To the Graduate Council:

I am submitting herewith a thesis written by Mark Edward Harmon entitled "The Influence of Fire and Site Factors on Vegetation Pattern and Process: A Case Study of the Western Portion of Great Smoky Mountains National Park." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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We have read this thesis
and recommend its acceptance:

Accepted for the Council:

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Graduate Studies and Research

THE INFLUENCE OF FIRE AND SITE FACTORS ON VEGETATION PATTERN AND PROCESS: A CASE STUDY OF THE WESTERN PORTION OF GREAT SMOKY MOUNTAINS NATIONAL PARK

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

Fire history, the initial effect of fire disturbance on community structure, the response of communities one and two years after fire disturbance, and the present-day vegetation pattern were examined in the westernmost portion of the Great Smoky Mountains National Park in Tennessee and North Carolina.

Sectioning of fire scars, field observations, historical accounts, and fire control records indicated that the fire disturbance regime has changed dramatically during the last 200 years. Man-caused fires have probably been an important disturbance since Indians migrated into the area over 12 thousand years ago. Between 1790 and 1940, Euro-American man frequently burned the landscape. On south facing upper slopes the mean fire interval between 1860 and 1940 was 12.7 years. Field observations suggested that south facing upper slopes burned most frequently while north facing lower slopes and ravines burned least frequently. The interval between fires increased with increasing elevation. Under the present fire suppression policy, the fire disturbance regime probably resembled no other period in the last thousands of years. Estimates of lightning-caused fire frequency and potential size indicated that a policy which allows some natural fires to burn unhindered will not maintain the current or the historical vegetation pattern.

Fire disturbance severity was found to be a function of fuel, topography and weather. South facing upper slopes appeared to be the topographic positions most prone to severe fires. Disturbances to the canopy such as southern pine bark beetle attack also increased the

chances of severe fire. Canopy closure, litter depth, species richness, basal area and stem density all decreased immediately following fire. Fire disturbance can be considered both a product of the community (endogenous) and a product of the environment (exogenous). The ability of trees to survive fires was a function of severity, species, diameter at breast height, bark thickness and the ability to initiate epicormic branches. Rapid growth rates were also of survival value when fire intervals were short.

Seedlings, seedling sprouts and root collar sprouts were important reproductive forms one and two years after fire. The relative importance of each reproductive form was a complex function of position along the topographic-moisture gradient, litter depth, canopy closure, fire severity and community structure prior to disturbance. The ability of most species to generate sprouts indicated few species were actually eliminated from a site by fire. Yellow poplar, pine, sumac, sourwood, devil's walking stick, black locust and princess tree seedlings were most abundant in severely burned forests.

Forest canopy data from 100 permanent plots were examined using indirect ordination, direct ordination and community classification. Slope position, aspect, slope steepness, potential solar beam irradiation (SBI), concavity, elevation, disturbance by man and the time since last fire were all important in determining species distributions. Forests which were not recently cleared by man for agriculture or timber were divided into 7 cover types. From mesic to xeric sites these included: cove hardwoods, hemlock, mixed hardwoods, mixed oak, white pine, chestnut oak-scarlet oak and yellow pine. Forests cleared by man had old-field

pine on xeric sites and successional hardwood on mesic sites. Major successional change is expected in the old-field pine, successional hardwoods and yellow pine cover types. Continued fire suppression will lead to a substantial decrease in the yellow pine cover type in the next 50 years. Allowing some lightning-caused fires to burn unhindered will probably not maintain the present extent of the yellow pine cover type.

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I. INTRODUCTION

A program to suppress all fires was started in the Great Smoky Mountains National Park (GRSM) when land was purchased for the park's creation between 1930 and 1940. The GRSM fire suppression policy reflected the widely held view that fires in forest ecosystems were purely destructive events. Yet, fire's destructive capability is only one facet of fire disturbance. Because fires promote birth and growth in many forests, they may also be considered constructive events.

Long before modern man could offer forests "protection," fires set by lightning, volcanic activity, and man commonly spread across the landscape. Fires have had such a steady and long-term influence in some regions that genetic traits which are specifically adapted to fire have evolved. The serotinous cones of table mountain pine are an example of the natural selection pressure exerted by fires (Barden 1979, Zobel 1969). Although fire tends to eliminate some species, there is a host of species which benefits from the situations created by fire. Total fire suppression can potentially alter the structural, functional and evolutionary characteristics of many ecosystems. By eliminating the role of a natural process, total fire suppression has in effect contradicted a basic tenet of wilderness and National Park Service management. After more than 40 years of total fire suppression, managers, conservationists and scientists are attempting to restore the natural role of fire in GRSM. But what was the role of natural fire and to what extent has man either through starting or suppressing fires changed the role fire played in maintaining a landscape pattern?

In the spring of 1977, studies relating to the natural role of fire were started in GRSM under the direction of Dr. Susan P. Bratton. The westernmost portion of GRSM was chosen as a case study because: (1) agricultural and commercial land clearing had been minor, (2) a recent and large lightning fire had occurred in the area and (3) the widespread occurrence of pine forests indicated that area might be susceptible to changes initiated by fire suppression. The general objective of these studies was to examine the mechanisms whereby fire influences vegetational pattern and process and to test the hypothesis that man has changed the role of fire. Four topics concerning fire were defined: fire history, present vegetational pattern, the characteristics of fire disturbance and the response of vegetation after fire. All four subjects were important in understanding fire and man's influence on vegetational pattern and the major objectives on each topic are outlined below:

1. Fire history--what effect has man had in terms of starting and suppressing fires and what influence does topography, elevation, drought, etc., have on the occurrence and frequency of fire?

2. Present vegetation pattern--how do environmental gradients and historical factors influence the distribution of tree species and how are species arranged on these gradients?

3. Characteristics of fire disturbance--how do community and environmental factors influence the initial impact of fire; what are the immediate changes in vegetational structure wrought by fire and what are the attributes which allow trees to survive fires?

4. Vegetation response after fire--what role do sprouts and seedlings play after fire and how do the characteristics of fire disturbance, the previous vegetational structure and environmental gradients affect these roles?

The definition of the word natural in the context of fires is complex and polemical. Naturalness is equated with the pre-Columbian landscape for the purposes of National Park Service management. This definition, therefore, includes the Indian as a natural factor and defines natural fires as being started by Indians and lightning. I have separated the causes of fires into three classes: modern man, which includes the Euro-American settlers; pre-Columbian Indian; and lightning.

Finally, a major assumption made throughout the thesis is that the key to understanding the past lies in the processes of the present. This assumption is similar to that used in geologic interpretation. In this regard the fire history record and the present vegetation pattern are analogous to the stratigraphic record. To understand the implications of this record, the present response of vegetation to fire has been examined.

II. STUDY AREA

Physical Setting

Physiography. The study area encloses approximately 9100 ha in the westernmost portion of the Great Smoky Mountains National Park (GRSM) (Figure 1). The Great Smoky Mountains are part of the Unaka Mountains, a western extension of the Blue Ridge Province (Fenneman 1938). Within the study area a series of regularly spaced SW-NE trending ridges and valleys form a transition zone between the Great Valley and the main crest of the Unaka Mountains. Elevation ranges between 259 m (850 ft) at the mouth of Abrams Creek and 942 m (3100 ft) at the summit of Mount Lanier. Abrams, Hesse, Parsons, Shop and Tabcat Creeks are the major drainages; Abrams Creek forms the largest watershed.

Geology and soils. The geology of GRSM has been described in detail by King et al. (1968). Most of the study area is underlain by Cades Sandstone and Whilhite Formation of the Ocoee Series. These rocks are Precambrian in age. Cades Sandstone is a slightly metamorphosed, evengrained feldspathic sandstone which underlies broad ridges. In contrast, the Whilhite Formation is largely sandstone and shale with lenses of conglomerate, quartzite, limestone and dolomite. Ridges formed in the Whilhite Formation are often capped with quartz pebble conglomerate and are very narrow when compared to ridges formed on Cades Sandstone. The northwesternmost corner of the area is underlain by Cambrian aged Nichols Shale and Nebo Quartzite both of the Chilhowee Group.

Figure 1. Map of the study area in the Great Smoky Mountains National Park, North Carolina and Tennessee.

The original Morton Butler Tract was a "virgin" forest purchased for timber products. However, commercial harvesting of trees was not undertaken before the land was purchased by the National Park Service. Inholdings were tracts of land that had been cleared by settlers prior to purchase by the National Park Service.

The numbers of the major drainages correspond to: (1) Abrams Creek, (2) Panther Creek, (3) Hesse Creek, (4) Maynard Creek and (5) Tabcat Creek.

Source: Morton Butler File, Great Smoky Mountains National Park Archives.

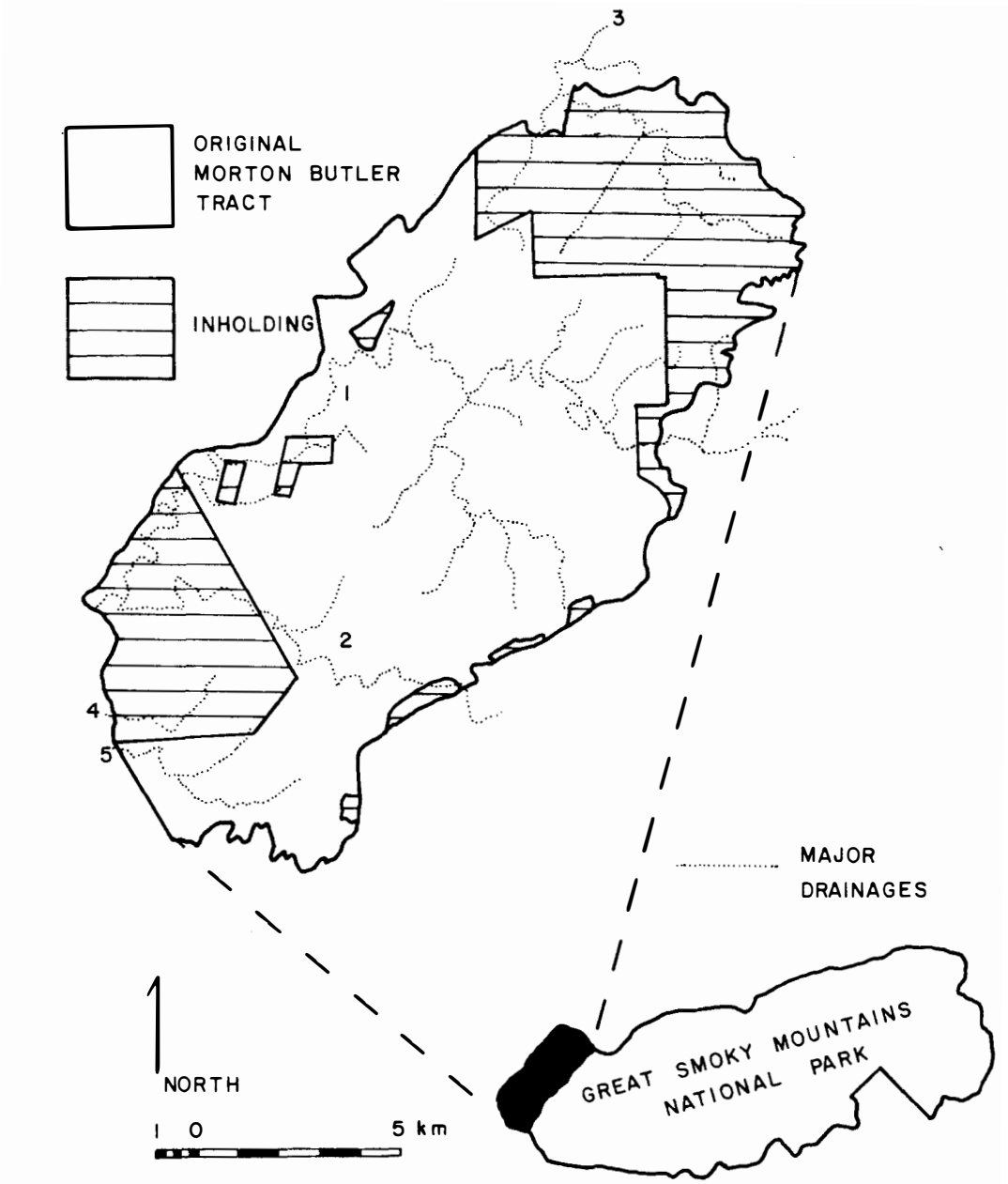

ORIGINAL
MORTON BUTLER
TRACT
INHOLDING
1
2
3
4
5
MAJOR
DRAINAGES
NORTH
1 0 5 km
GREAT SMOKY MOUNTAINS
NATIONAL PARK

Figure 1

Soils of the study area have been mapped as belonging to the Ramsey soil series (Elder 1959). Ramsey soils can be generally described as lithosols that have poor horizon development, strong acidity, and low fertility.

Climate. The climate of GRSM is very complex and is strongly influenced by differences in elevation and topography (Shanks 1954, Shanks 1956, and Smallshaw 1953). Mean annual precipitation* is 155 cm at Chilhowee Ranger Station (305 m) and 172 cm at Cades Cove Ranger Station (578 m). Smallshaw (1953) and Shanks (1954) found an increase in precipitation with an increase in elevation; their data indicate that annual precipitation at the highest point of the study area is 195-200 cm. Precipitation is distributed evenly throughout the year, although water deficits are likely to occur during April, July, September, October and November.

At 304 m the mean January maximum is 11.7°C, the mean January minimum is -1.1°C, the mean July maximum is 31.9°C and the mean July minimum is 18.7°C (Dickson 1960). Temperature decreases with increasing elevation (Shanks 1954, Shanks 1956), and a difference of approximately 3.3°C in mean growing season temperatures is expected between the highest and lowest points of the study area. Gatlinburg has a mean of 171 days above 0°C during the year (Dickson 1960). In general the number of frost-free days should decrease as elevation increases. Shanks (1954) classified the climate of GRSM below 456 m as humid mesothermal, and above 456 m but below 1672 m as perhumid mesothermal.

