 ha of oak-chestnut forest in GRSM. Since mortality of mature trees was total, the pattern of canopy opening followed Whittaker's gradient diagram. The disease is apparently somewhat cold intolerant, so there was also a gradient response in the pattern of disease spread. The trees in the upper elevations were the last to die – some still had live branches when Whittaker sampled in the late 1940's (Fig. 8).

The recovery response of the forest community was also related to environmental gradients, since the nature of *Castanea* replacement was a function of its original density (Woods & Shanks, 1959). Where density was high, both replacement by established saplings of shade-tolerant species and seed reproduction by shade-intolerant species were important. In sites with lower densities of *Castanea*, canopy expansion by adjacent trees was the dominant process. This prevented the establishment of shade-intolerant species and the release of advanced reproduction. In general, *Acer rubrum*, *Quercus prinus* and *Quercus rubra* increased in importance as *Castanea* declined. From Whittaker's work, one could predict that most of the intolerant replacement occurred in high elevation and low elevation subxeric forests.

A second example of a host-specific introduced parasite is the balsam woolly aphid (*Adelges piceae*), the most damaging exotic insect now in the park. First found in GRSM in 1963, the aphid threatens to eliminate mature *Abies fraseri* in its

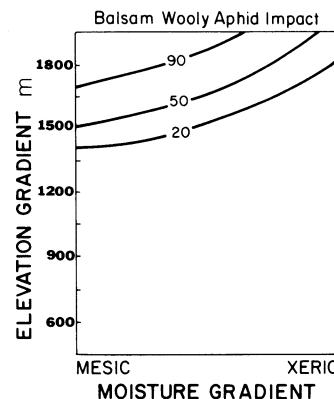


Fig. 9. *Abies fraseri* as a percentage of the forest canopy stems (after Whittaker, 1956). If balsam woolly aphid kills all the *Abies fraseri* in the park, these percentages should also represent the mortality for this tree species.

6 000 ha range (Fig. 9). Initial infestations occurred at the spruce-fir/hardwood ecotone (Eager, 1978) but have subsequently spread to include stands all along the elevation gradient. Trees may take years to succumb, but death sometimes occurs in as few as three growing seasons (Johnson, 1977). Because *Abies fraseri* increases in importance with elevation, the pattern of invasion is the reverse of the pattern of potential impact.

Attack by balsam woolly aphid causes an increase in light and alters microclimate in dense fir stands. Understory shrubs, herbs, and reproduction respond quickly to this disturbance by growing more vigorously (Eager, 1978). Lichens in dead fir canopies also dramatically increase after needle drop. An increase of seed reproduction has not yet been documented, but an increase in *Betula lutea*, *Sambucus canadensis*, *Rubus canadensis*, *Sorbus americana*, and *Amelanchier laevis* should be expected. *Abies fraseri* may reach a mature size and reproduce before aphid attacks. If this occurs, then one can envision a mosaic of *Abies fraseri* populations: some mature with aphids and others immature and relatively free of aphids. However, Hay *et al.* (1978) believe it is only a matter of time before *Abies fraseri* is entirely eliminated, removing an endemic species from the already species-poor high elevation flora. *Abies fraseri* tends to support more epiphytic mosses and liverworts than red spruce; hence, the loss of fir may also lead to local extinctions in the cryptogamic flora (Fig. 9).

A more complicated case is the effect of the exotic European wildboar (*Sus scrofa*), a disturbance which is not related to any single plant species or single environmental gradient. The movements and habitat preferences of wild boar, are a function of the animal's direct response to variables such as temperature (the wild boar move to lower elevations and bed on warmer southwest facing slopes in winter), and the availability of favored food items (Bratton, 1975). Wild boar rooting reaches maximum disturbance levels in grey beech forest from 1450–1800 m (Fig. 10). Bratton *et al.* (1982) related boar rooting to understory composition. They found some understories to have almost no hog activity but others to have high levels of rooting. This distribution was negatively correlated with density of *Rhododendron maximum* and other ericads, and positively correlated to occurrence of mesic herbs and more open understories. As a complicating factor, recently burned stands have more hog rooting, presumably due to increased availability of herbs, insects or both (Bratton *et al.*, 1982).

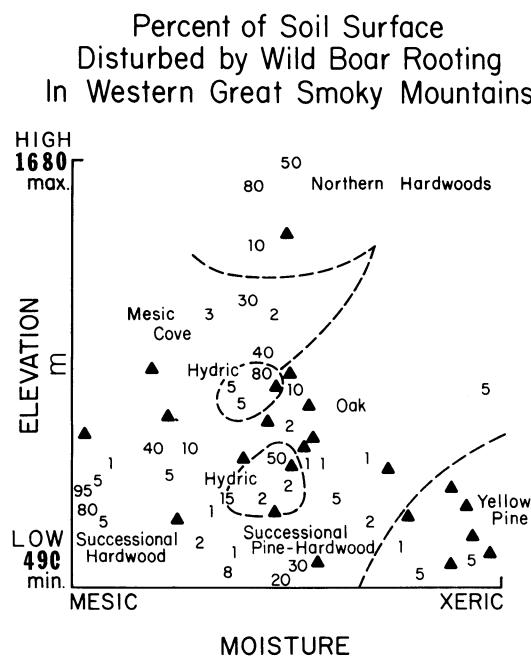


Fig. 10. Percent of soil surface disturbed by wild boar rooting. Triangles indicate no hog activity. Note the greater intensity of rooting in mesic sites (after Bratton *et al.*, 1982).

## Conclusions

We have used Whittaker's original (1956) analysis to show that superimposed on the gradient pattern of forest composition in GRSM are similar disturbance patterns which also can be treated as gradients. The vegetation pattern reported by Whittaker is not independent of these disturbance factors, nor are these factors independent of the vegetation. Modification of disturbance frequencies and intensities by management activities such as fire suppression may result in slow shifts in the distributions of both individual species and of whole communities. Species responses to disturbance are probably the result of both physical environmental considerations (e.g. conifers are tolerant of xeric conditions), and of disturbance patterns, (e.g. pines recolonize bare soil quickly after severe fire). Certain aspects of recovery, such as accumulation of leaf litter or humus are correlated with physical environmental gradients and may in turn influence disturbance frequencies and intensities. Recent anthropogenic disturbances also show a relation to landscape gradients.

Ecosystem responses to disturbance on a landscape basis are complex and integrate multiple factors. Since disturbance gradients may parallel physical environmental gradients, the two may be difficult to distinguish. Adding disturbance parameters to Whittaker's original study of the Great Smoky Mountains can provide us with an increased ability to understand species composition and vegetation change.

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