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*Based on 5 years of data collected from 1972-1976 (Larson and Silsbee, unpublished data).

In the Southern Appalachians the number of days with one or more thunderstorms averages between 50 and 60 per year (Visher 1954), July having the highest number. Lightning activity in the Southern Appalachians occurs when relative humidity exceeds 75% and is usually accompanied by precipitation (Barden 1974). Both of these factors moisten forest fuels and reduce the initial spread rates of lightning-caused fires. However, if lightning-caused fires continue to burn into drier and/or warmer weather conditions then fire behavior becomes more extreme (e.g., faster rate of spread, higher intensity). Barden (1974) found that large man-caused fires tended to start on days with lower relative humidity than large lightning-caused fires. Hence, man-caused fires tend to be intense even on the starting date.

Historical Influences

Indian habitation. As early as 12 thousand years ago, the Little Tennessee River valley was inhabited by small bands of Indians who were primarily hunters (Dickens 1976, Goodwin 1977). Archaeologic sites have been found in Cades Cove which date from the early Archaic to the late Mississippian Periods (Bass 1977). Dickens (1976) has traced the development of aboriginal culture in the Southern Appalachians from ca. 10,000 B.C. to 1838 A.D. During the Archaic Period (ca. 8000 B.C. - 1000 B.C.) hunting and gathering were the dominant means of sustenance. The Woodland Period (ca. 1000 B.C. - A.D. 1000) was a transition from Archaic culture to the Mississippian Period when agriculture was the primary food source. During this period settlements exhibited a nucleated-village pattern, and a stratified social structure. Corn

(Zea mays), beans (Phaseolus spp.), squash (Cucurbita spp.) and sunflowers (Helianthus spp.) were cultivated during the Mississippian Period and the forest was utilized for firewood, game, nuts, berries and herbs. During this period fire was evidently used extensively by the Cherokee (and presumably other Indians as well) to clear land for agricultural use, enhance berry crops, expose nuts on the forest floor, drive game, and improve travelling conditions (Day 1953, Goodwin 1977). Prior to contact with European man, the Cherokee were estimated to have 60 permanent settlements in the Little Tennessee River Valley (Goodwin 1977). After 1650, the Cherokee began to trade with European man, and by 1775 disease and warfare had drastically reduced the population density. By 1800 the original nucleated village pattern was replaced by widely scattered individual homesites (Dickens 1976). In 1838 the Cherokee were forcibly removed from the Southern Appalachians.

Euro-American settlement. In 1821 the first legal land grant was claimed in Cades Cove and by 1830 the population had grown to 271 persons. The highest population count (685) was in 1850, which was followed by a rapid decline to 275 in 1860. After 1860 the population gradually increased to 540 in 1920. Land was acquired by the U. S. Interior Department between 1920 and 1930 (Shields 1977) for inclusion in GRSM, after which the population has steadily decreased.

Within Cades Cove most agricultural clearing occurred in the major valley bottom, and lumbering was for local purposes only (Shields 1977). Evidence of extensive clearing was observed in the Hesse Creek drainage (M. Harmon, personal observation), and along Tabcat and Maynard Creeks

(Heritage 1939). At the turn of the century, only 3.2% of the lower Abrams Creek, the south face of Chilhowee Mountain, and the Deals Gap area were cleared for agriculture (Ayres and Ashe 1905). Between 1912 and 1913 Morton Butler acquired the majority of the study area. Although Morton Butler's original intent was commercial logging, this operation was not established and a large portion of uncleared land was acquired by the Park Service (Lambert 1958).

Euro-American man impacted the forest by burning and allowing livestock to range freely (Ayres and Ashe 1905, Heritage 1939, Morely 1913, Shields 1977). Fire was used to increase wild berry production (Shields 1977), gather chestnuts (Castanea dentata fruit), and provide forage for cattle (Morely 1913).

Chestnut blight. Between 1925 and 1930 chestnut blight (Endothia parasitica) began to kill the American chestnut* in the Southern Appalachians (Woods and Shanks 1959). Gaps in the canopy formed by the demise of American chestnut were filled primarily by red maple, chestnut oak, and red oak. Woods and Shanks (1959) observed that as gap size left by dead chestnut increased, the importance of intolerant seedling reproduction increased. Thus, seedlings of black locust, sweet birch, yellow poplar, sassafras and sourwood also tended to replace the dead chestnuts in sites with extensive damage.

Southern pine bark beetle. The southern pine bark beetle (Dendroctonus frontalis) is a native insect which attacks yellow pines

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*Common names of vascular plant species will be used throughout the text. See Appendix, Table 29, for the scientific names.

(pitch, shortleaf, Virginia and table mountain pines). Kuykendall (1978) examined the occurrence of beetle infestations within GRSM, and observed the structure of forests following attacks. The first record of bark beetle outbreaks was made in the 1890's in West Virginia. From 1913 to 1916 another outbreak occurred in Tennessee and Virginia. Two bark beetle outbreaks have been observed in GRSM during the last 26 years: (1) 1954 to 1958 and (2) 1967 to 1977. Kuykendall found that after beetle infestation the typical replacement species were white pine and mixed hardwoods on submesic old field sites. Replacement species on sub-xeric and xeric fertile sites were predicted to be chestnut oak and scarlet oak, while xeric infertile sites were dominated by scarlet oak and scattered yellow pines.

III. METHODS

Present Vegetational Pattern

Field Methods

During the summers of 1977 and 1978 forest vegetation was sampled as part of a vegetation survey for the Great Smoky Mountains National Park. One hundred stands were selected to give a systematic sampling of topographic-moisture, elevation and fire disturbance gradients. Lumbering and agriculture influenced 8 stands; the remaining 92 stands were affected by selective cutting, livestock grazing and fires. On 17 of these 92 stands fires had occurred within 2 years of the sampling.

Once a site was selected (usually from a topographic map) a 0.1 ha plot (50 m by 20 m) was randomly located within homogeneous vegetation. Whenever possible, obvious vegetational boundaries were avoided. Except for ravines and draws, the long axis of the plot was oriented parallel to the land contour. In ravines and draws the plot's long axis was oriented parallel to the topographic feature or cutting across contour lines.

Each plot was permanently marked with four 1.9 cm diameter steel rods to facilitate long term monitoring (Appendix, Figure 27). Each steel rod was in turn referenced by azimuth and distance to a "witness" tree marked with a numbered aluminum tag. Routes between the plots and a trail or road were crudely mapped using pace and compass. The occurrence of prominent features (e.g., waterfalls, ledges) along the route to plots was also noted. Finally, plot locations were marked on topographic maps.

Vegetation. Within each plot woody plants above 0.5 cm diameter at breast height (dbh) were tallied by 1 cm size classes. These plants were defined as trees. During 1977 trees larger than 10 cm dbh were mapped by recording distance and azimuth from points 5, 15, 25, 35 and 45 m along the major plot axis. Standing dead trees above 10 cm dbh were also noted in the tree tally by the lowest taxonomic level possible.

All woody plants less than 0.5 cm dbh were defined as shrubs. For the purposes of sampling each 0.1 ha plot was divided into 5 rectangular sections with 10 m and 20 m sides (Appendix, Figure 27). Shrubs were sampled in 25, 4 m^2 quadrats which were grouped into sets of 5. One set of 5 was used to sample each 10 m by 20 m section. The location of each set of 5 was chosen randomly and was recorded for resampling. The percent of the ground covered by shrubs and stem density was recorded for each quadrat. Shrub stems were grouped into 3 diameter classes at a height of 5 cm above the ground (0-2 mm, 2-6 mm and > 6 mm). In 1978, ericaceous shrubs and Smilax spp. were excluded from the stem counts and were recorded as cover. In the lower right-hand corner of each shrub quadrat, herb cover was recorded in a 1 m^2 quadrat. There were a total of 25 herb quadrats. When seedlings of hemlock, red maple and yellow poplar were less than 5 cm in height, they were sampled as cover in the herb quadrats. The maximum cover a shrub or herb species could have was 100%. Taxonomic nomenclature follows Radford et al. (1968).

Environmental variables. On each plot the slope, aspect, topographic form, elevation, degree of concavity, presence of running water, boulders, soil charcoal and disturbances by southern pine bark beetle, windthrow, chestnut blight, and European wild boar rooting were noted.

Disturbance severities were ranked from 1 to 5 depending upon the percentage of the plot involved. Slope was measured with a Suunto clinometer at plot center and along both ends of the plot. Concavity was determined by measuring the slope along the center line of the plot from the center point (Appendix, Figure 27). Elevation was determined both from a topographic map and an altimeter. A Brunton compass was used to determine aspect. Slope position was derived from topographic maps by measuring the horizontal distance from a ravine and expressing this number as a percentage. Distances to primary and secondary streams and to major ridges were obtained from topographic maps. A combination of slope and aspect was transformed to potential solar beam irradiation (SBI) using tables (Frank and Lee 1966). The units of SBI are expressed as 1000 langleys per year.

Data Analysis

After keypunching and verification, stand data for trees and shrubs were summarized by 2 FORTRAN programs developed by Dr. Susan P. Bratton. The stand summary card deck was processed by a second set of FORTRAN programs also developed by Dr. Susan P. Bratton to create a species-plot matrix. The species-plot matrix was used to generate a resemblance or distance matrix (Gauch 1976) which was used for ordination analysis.

Vegetation patterns were interpreted by means of 3 standard procedures: (1) indirect ordination, (2) direct ordination and (3) community classification. A considerable body of literature reports the merits and disadvantages of each approach (McIntosh 1967, Whittaker 1975) and only a brief summation of salient points is presented here.

Ideally, community classification strives to group numerous samples into a smaller number of distinct, natural units. Natural communities, however, are rarely discrete units, and the separation of one sample from another becomes an arbitrary process. Although stands can be objectively classified (e.g., Orloci's sum of squares method, 1967) most techniques are hierarchial in nature. Hierarchial classification techniques assume that classes at any level are subclasses of classes at a higher level. There is no basis, as of yet, to decide if community classification should be hierarchial or reticulate in nature (Pielou 1977). In contrast, ordination is a process of arranging samples continuously in relationship to one or more gradients or axes (Goodall 1954). "Ordination has two great advantages over classification; it obviates the need for setting up arbitrary criteria for defining classes, and there is no need to assume that distinct classes (if there are any) are hierarchically related" (Pielou 1977).

Indirect ordination uses the correlation of species between plots to arrange the sample stands independent of environmental variables. The relationship of environmental variables and indirect ordination models can be assessed by observing the correspondence of the two sets of information. However, the relationship of environment to the indirect ordination model can be quite complex if environmental gradients interact (e.g., fire frequency and moisture). The indirect ordination model can also be quite useful in interpreting the way species intermingle. Examination of species distributions along environmental gradients is called direct gradient analysis (Whittaker 1973). One major advantage of direct over indirect ordination is that the

interaction of environmental gradients can be assessed more easily. Communities as well as species can be considered to occupy positions along environmental gradients.

Indirect ordination. Bray-Curtis polar ordination (BC) with modification by Beals (1960) and principle component analysis (PCA) were used as indirect ordination techniques. The FORTRAN programs used in the ordination analysis were developed by Dr. Hugh G. Gauch (1976) of Cornell University. Endpoints on ordination axes are chosen subjectively when using BC by examining the resemblance matrix. Distortion along the axes was reduced by rejecting endpoints which were not at least 50% similar to 3 or more plots (Newsome and Dix 1968). Distortion along the higher order (N) axes was reduced by choosing endpoints which were within the 40-60% range of lower order (N-1) axes (Newsome and Dix 1968).

Direct ordination. Polynominal regression and analysis was used to test the relationship between species distributions and environmental gradients. Least-squares fit of multiple polynominal regression equations and F-tests were calculated using the SAS76 procedure STEPWISE (Barr et al. 1976). Species density and basal area were the major dependent variables; elevation, slope position, aspect, concavity index, potential solar beam irradiation (SBI), years since burn (YSB) and their second order products were used as independent variables. The overall regression was judged significant if $P < .05$, and individual independent variables were rejected if the type II sum of squares was not significant at $P < .10$. Pearson's product moment correlation

coefficients (r) were calculated between all independent variables to test for independence by using SAS76 procedure CORR (Barr et al. 1976).

Canopy cover types. The 100 canopy plots were divided into 9 cover types based on the basal area dominance of a species or species group and disturbance history. The division was wholly arbitrary--each plot was assigned to a cover type when 33% or more of the basal area was composed of a species or species group. When 2 or more groups were dominant, the group with the higher value was used as the cover type. Cover types were used here to indicate the distribution of less common species and as a convenient generalization of species dominance on the landscape.

Fire History

Field and Laboratory Methods

GRSM fire records and fire scars on trees (Arno and Sneck 1977, Houston 1973) were used to determine fire history. Fire scars were distinguished from other basal wounds by (1) upslope position, (2) presence of charcoal, (3) presence of numerous overlapping scars and (4) the absence of rocks or logs which might have caused wounding. Sections with fire scars were removed from pine trees on or near the plot sites. Hardwoods were also examined but the wood was too decayed to age fires with any reliability. Stumps were also examined for fire scars and were cross-correlated to fire scar records on live trees to extend stand histories. Fire scars were removed by handsawing a wedge-shaped section from the basal wound. Each section was air dried, sanded and examined with a hand lens.

Data Analysis

The mean interval between fires was calculated using untransformed values. These data were transformed to a natural logarithmic scale to compare the mean fire interval above and below an elevation of 610 m. The t-test was used to compare mean intervals.

Fire rotation was defined by Heinselman (1973) as the number of years required to burn over a study area. Fire rotation is dependent on both fire frequency and size. When a study area is homogeneous in terms of vegetation, topography, climate, etc., the fire rotation equals the mean fire interval. The fire rotation for the westernmost portion of GRSM was calculated one of two ways:

(1) For the period 1940 to the present the fire rotation equaled the total area divided by the area burned per year. Hypothetical lightning-fire rotations were calculated the same way.

(2) For the period 1830 to 1940 the possible ranges of the fire rotation were calculated. The lower range assumed all forests burned as often as pine forests. The upper range assumed pine forests were the only forests that burned and that they composed one-third of the study area.

Characterization of Fire Disturbance

Field Methods

Tree mortality caused by fire was assessed on 17 plots 1 to 2 years after fire occurrence. Trees on each 0.1 ha plot were divided into 3 categories: (1) dead before fire, (2) alive, and (3) dead after fire. Trees were tallied by species in 1 cm size classes. On recently

burned plots a canopy openness index was derived by determining the percentage of points on a convex mirror that were obscured by live canopy vegetation. On each plot the canopy openness index was measured in the center of each 10 m by 10 m section for a plot total of 250 points.

The attributes which enable trees to survive fire examined in this study were bark thickness, ability to initiate epicormic branches and growth rates. The presence of epicormic sprouts was recorded on all the live trees in 8 of the recently burned plots. An estimate of tree diameter growth rates was made by coring 11 dominant yellow pines, 9 suppressed yellow pines, 10 oaks and 5 other hardwoods (red maple, sourwood, blackgum and pignut hickory) on upper slope positions. Each core was taken at breast height on the uphill side, stored in a paper straw, dried, mounted on a grooved board and sanded before examination with a hand lens. Growth was measured for 10 year intervals starting from the pith. A bark punch was used to determine bark thickness at breast height and at 1 to 3 dm above the ground. Three measurements were taken on each tree at each height for a total of 6 measurements. Measurements were always taken on bark "ridges." Individual trees were chosen while walking through forests which contained small and large size classes of desired species. An effort was made to sample one tree for each species from each 1 cm size class that was available.

Data Analysis

Fires were grouped into 2 severity categories: "cool" and "hot" depending upon the portion of basal area removed. Cool fires were defined as having removed 25% or less of the original basal area.

Unfortunately, the intensity and residence time of each fire were not measured. As these parameters increase the stand mortality should also increase, but it must be emphasized fire intensity was not measured in this study. Tree survival data for trees less than 10 cm dbh were pooled for cool fires. The probability of a tree surviving cool fires was then modeled as a logistic function of dbh. Bark thickness was transformed to a percentage of dbh and an average percentage was calculated for each species. Survival of cool fires was then modeled as a logistic function of calculated bark thickness at both ground and breast height levels. All logistic function parameters were estimated using SAS76 procedure NONLIN (Barr et al. 1976). Growth rates, the relationship of canopy openness and species richness to severity were calculated and tested using regression analysis. Indirect ordination was used to generate the vector of species composition change caused by fire. This technique is similar to the one used by Austin (1977) to follow species changes associated with succession. The Bray-Curtis algorithm was used to ordinate the 17 recently burned forests. Stand compositions before fire were assumed equal to the trees alive after fire and the trees killed by fire.

Early Response to Fire Disturbance

Field Methods

Shrubs were sampled in 17 recently burned stands to determine the importance of tree reproduction after fire. The sampling scheme was identical to the one used in unburned plots (see page 13). The ability of hardwood trees girdled by fire to sprout from the base was

assessed 2 years after fire occurrence. Trees with sprout clumps were separated by species and 2 cm dbh size classes. On each sprout clump, the number of live sprouts, the number of dead sprouts and the height of the tallest sprout were recorded. The total number of sprouts (dead and live) at year 2 was used as an estimate of the number of sprouts 1 year after fire.

Terms used concerning sprouting are defined to reduce confusion and to facilitate comparisons with other investigators. Epicormic sprouts arose from dormant buds on above ground portions of the stem. In the present study, epicormic sprouts were confined to the stem 0.5 m or more above the ground. This height was chosen because trees were not always girdled by fire at ground level. Root collar sprouts developed from dormant buds on tree stem tissue 0.5 m or less above the ground level. When these sprouts arose from trees less than 0.5 cm dbh they were termed seedling sprouts. Shoots sometimes arose from adventitious buds on root tissue; these sprouts were termed root suckers. Sprouts also arose from adventitious buds formed in wound tissue. The term sprout clump was used to designate all the sprouts arising from the base of one tree and included sprouts formed by adventitious and dormant buds. On recently burned plots the percentage of canopy opening and the residual humus litter (O2) were assessed. The depth of O2 which was not consumed by fire was measured in the center of each 4 m^{-2} shrub plot.

Data Analysis

Hardwood reproduction originated from seed, seedling sprouts, root suckering and root collar sprouts. An estimate of seedling

reproduction after fire was made by balancing the total stem density against the density of root collar sprouts, root suckers, and seedling sprouts. The number of root suckers could not be determined without detailed excavation. I assumed the density of root suckers was not high enough to influence the estimate of hardwood seedling reproduction. Based on the observations of Sander (1971) each seedling girdled by fire was assumed to generate one sprout. No data on seedling density prior to fire were available for burned stands, although densities for similar unburned forests gave approximate estimates.

The relationship between the dependent variables, numbers of sprouts per sprout clump and sprout height and the independent variables canopy openness, litter depth and tree diameter was tested using SAS76 procedure STEPWISE (Barr et al. 1976). The dependence of pine seedling density on canopy openness, litter depth and time since fire occurrence was also tested using procedure STEPWISE.

IV. FIRE HISTORY

Introduction

The importance of fire as a disturbance and as an evolutionary influence depends upon frequency, extent, severity and location on environmental gradients. In constructing a disturbance regime, one must examine the way in which these parameters vary in space and time. Increased variation of the disturbance regime implies an increased variation in habitat.

Historically the influence of fire on the study area can be divided into 5 periods:

(1) prior to man, when lightning was the primary cause of fire starts (before 10,000 B.C.).

(2) Indian hunting (ca. 10,000 B.C. to A.D. 1000).

(3) Indian agriculture (ca. A.D. 1000 to A.D. 1830).

(4) Euro-American agriculture (ca. 1830 A.D. to A.D. 1930).

(5) National Park Service Management, when fire suppression was initiated (1940 A.D. to present).

In the last 4 periods man as well as lightning started fires.

Results

Recent fire evidence. Scars and/or charcoal formed by fire were found in 88% of the vegetation plots. Former agricultural lands lacked fire evidence partially due to increased fire protection after abandonment and park establishment. Fire evidence was also absent from 78% of the sheltered draws and ravines. Since those sites remain moist (except

during severe droughts) a low fire incidence would be expected. Heritage (1939) observed that ravines and lower slopes generally lacked fire damage.

Fire scar evidence. A total of 43 pine trees was sectioned and 115 scars were revealed. The oldest fire scar examined was formed in approximately 1856. The absence of fire scars before 1855 may have been caused by a combination of rapid decay rates and the burning of older stumps. At present, the hypothesis that fires did not commonly occur prior to 1850 cannot be rejected by fire scar evidence alone.

Almost all (97%) of the pine forests examined were burned last between 1920 and 1949 (Table 1). The years 1925-26 accounted for 23% of the last fires to form scars and corresponded to a known drought (Hursh and Haasis 1931). Chestnut stumps in many north facing vegetation

Table 1. Year of Last Fire in 26 Pine Forests Based on Fire Scars.

Decade Stand Was Last Burned	Number	Percent
1940 - 1949	8	31
1930 - 1939	9	35
1920 - 1929	8	31
1910 - 1919	1	3
1900 - 1909	0	0

plots had multiple fire scars but no charring on the outer portions of the stumps. Downed chestnut logs were also without charring. This evidence implied that many north facing stands have not burned since 1930.

The fire interval is defined here as the number of years between scar formation. The arithmetic mean fire interval for 63 scars from pine forests of the Euro-American agricultural era was 12.70 years. The shortest interval during this era was 2 years, whereas the longest interval was 49 years. The frequency distribution of fire intervals was strongly skewed to the right, which suggested a logarithmic mean represented the central tendency better than the arithmetic mean. The logarithmic mean fire interval for pine forests sampled was 9.98 years. Pine forests below 610 m had a logarithmic mean fire interval of 9.17 years; pine forests above 610 m had a logarithmic mean fire interval of 11.34 years. The t-test indicated the mean fire interval for forests above 610 m was significantly larger than that below 610 m ($t = 2.428$, $0.05 > p$). Barden (1974) also observed that lightning- and man-caused fires were more frequent per unit area below 610 m than above this elevation.

One dead black locust was sectioned on a north facing ridge-top revealing 5 scars with a logarithmic mean fire interval of 9.55 years ($s = 2.02$). This evidence indicated some northern upper slopes burned as frequently as southern slopes. The number of scars observed on trees without cutting can serve as a rough indication of fire recurrence. This method is likely to underestimate the number of scars. North facing lower slopes had the fewest scars per tree (0.84) and south facing

upper slopes had the greatest (2.65). South facing lower slopes (2.09) and northern upper slopes (1.65) had an intermediate number of scars per tree. This suggested that, during the last 200 years, the decreasing order of fire frequency by site was south upper > south lower > north upper > north lower.

Fire scars on pine trees occurred more frequently in some years than others. Years with 3 or more trees with fire scars in the data set included 1880-81, 1887-88, 1894-95, 1903-04, 1906-07, 1909-12, 1922-23, 1925-26, and 1930-34. Hursh and Haasis (1931) presented data on precipitation from 1903 to 1929. Their data for Asheville, North Carolina indicated below normal precipitation in 1904, 1907, 1910-13, 1917, 1919, and 1921-26. These years corresponded well to those with 3 or more fire scars and suggested that years with lower than average precipitation also had more and/or larger fires.

Discussion

Fire scar evidence. Fire histories can be reconstructed using fire scars, but the method does have serious limitations. Fires do not create scars unless they are intense enough to kill a portion of a tree's cambium (Lachmund 1921). Once a tree becomes scarred, the formation of new scars may be enhanced (Kilgore and Taylor 1979). Abnormalities in growth ring formation may reduce the accuracy of scar age determinations (Craighead 1927).

Ignition sources. It was impossible to distinguish between fire scars caused by lightning and man. Between 1930 and 1978 there were 12

recorded lightning fires in the study area, or an average of 1 every 4 years. To account for the observed frequency between 1850 and 1930, lightning fires had to be very frequent or large. Between 1940 and 1969 lightning started only 15% of all GRSM fires (Barden 1974). Before the establishment of GRSM, man probably accounted for an even larger portion of fire starts. According to Ayres and Ashe (1905) fires were set in the Cades Cove area by Euro-American settlers "as often as they would run." Lambert claimed (1958) "30-50 percent of the land of Swain County has been burned over every year for a long period." Heritage (1939) observed "from 65-75 percent of the entire area has been burned over at least once in the past twenty-five years [1914 to 1939]."

Although there was evidence indicating the Indians used fire (Day 1953, Goodwin 1977), the proportion of Indian versus lightning fires was difficult to establish. Indians may have started as many or more fires than lightning, but further research is required to answer this question.

Fire rotation in a historical perspective. Between 1960 to 1971 the mean size of lightning- and man-caused fires was 3.4 and 5.4 ha, respectively (Barden 1974). GRSM fire control records between 1930 and 1978 for the study area indicated 2.5 lightning fires every 10 years and 6.7 man-caused fires every 10 years. Under a continued policy of full fire suppression, the fire rotation period for the 9100 ha study area would be over 2000 years.

The impact which natural lightning fire has on the rotation period can only be approximated. Assuming man-caused fires were

eliminated entirely and given the current lightning fire regime, it would take over 10 thousand years to burn the entire study area. Without fire suppression, the mean fire size will increase. For example, 2 lightning fires which were not suppressed in 1976 and 1977 burned 57 ha ($\bar{x}$ = 28 ha). If this area were burned by each lightning fire and the number of fires remained at 2.5 per 10 years, then an average of 7 ha would be burned by lightning fires each year. Under this disturbance regime 1300 years would be required to burn the entire study area. By assuming a fire will not cross a primary order stream, the maximum area a fire is likely to burn was calculated. The average area that might burn in the study area is approximately 300 ha. Even if all fires attained this size, the fire rotation would be over 100 years.

Data from fire scars sampled in the present study indicated a fire rotation of less than 30 years but greater than 10 years for the Euro-American settlement period while observations provided by Lambert (1958) and Heritage (1939) indicated a fire rotation of 5 to 38 years.

Under the influence of Cherokee and other Indian cultures, the fire rotation period in the study area may have been less than 500 years. Clearly, further study on the impact of Indians would be desirable.

Summary

During the periods of Euro-American settlement and NPS management, man was the major cause of fire. Between 1830 and 1940 the fire rotation was between 10 and 30 years. Under fire suppression, the fire rotation increased to 10 thousand years. The exact role of

pre-Columbian Indians in burning the study area is not known and further research is required.

Evidence of fire was present in most forests regardless of aspect, slope position and elevation. During the period of Euro-American settlement, fires in pine forests were more frequent at lower elevations. Fires were most frequent on south facing upper slopes and least frequent on north facing lower slopes.

Years with less than average rainfall were more prone to have fire scars. However, it was difficult to assess whether man or lightning was the primary cause of fire starts during drought events. Most south facing slopes and north facing upper slopes have not burned since NPS management was initiated in 1930. Under a continued fire suppression policy, the chances of a forest burning are very low. Allowing some lightning fires to burn will decrease the fire interval, but only to a small degree relative to that during the periods of Euro-American habitation.

V. CHARACTERISTICS OF FIRE DISTURBANCE

Introduction

Forest composition reflects a balance of seed sources, seed germination, and the ability of the resultant seedlings to survive and grow. Shifts in this balance result in composition fluctuations which may be caused by either endogenous or exogenous factors (Webb et al. 1972, White 1979). Exogenous factors represent strictly environmental agents, whereas endogenous factors are only influenced by characteristics of the plant species themselves. In reality, few factors are truly endogenous or exogenous; rather one can envision a continuum of endogenous and exogenous combinations. Although fire has been traditionally viewed as a strictly exogenous factor, the presence of fire-promoting, resisting and dependent traits suggests fire is partially endogenous (White 1979). Hence, changes due to fire may be as much a result of community structure and composition as of environment.

Fire disturbance influences individual plants by reducing stature (e.g., killing above ground parts in sprouting species), opening wounds, enhancing seed germination, reducing competition and death. Species, as well as individuals, vary in their ability to resist and/or exploit fire induced changes. Frequent fires over a long time span may become an evolutionary agent and thus affect the position of fire on the exogenous-endogenous gradient.

Clearly, the relationship between fire, other environmental factors and plant communities is holocoenic (Billings 1952). The following section attempts to separate the effects of fire, environment

and species on forest structure and mortality. Finally, a preliminary model summarizing the effect of these 3 variables is presented.

Results

Fire behavior and stand mortality. Theoretically, tree mortality should increase with higher fire intensity, higher ambient temperatures and lower wind speeds (Bryam 1958, Storey and Merkle 1960, Van Wagner 1973). Unfortunately, fire intensity, ambient temperature and windspeed were not measured on the fires examined here.

Crown fires are rare in the Southern Appalachians (Barden 1974). Most of the fires examined in the present study were probably surface fires (Brown and Davis 1973), although hot fires tended to "crown-out." With one exception, all burned sites examined with high mortality corresponded to areas with heavy southern pine bark beetle-kill. Stands with beetle-kill had considerable mortality during both summer and winter fires. Tree boles downed before the fire were charred but not consumed unless in an advanced state of decay. Branches smaller than 8 cm diameter, twigs, and soil organic horizons are greatly reduced on high mortality sites (Harmon 1980). Evidently the accumulation of fine fuels within beetle-kills increased fire intensity and hence mortality.

Fires burning on slopes create updrafts which preheat fuels and fire sensitive plant tissues (Schroeder and Buck 1970). Preheating serves to increase the ambient temperature and could increase mortality. On 2 of the 6 severely disturbed sites investigated, slope and topographic position appeared to explain high stand mortality.

Canopy openness. The portion of sky obscured by live trees decreased significantly as the amount of basal area and stems removed by fire increased (Figure 2). A linear model with an intercept near 0 was an adequate regression model for both independent variables. The intercept for the basal area equation was higher than that of the stem equation. Amounts of canopy opening present in undisturbed forests varied between forest cover. The basal area equation also predicted 100% canopy opening with 100% removal, but the stem equation predicted 84% canopy opening. The basal area model, therefore, appeared to be more realistic than the stem density model in terms of predicting canopy opening.

Fuel reduction. Approximately 90% of the O1 litter horizon was removed by fire in pine and oak forests regardless of season (Harmon 1980). Removal of O2 litter horizon was influenced by forest cover and season. Fires in oak forests tended to remove less than 50% of the O2. Summer fires removed over 80% of the O2 in pine forests while winter fires removed less than 40%. The seasonal differences in O2 litter horizon consumption were probably related to moisture content. Van Wagner (1972) demonstrated the inverse relationship between O2 moisture content and fuel consumption by fire in pine forests.

Species richness. Fire disturbance tends to remove species as well as individuals from the canopy strata. The degree to which fire reduces species richness* theoretically varies with the original number

*Species richness is defined as the number of species per unit area.

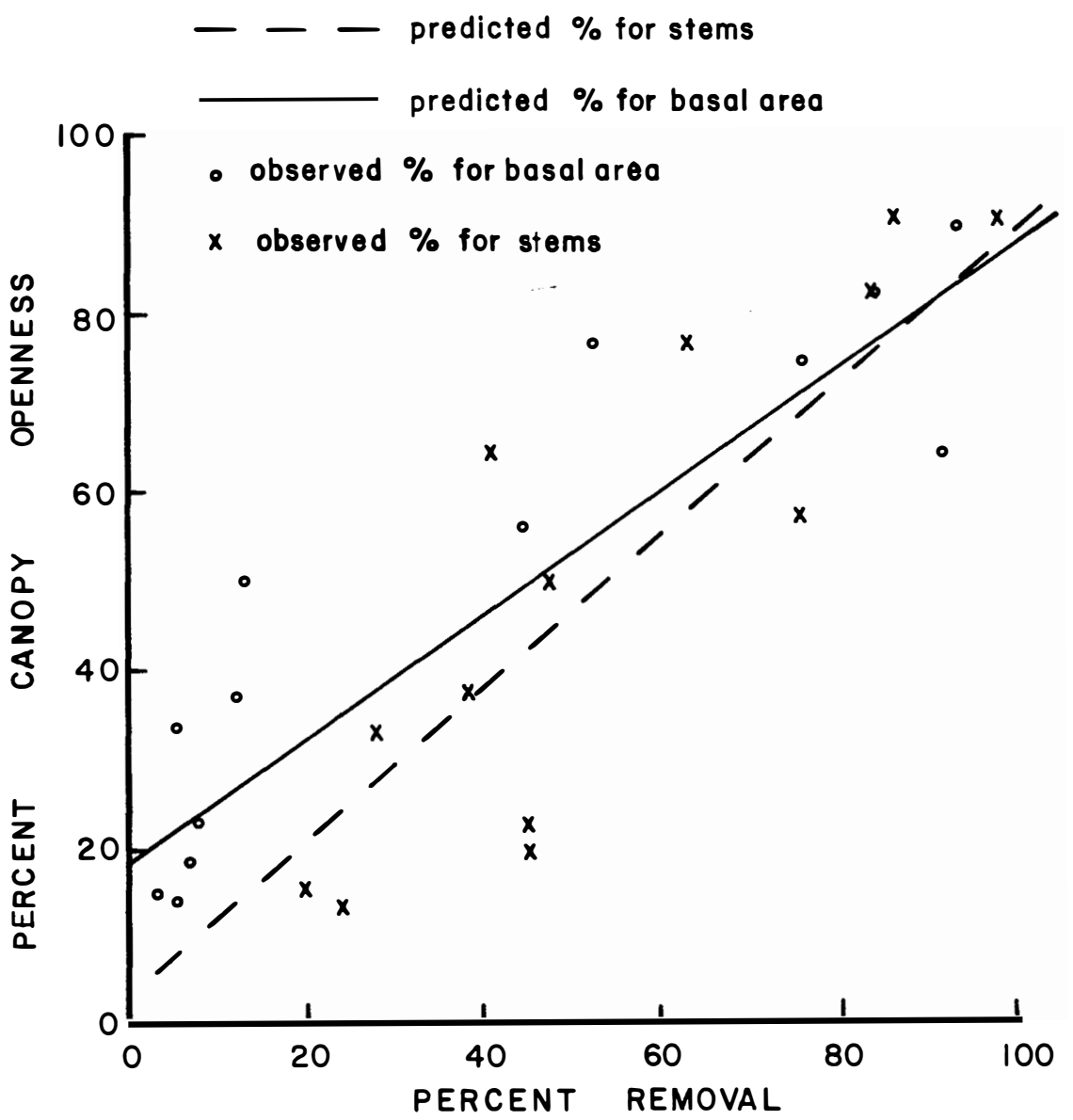


Figure 2. Estimated increase in percent canopy opening as a function of the percentage of basal area and stems removed by fire.

of species, size structure, composition, susceptibility of species to fire and the severity of disturbance. For example, a forest with a set of fire resistant species is less apt to change in richness than a forest with a suite of susceptible species. A forest with a rich upper canopy and a few lower canopy species would be expected to lose fewer species than a forest with an inverse structure.

Fire disturbance removed up to 9 species per 0.10 ha, but even in cases of 99% stem removal 3 species remained. Canopy richness decreased significantly as the percentage of stems removed increased (Figure 3). The linear model used was only appropriate over a range of 15% to 99% stem removal. Although fires tended to decrease canopy richness, the disturbance had to be quite severe (i.e., over 75% stem removal) to remove one-half or more of the original species.

Initial shifts in species composition. Two questions concerning composition can be asked after a fire:

(1) Are compositional changes proportional to severity?

(2) Are compositional changes consistently biased?

As fire severity increased, the stem and basal area compositional similarity* decreased (Figure 4). The relation between fire severity and compositional change appeared to be curvilinear. The general convex upwards curve shape indicated that, as fire severity increased, the rate of compositional change increased.

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*Compositional similarity is based upon a modified index of Jaccard (Muller-Dombois and Ellenberg 1974).

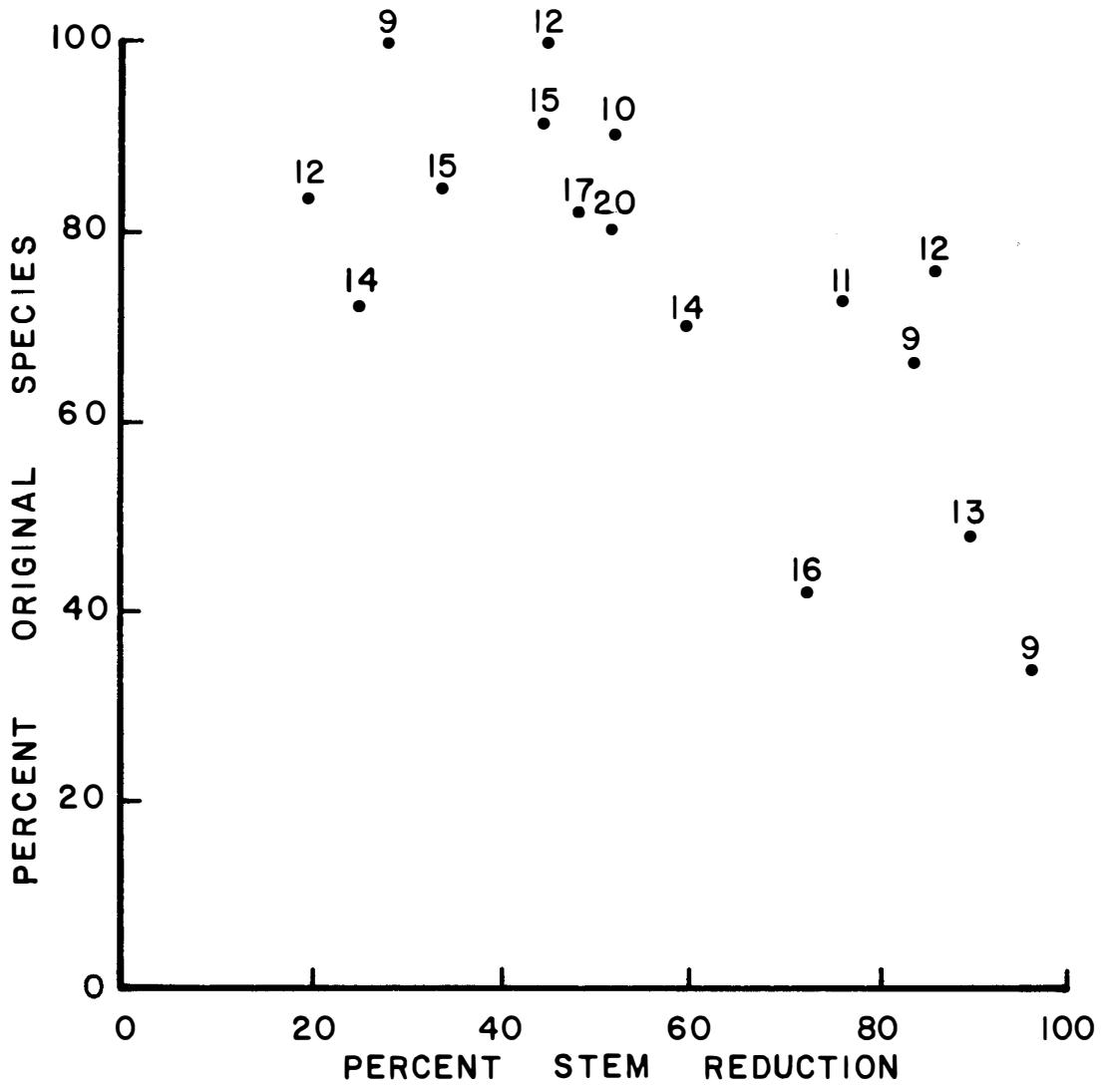


Figure 3. Decrease in species number per 0.1 ha as a function of the percent stem reduction caused by fire.

The numbers above circles represent the original number of species.

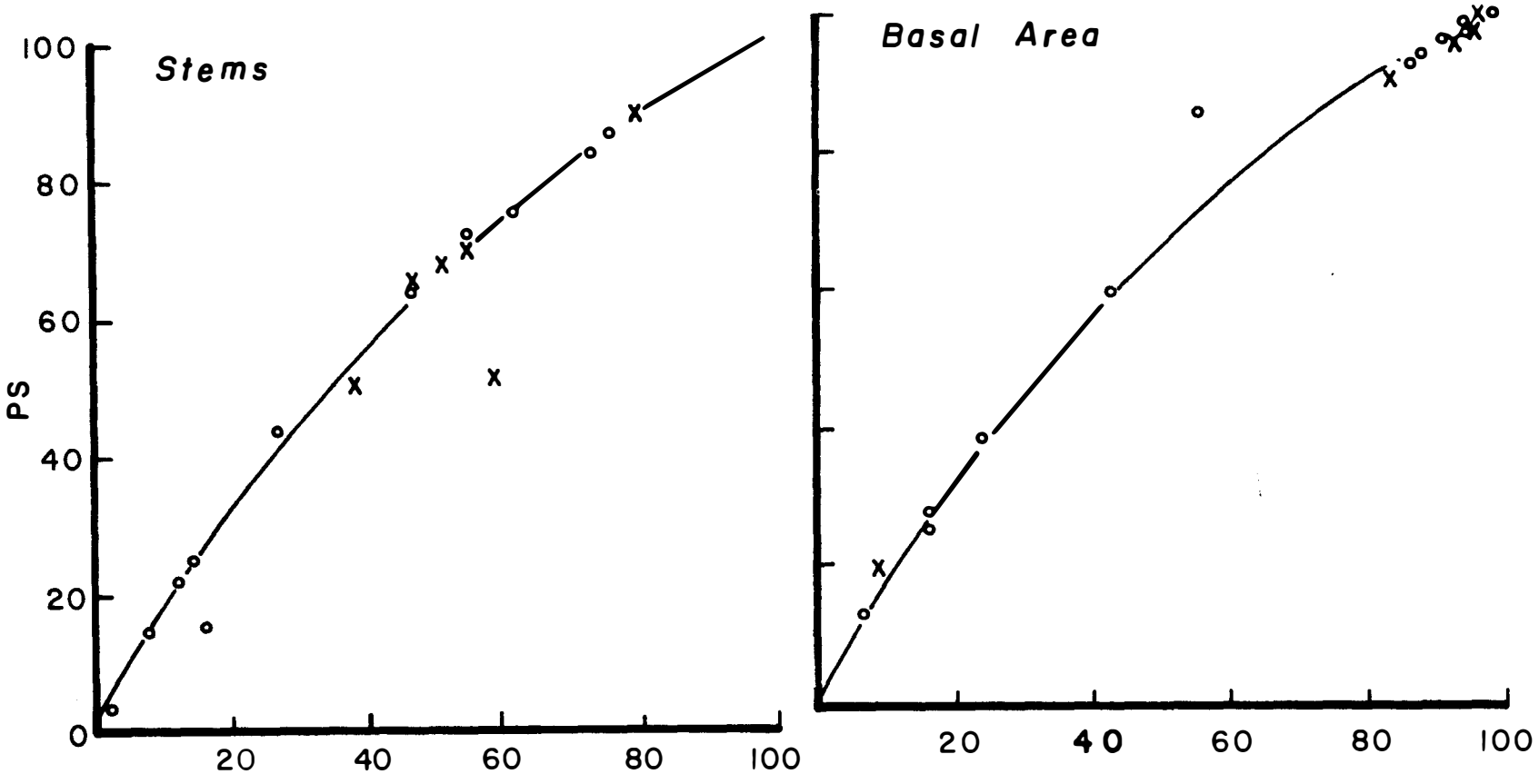


Figure 4. Change in canopy composition as a function of basal area and stem removal caused by fire.

The open circles represent yellow pine forests and the X's represent oak forests.

The length of the disturbance vector was proportional to disturbance severity for both basal area and stem density ordinations (Figures 5-6). The directions of stem composition changes were also consistent within a forest cover. After cool surface fires in both pine and oak forests, little change occurred in stem composition. Usually oak and pine stems increased in dominance as smaller understory trees such as blackgum, sassafras, hickories, dogwood, red maple, sourwood and mountain laurel were girdled and killed. After a hot fire in oak forest stem composition shifted toward hardwoods other than oak. Hot fire in pine forest caused a consistent increase in the percentage of pitch pine and scarlet oak stems and a decrease in hardwoods. Shifts in basal area composition after fire also indicated a consistent bias. As in the case of stem composition, little change in basal area dominance was associated with cool fires. After severe fire in oak forest there was a relative increase in pitch pine and Virginia pine basal area. However, not all oak forests contain pines, so the shift toward pine only occurred in pine-oak transitional situations. When pine forests were severely disturbed, pitch pine and table mountain pine relative basal area increased at the expense of Virginia pine. The higher survival of pitch and table mountain pines after severe fire disturbance may reflect their generally larger size and thicker bark compared to Virginia pine. Pitch pine also produced epicormic branches after defoliation, a trait which enhanced the probability of fire survival.

Epicormic sprouting ability. Convective heat plumes may elevate leaf and bud tissues to lethal temperatures causing defoliation and

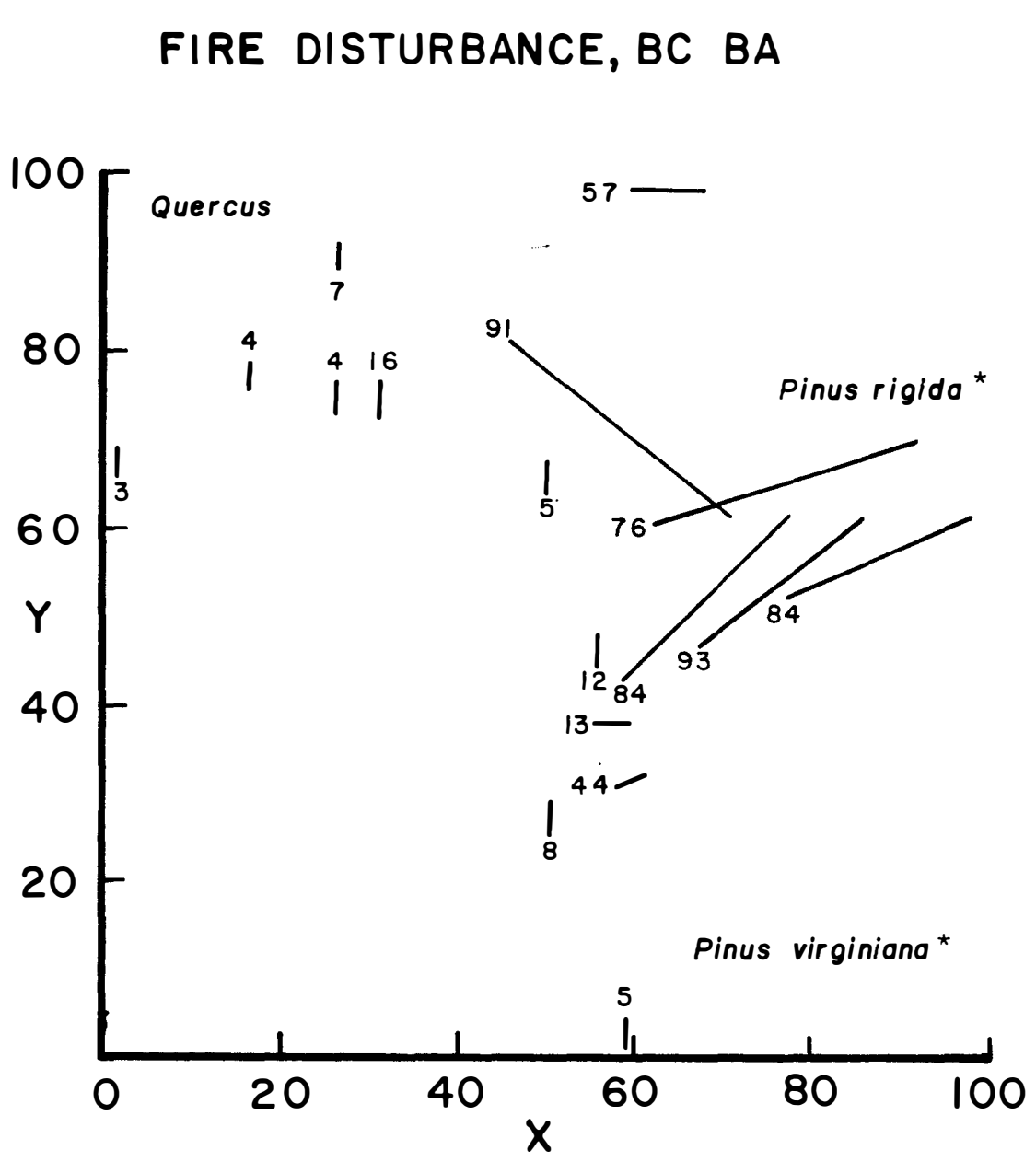


Figure 5. Vectors of basal area composition change caused by fire.

The numbered end of the vector indicates the position before fire, while the number represents the percent basal area removed by fire. The endpoints of the vectors represent the position of a plot before and after fire in the Bray-Curtis ordination.

*The common names of species from all figures are presented in the Appendix, Table 29.

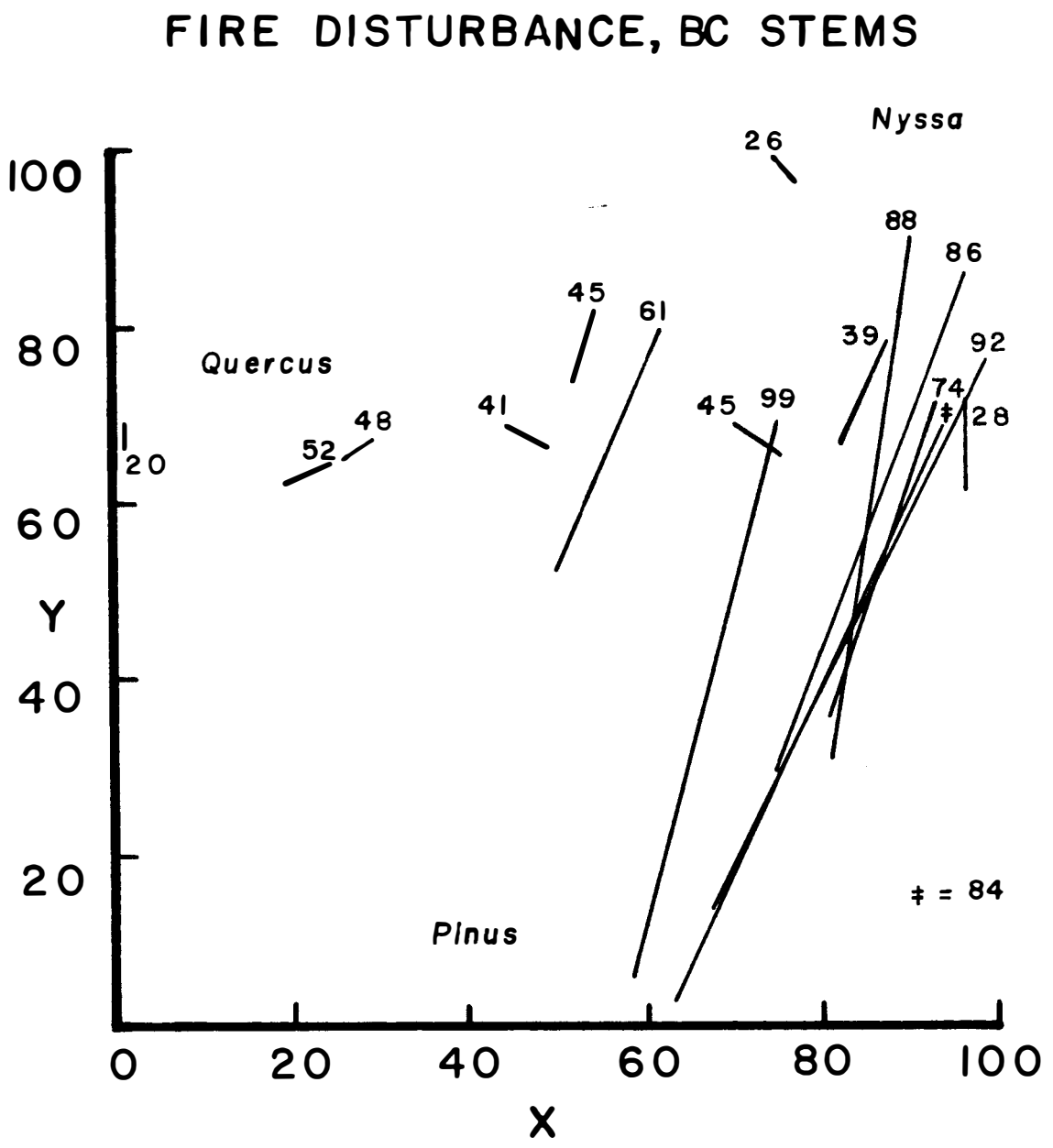


Figure 6. Vectors of stem composition change caused by fire.

The numbered end of the vector indicates the position before fire, while the number represents the percent stem density removed by fire. The endpoints of the vectors represent the positions of a plot before and after fire in the Bray-Curtis ordination.

death of exposed buds. In contrast to cambium (which is protected by bark) leaves and buds have very little thermal protection (Hare 1961). When only defoliation occurs, many species can activate buds that were dormant prior to defoliation (Churchill et al. 1964, Collins 1961, Storey and Merkel 1960). Death of all exposed buds will result in the death of the above ground portions of a tree unless an individual is capable of epicormic sprouting.* Resistance to cambial girdling and epicormic branching both enhance the ability of a tree to maintain its stature after fire disturbance.

Leaf scorch height in severely burned stands exceeded the height of trees less than 10 cm dbh. Trees less than 10 cm dbh with epicormic sprouts on these sites represented individuals that withstood defoliation and stem heating. The proportion of trees which withstood stem heating but failed to initiate epicormic sprouting after defoliation or death of exposed buds could not be determined.

A chi-square test indicated that trees less than 10 cm dbh on severely burned sites exhibited significantly different proportions of epicormic branching according to species (Table 2). Sassafras stems had no epicormic sprouts, while most blackjack oak stems had epicormic sprouting. Although hemlock, white pine, Virginia pine and table mountain pine were not examined quantitatively, no epicormic sprouts were observed on these species. Epicormic sprouting in pitch pine was less than the mean for the other species examined. Nonetheless, the ability

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*Epicormic sprouting is defined here as the initiation of sprouts from dormant buds at least 0.5 m above the ground.

Table 2. Number of Stems Surviving Severe Fire Event with Epicormic Sprouting on the Main Stem.[a]

Species[b]	Stems with Epicormic Sprouting: Percent of Observations	Stems with Epicormic Sprouting: Total Number of Observations
Nyssa sylvatica	39	119
Oxydendrum arboreum	27	15
Pinus rigida	16	49
Quercus marilandica	89	9
Quercus prinus	25	20
Sassafras albidum	0	69
Total	25	281
$\chi^2 = 42.302$	df = 5	P<.01

[a]The trees for this analysis were all less than 10 cm dbh.

[b]The common names of species from all tables are presented in the Appendix, Table 29.

to produce epicormic sprouts gave pitch pine an advantage over most other conifers when convective heating was extreme (e.g., a head fire). Shortleaf pine is also capable of epicormic sprouting (Stone and Stone 1954) and is probably quite similar to pitch pine in this trait.

Fire survival. As the severity of fire increased, the number of trees killed in each size class also increased (Figure 7). It was more useful, however, to consider the probability of survival rather than the absolute number (which varied with density). The probability of survival, P(Surv), is defined as the proportion of trees surviving a fire. As long as the total number of individuals observed is large, this proportion will approximate the actual probability (Dwass 1970).

Trees over 9 cm dbh had a very high P(Surv) in both the cool and medium fire situations (Figure 8). When fires were hot only a few individuals survived either because of very large size, genetic attributes (e.g., very thick bark and epicormic branching) or the presence of cool pockets, a factor that allowed some small, fire susceptible species to survive. Stickle (1935) also found that survival increased with size and decreased with fire intensity. Overall stand survivorship is generally considered a function of size distributions, species and fire intensity.

Survival after a cool fire increased significantly as a function of dbh for each species examined (Appendix, Table 9 and Figure 9). The chi-square test indicated that the observed number of survivors did not deviate significantly from the number predicted by the curvilinear logistic regression model.

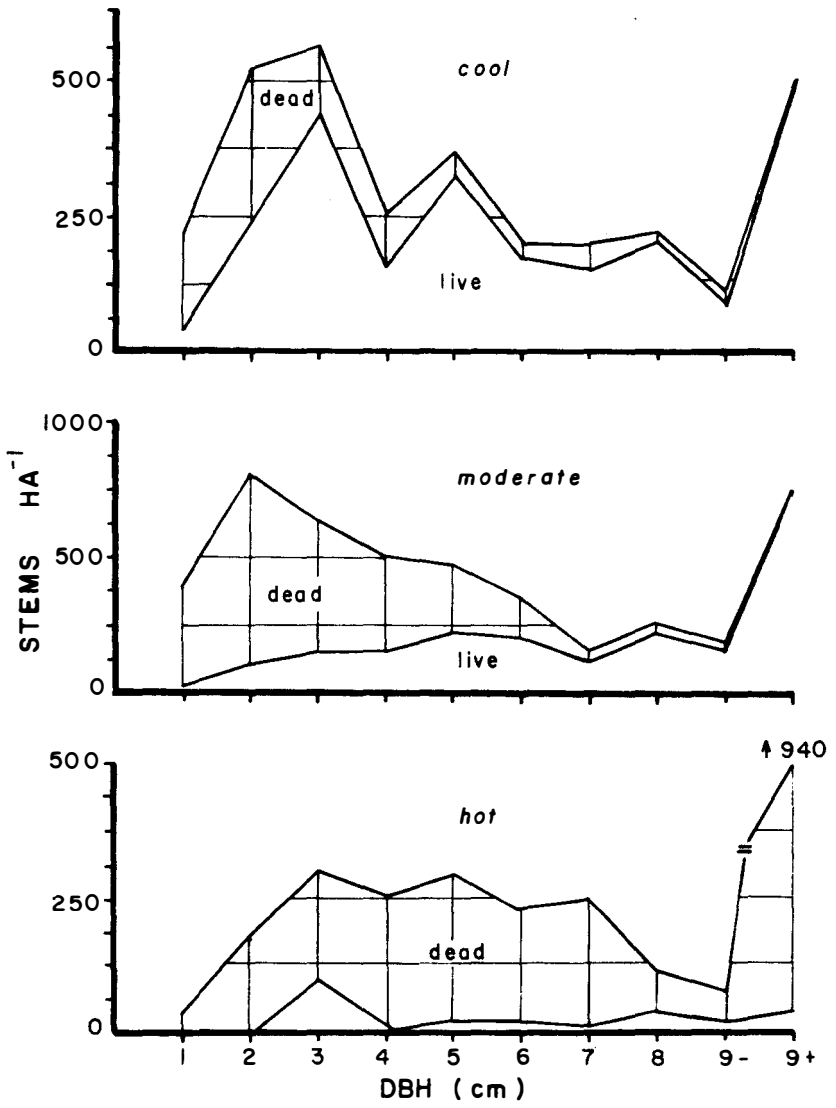


Figure 7. Stem mortality as a function of fire severity and tree size.

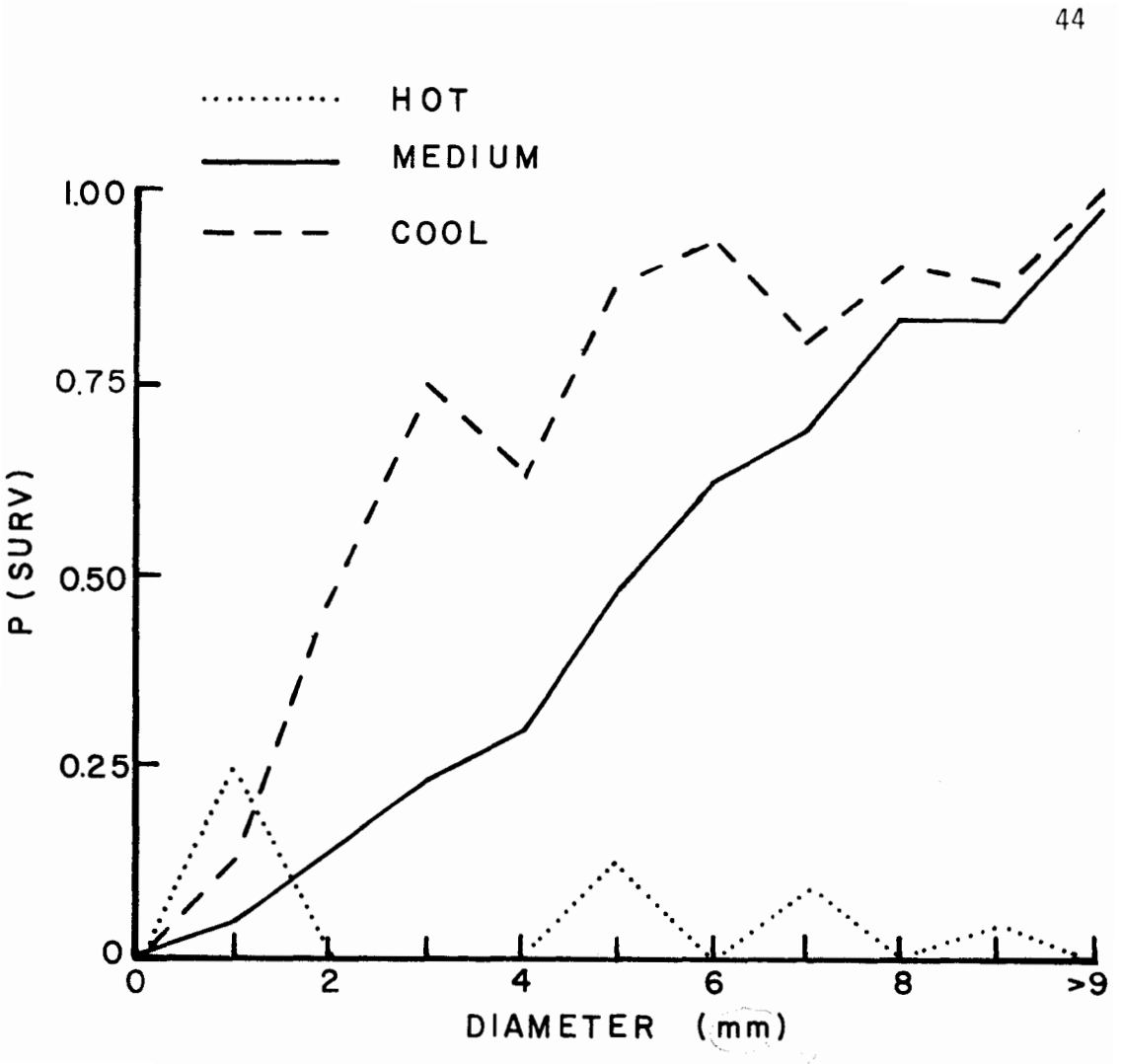


Figure 8. Survival of trees as a function of diameter at breast height and fire severity.

Cool fires reduced the basal area less than 25% while hot fires removed over 50% of the basal area.

Figure 9. Survival of canopy trees after cool surface fire as a function of size and species.

The probability of survival, P(Surv), is described as a logistic-type function of size. Curvilinear regression estimates of the logistic-type functions are presented in the Appendix, Table 9.

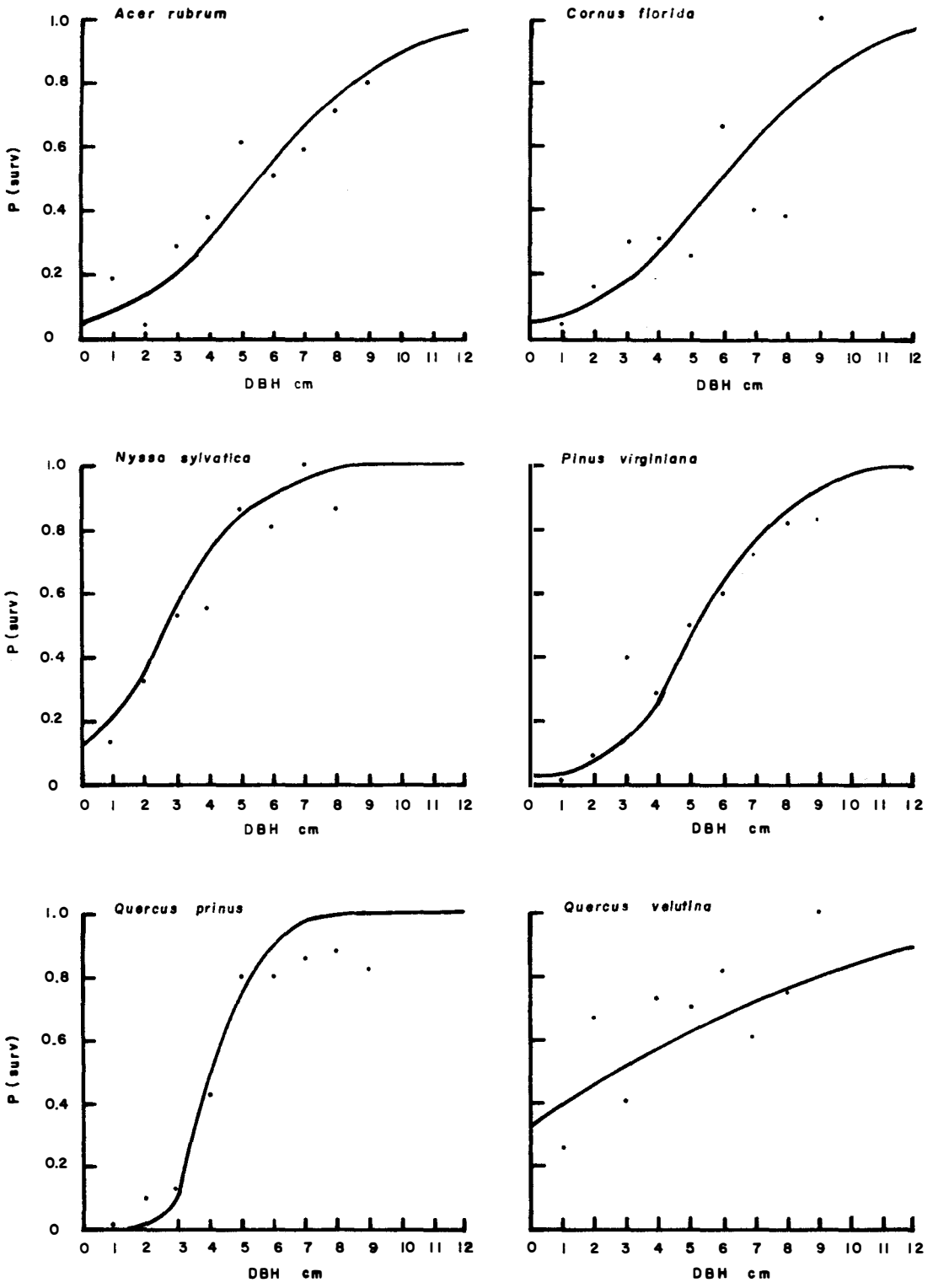

Acer rubrum
Cornus florida
Nyssa sylvatica
Pinus virginiana
Quercus prinus
Quercus velutina
P (surv)
DBH cm
0
0.2
0.4
0.6
0.8
1.0
0 1 2 3 4 5 6 7 8 9 10 11 12

Figure 9

The regression models indicated differences between species as size increased. For example, blackgum survived better than chestnut oak when less than 3 cm dbh. However, as chestnut oak exceeded 3 cm dbh it became quite similar to blackgum in survival. Red maple survival when trees were less than 3 cm dbh was higher than for chestnut oak and pines. When trees exceeded 3 cm dbh, survival of chestnut oak and pines equaled or exceeded that of red maple. The changing relationship of survival to size between species made it difficult to order species linearly from fire intolerant to fire resistant. The steep slopes of chestnut oak, Virginia pine, white pine, pitch pine, blackgum, sourwood, and sassafras indicated high resistance to fire. Red maple, dogwood and the hickories had low resistance to fire.

Use of calculated bark thickness as an independent variable in predicting cool fire survivorship generated significant curvilinear regression models (Figures 10-11). Both the ground level and breast height bark thickness predicted some survival when bark thickness was 0. The breast height level model predicted higher survival than the ground level model when bark thickness equaled 0. This result was expected since ground level thickness was generally higher than dbh level thickness. Both models predicted nearly complete survival of cool surface fires when bark thickness exceeded 10 mm.

A number of observations were held in reserve to test the goodness-of-fit of both models using the chi-square test. Survival predictions from the breast height and ground level models did not deviate significantly from those observed. In many cases the ground level model is preferable to the breast height model, since heat release and protection is most critical at ground level.

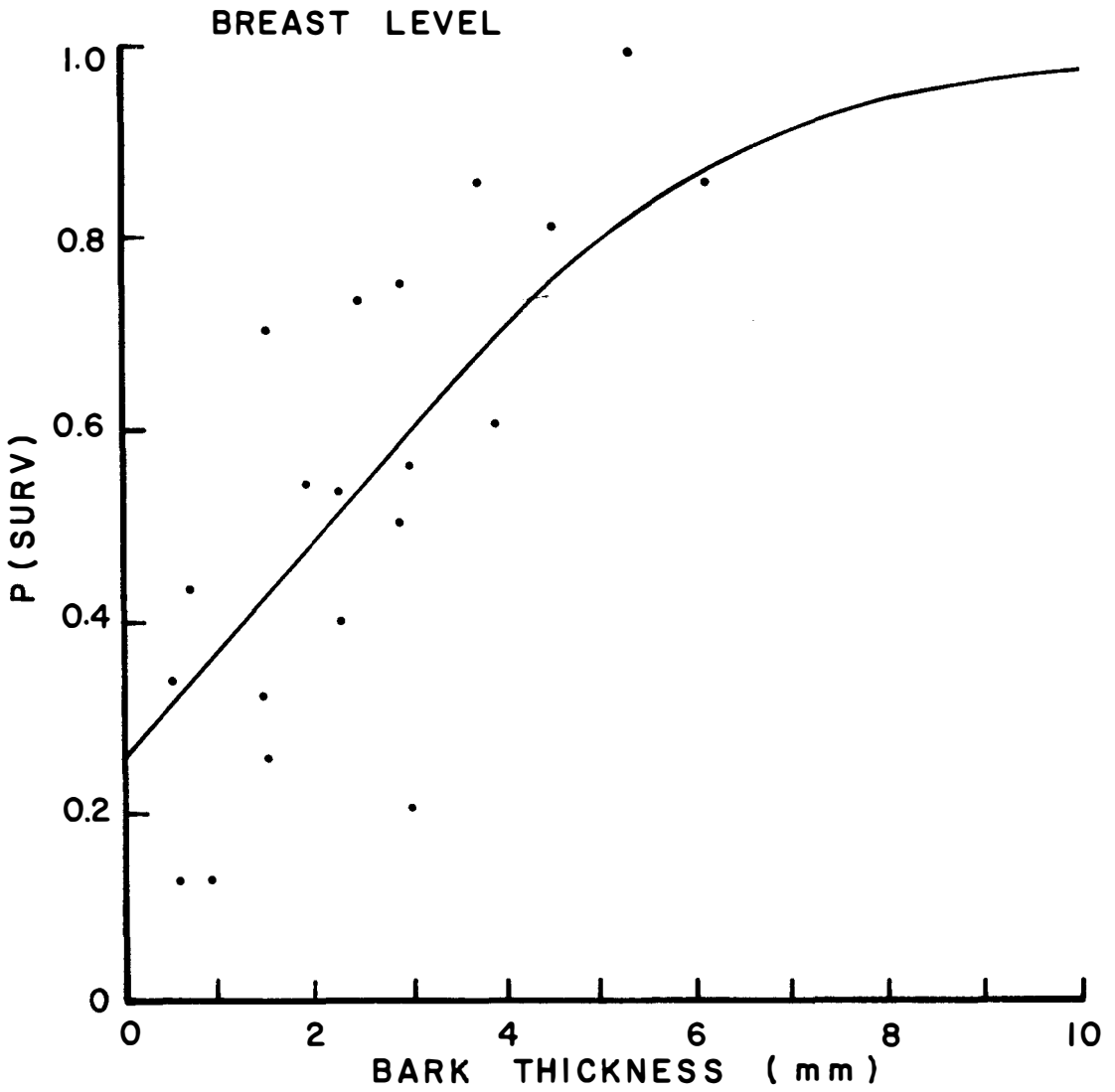


Figure 10. Survival of canopy trees after cool surface fire as a function of bark thickness at breast height.

$P(surv) = [1 - \exp(1.04 - 4.85\ BT)]^{-1}$, $r^2 = 0.89$, $p<0.01$, where BT is bark thickness at dbh level in cm and P(surv) is the probability of survival after cool ground fire. Dots represent observations independent of data used for regression analysis. The goodness-of-fit between the independent observations and the regression was tested using chi-square $X^2 = 23.91$, df = 19, $0.5>p>0.1$.

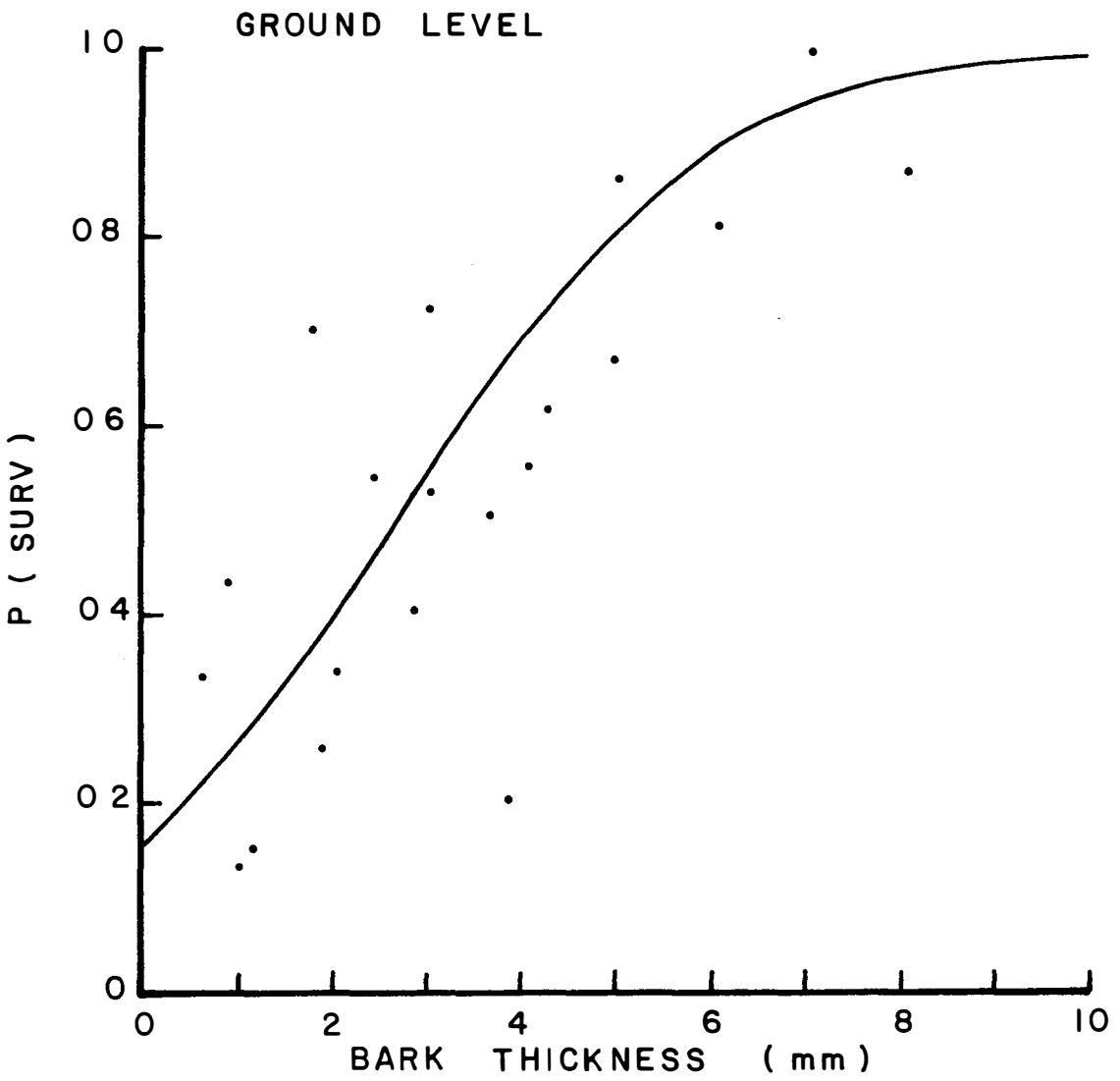


Figure 11. Survival of canopy trees after cool surface fire as a function of bark thickness at ground level.

$P(surv) = [1 - \exp (1.74 - 6.43\ BT)]^{-1}$, $r^2 = 0.88$, $p < 0.01$. BT is bark thickness at ground level in cm and P(surv) is the probability of survival after cool ground fire. Dots represent observations independent of data used for regression analysis. The goodness-of-fit between the independent observations and the regression was tested using chi-square. $X^2 = 18.63$, df = 19, $0.5>p>0.1$.

Survival-size relationships can be calculated by combining bark thickness data (Table 3) and the survival-bark thickness regressions (Figures 10-11). Although these predictions are useful they are subject to some limitations: (1) the bark of 2 species may be of equivalent thickness, but one may be a better insulator than the other (Spalt and Reifsnyder 1962) and (2) all tree death is not due to cambial girdling, defoliation or the heat death of exposed buds may also be important causes of mortality. Given 2 species with similar bark characteristics, the species with greater defoliation tolerance would be more likely to survive fires. Tolerance to defoliation may be expressed by traits such as epicormic branching or a growth form which increases the height of foliage above the ground.

Bark thickness. Although bark thickness usually increased from dbh to ground level, in the yellow pines it more than doubled. Therefore, yellow pine resistance to cambial girdling at ground level greatly exceeded that predicted from bark thickness at breast level.

Table 3 presents bark thickness data and ranks each species according to predicted resistance. Using ground level bark thickness blackjack oak was the most resistant species while yellow birch, buckeye and beech were the least resistant. Using breast height bark thickness placed blackjack oak as the most resistant and yellow birch as the least resistant. However, a major decrease in rank occurred for Virginia pine and table mountain pine when breast height bark thickness was used.

Table 3. Bark Thickness as a Percentage of Diameter at Breast Height.[a]

Species	Bark Thickness: Breast Height %	Breast Height Rank	Ground Level %	Ground Level Rank	N
Acer pensylvanicum	2.5	26	3.3	24	9
Acer rubrum	2.5	27	3.3	25	27
Aesculus octandra	2.7	24	2.8	27	6
Aralia spinosa	5.5	9	8.2	6	12
Betula lutea	2.3	28	2.4	28	45
Carya spp.	4.9	12	6.1	13	33
Celtis occidentalis	5.9	6	4.5	20	9
Cornus florida	2.9	22	3.5	22	18
Fagus grandifolia	2.8	23	3.0	26	42
Halesia carolina	3.5	19	3.8	21	24
Liriodendron tulipifera	4.7	15	5.9	14	72
Magnolia tripetala	4.4	16	6.2	12	18
Nyssa sylvatica	7.6	3	10.1	3	18
Oxydendrum arboreum	5.9	7	5.3	18	15
Pinus pungens	4.8	13	8.3	5	24
Pinus rigida	9.0	2	12.0	2	51
Pinus strobus	7.5	4	9.7	4	45
Pinus virginiana	3.0	21	7.9	7	42
Quercus alba	4.7	14	5.9	15	18
Quercus coccinea	4.0	17	6.4	11	15
Quercus prinus	6.7	5	7.8	8	39
Quercus rubra	2.7	25	5.1	19	15
Quercus velutina	5.7	8	5.6	16	15
Rhus typhina	3.3	20	3.4	23	15
Robinia pseudoacacia	5.3	11	7.2	9	27
Sassafras albidum	5.5	10	6.7	10	18
Tsuga canadensis	3.8	18	5.3	17	36

[a]Thickness at ground level (0.25 m) and breast height are included. Species are ranked from the thickest to the thinnest bark.

Growth rates. There were significant differences between species in their ability to grow on south facing slopes (Figure 12). The t-test indicated that dominant pines grew significantly faster than oaks, hardwoods or suppressed pines. Oaks, in turn, grew faster than suppressed pines and hardwoods (e.g., red maple, blackgum and sourwood). Suppressed pines and hardwoods grew at equivalent rates. The growth rates of hardwoods (aside from red maple, blackgum, hickory and sourwood) on south facing slopes were probably lower than the estimated dbh growth rate of 0.217 cm yr^{-1}. Dominant pines had growth rates exceeding 0.492 cm yr^{-1}, while suppressed pines had roughly one-half this growth rate (0.252 cm yr^{-1}). Oaks (chestnut, black and scarlet) were estimated to grow at a rate of 0.319 cm yr^{-1} on south facing slopes. Although the sample size was quite small (N=35 trees), it illustrated the differences expected between species.

As tree diameter growth rate increases, the rate at which bark thickens, also increases. Fast growing trees will produce a thicker and therefore more heat resistant bark than slow growing trees. For example, given dominant and suppressed pines of the same age, the former should theoretically have bark twice as thick as the latter. Differential growth between species can, therefore, affect fire survival differences which are based on bark thickness.

Discussion

Weather, topography and fuels as determinants of fire severity. Fire severity is controlled by weather, topography, and fuel. Burning regimes differ with respect to these factors. Fire suppression has

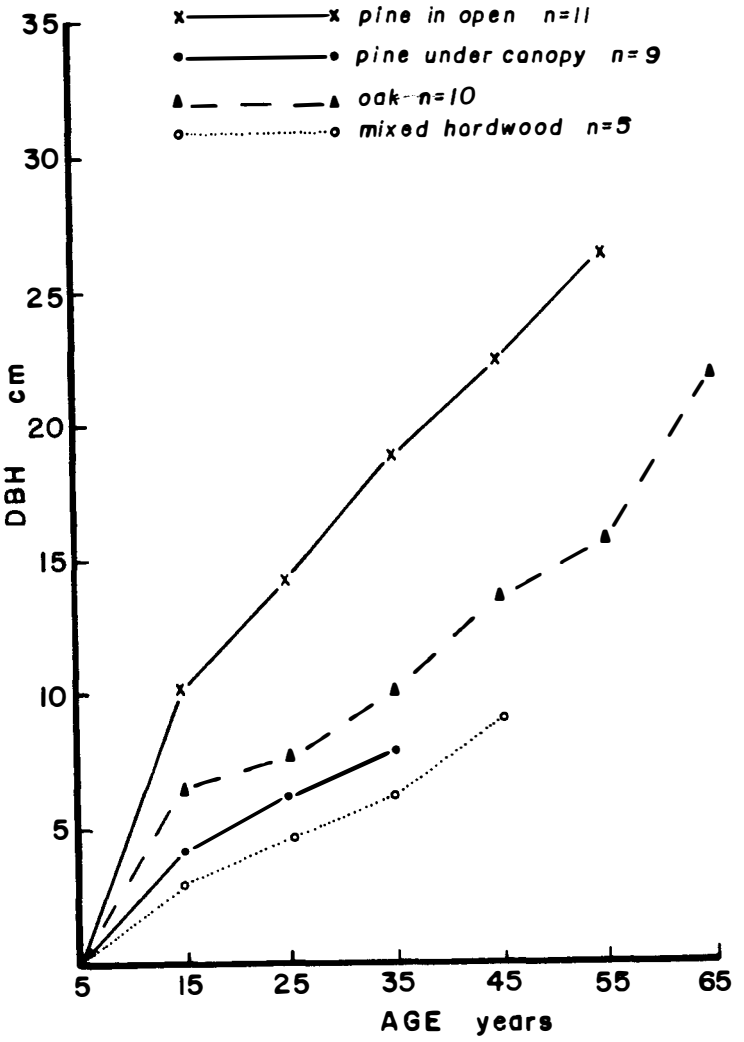


Figure 12. Growth in diameter at breast height (dbh) for yellow pines, oaks and hardwoods on south facing upper slopes.

Growth rates were estimated from diameter cores at breast height. Trees were assumed to reach breast height when 5 years old. Each data point represents the mean value.

increased dead fuels in forests and have increased the potential of fires to be more severe than those during Euro-American settlement.

Severely burned sites observed in this study often corresponded to heavy fuel accumulations after kills from southern pine bark beetle. Windthrow and fire also increased fuel accumulations. Windthrow is likely to cause very localized increases in fire severity in all types of communities. Trees adjacent to downed logs and stumps were often observed to be girdled and in some cases considerable green wood was burned. After 5 to 10 years most fire killed stems fall to the ground and increase the severity of the next fire.

The organic horizon accumulations in the forests of western GRSM differed greatly (Harmon 1980). In descending order of these levels were: cove hardwood with rhododendron, yellow pine, chestnut oak, mixed oak, oak-hardwood, and deciduous cove hardwoods. The amount of fuel entering the combustion process is dependent on fuel moisture, packing and mineral content. An increase in any of these factors reduces the quantity of fuel available for consumption, reducing potential severity. Mineral contents and bulk densities of hardwood and pine organic horizons did not differ greatly in eastern Tennessee forests (McGuiness 1958). Mutch (1970) demonstrated significant differences in fuel flammability between species; pine litter was more flammable than hardwood litter. Available fuel can be ranked by accumulation and relative moisture levels. For example, cove hardwood forests with rhododendron have heavy fuel accumulations but rarely dry sufficiently to permit combustion; severe fires are probably quite rare in this community. In contrast, yellow pine forests on south facing slopes have heavy fuel

accumulations and dry quickly; hence pine forests are more likely to have severe fires.

Topography affects fire severity by influencing fire behavior as well as fuel moisture content. Fires heading upslope will tend to cause greater canopy heating and defoliation than fires backing downslope (Hare 1961). Backing fires tend to burn slower, consume more fuel and cause more girdling than head fires (Hare 1961). In the present study forests on upper slopes and ridges were observed to be more susceptible to severe fires. Barden (1974) found that most lightning-caused fires started on upper slope positions indicating these will predominately be backing fires. Man-caused fires often start on middle to lower slopes and should cause more defoliation than lightning caused fires.

Seasonal weather changes influence fire severity. Cooler ambient temperatures during winter increase survival relative to warmer summer temperatures (Byram 1958, Storey and Merkle 1960, Van Wagner 1973). Barden (1974) hypothesized that the major differences in lightning- and man-caused fire behavior are attributable to weather. However, these comparisons were based on data taken under policies of fire suppression. If lightning-caused fires were allowed to burn into dry periods, spread rate and intensity would be expected to increase.

Initial changes in community structure. Fire increased the amount of light reaching the forest floor by increasing stem mortality. As the amount of basal area removed by fire increased, the canopy coverage significantly decreased. Increases in light penetrating to the forest floor increased the chance that light tolerant species will become

established. Sprouts from girdled trees are also favored by increased canopy openings. On exposed south facing slopes the increase in light may select against mesic species that are unable to tolerate an increase in leaf heat loads. By increasing soil temperature, canopy openings may speed decay rates and mineral cycling. The temporary increase in available nutrients from decay and combustion may influence the colonization of burned sites (Bormann and Likens 1979).

Although most fires removed species from the canopy, over 75% stem removal was required to reduce canopy richness by half. Since many species removed from the canopy strata remained in the stand as sprout reproduction, the decrease in canopy richness was often a temporary phenomenon. Species unable to sprout (e.g., hemlock) may have been locally eliminated by fire.

As fire severity increased, the degree of similarity to canopy composition prior to fire decreased for both pine and oak forests. Changes in species composition affect future stand composition by altering the composition of seeds reaching the site. Thus, the effect fire has on a given community is a function of severity and community composition. This supports the hypothesis that fire is both an exogenous and endogenous disturbance.

Fire tolerance. Individuals which are not killed by fire may be severely injured and have a lower competitive ability than individuals without injury. Thick bark, epicormic branching, high branches and decay resistant wood are traits which allow individuals to retain canopy stature after fires. Since larger size leads to thicker bark, rapid growth rates may also be selected for by frequent burning.

Survival of cool fires was correlated strongly to bark thickness. A similar correlation may exist for the severe fires. Bark structure may also influence fire survival (Spalt and Reifsnyder 1962). Flakey and corky barks tend to insulate better than compressed hard bark that has few air spaces. Thick bark also prevents partial girdling and wounds which allow the introduction of pathogenic infection and decay.

Some trees observed in this study did not survive in spite of the ability to sprout epicormically. Often these individuals were large oaks and pitch pines. Older and larger individuals may have had a lower probability of sprouting and survival than intermediate sized individuals (Woods and Cassady 1960).

In general, hardwoods should have an advantage over conifers in recovering from defoliation. Shortleaf and pitch pine were observed to recover from severe defoliation more often than Virginia, table mountain, and white pine and hemlock. Thick bark also complemented the ability to form epicormic branches.

Although decay and disease susceptibility were not studied here, both factors led to mortality after fire. After 3 to 4 years of decay, trees with basal wounds were observed to have stem breakage. Species observed with stem breakage included red maple, dogwood, blackgum, table mountain pine and blackjack oak. Since hardwoods decay faster than conifers (Allison and Klein 1961), they should be more susceptible to stem breakage. Thick bark therefore enhanced survival after fire by reducing the chances of basal wound formation (Nelson et al. 1933).

Ideally, very tolerant individuals survive the disturbance intact by resisting cambial girdling, wound formation and defoliation. Slightly less tolerant individuals sustain injury but are able to maintain canopy position by resisting cambial girdling, decay and pathogenic attack. If defoliation occurs epicormic branching also insures that canopy positioning is maintained. Even less fire tolerant individuals are killed above the ground but are able to maintain themselves on the site by forming basal sprouts. Individuals which survive fire only as seed are even less tolerant, while those that are removed completely are the least tolerant to fire. A major distinction between species is the maximum level of fire tolerance they attain. Thus, pitch pine is extremely tolerant to fire because it resists girdling, resists decay, initiates sprout growth, and persists as seed after disturbance. Sweet birch is less fire tolerant because it rarely resists girdling, decays rapidly and rarely initiates sprouts.

A model of fire disturbance. Fire tolerance and growth rates can be used to generate a model of fire disturbance (Table 3, page 51, Figures 10-12, pages 48, 49, and 53, respectively). Although growth rate data were only presented for south facing slopes, there is no reason a model of this general type would not apply to other topographic-moisture situations. Model predictions indicate that stand dynamics related to fire disturbance have changed considerably since fire suppression was initiated by the National Park Service. During the period of Euro-American settlement fires were so frequent that few trees reached a size capable of surviving even cool surface fires. Although yellow pines, chestnut oak, sourwood and black gum had similar bark thickness,

the rapid growth of yellow pine on open sites gave these species a survival advantage. However, yellow pines growing under the canopy grew slowly and were usually killed by cool surface fires. Hardwoods with thin bark (e.g., dogwood) rarely reached a size a cool surface fire could not kill on south facing slopes. Even so, the probabilistic nature of fire mortality and the variation in fire intervals insured the presence of some fire intolerant species on south facing slopes even during the settlement period. By pursuing an active fire suppression policy, National Park Service managers are allowing fire intolerant species time to grow into sizes which have a high probability of survival. On south facing slopes this means the growth of hardwood species into larger and more resistant size classes. On north facing lower slopes, dense thickets of young hemlock may establish because of fire suppression. When both hemlocks and hardwoods become large enough on their respective sites, the dynamics initiated by fire disturbance will change.

Summary

Fire severity was observed to be a function of topography and fuel in this study. Although no data on the subject are currently available for the western portion of GRSM, weather also is known to influence fire severity and may account for the number of man-caused fires with extreme fire behavior. The occurrence of canopy disturbance prior to burning also increased the chance of severe fire.

As fire severity increased larger and larger individuals were killed. When severity was held constant, mortality decreased with increasing stem size. Attributes allowing individuals to survive fire

were thick bark, epicormic sprouting, resistance to decay and resistance to pathogenic attack. Survival was significantly correlated with bark thickness for cool surface fires. Further research, incorporating data on epicormic branching, bark structure and branching patterns will lead to refinements in survivorship predictions for fires of varying severity.

Differential growth rates combined with fire tolerance to influence disturbance dynamics. On south facing slopes dominant pines grew more quickly than oaks, hardwoods or suppressed pines. Fire regimes before the establishment of GRSM favored individuals with thick bark, rapid growth rates, and the ability to sprout. Effective fire suppression has allowed species with thin bark and slow growth rates to enter size classes that are resistant to all but the most severe fires.

Fires influenced community structure by creating canopy openings and removing organic soil horizons. As the amount of basal area and number of stems removed by fire increased, the amount of canopy opening increased. Not all fires removed thick organic horizons, especially if moisture contents were high. Fires, therefore, created a very heterogenous habitat in terms of light and organic matter. Species richness was reduced when over 20% of the stems were killed.

Finally, fire disturbance caused consistent changes in species composition in pine and oak communities. Fire disturbance was controlled by community as well as environmental factors, and must be considered both an endogenous and exogenous factor.

VI. EARLY RESPONSE TO FIRE DISTURBANCE

Introduction

A flush of sprout and seedling reproduction follows fire disturbance. This phase of community reorganization leads to a recovery of ecosystem process, structure and regulation after disturbance (Bormann and Likens 1979).

The pattern of community reorganization after fire is complex in Southern Appalachian forests, and is a function of elevation, position along the topographic-moisture gradient, community structure prior to disturbance, organic matter removal and fire severity. As fire severity increases canopy opening also increases, allowing shade-intolerant species to colonize the burned site. Furthermore, the exposure of mineral soil should favor the establishment of seedlings requiring both light and mineral soil (e.g., pines). Consumption of organic horizons also removes stored seed and may increase the importance of seed rain during the reorganization phase. Although woody vegetation is often killed above the ground by fire, the ability to form root collar sprouts insures persistence. In certain situations, root collar sprouts may grow faster and survive better than seedlings (McQuilkin 1975). Rapid and dense growth issuing from trees killed above the ground may reduce the importance of shade-intolerant seedling reproduction.

In the following section, the importance of seedling and sprout reproduction during the reorganization phase in oak and pine communities is assessed. The effects of position along the topographic-

moisture gradient, community structure prior to disturbance, organic matter removal and fire severity on the reorganization phase are also examined.

Results

Sprout reproduction. The following species produced sprouts after the above ground portion of the stem was killed by fire: pitch pine, shortleaf pine, blackjack oak, scarlet oak, black oak, chestnut oak, white oak, sourwood, mountain laurel, rhododendron, dogwood, blackgum, red maple, pignut hickory, mockernut hickory, black locust, persimmon, sassafras, shadbush, white ash, chestnut, Fraser magnolia, and yellow poplar. No sprouts were observed on fire girdled stems of sweet birch, hemlock, white pine, Virginia pine and table mountain pine. The woody species excluded from this list were not examined on burn scars.

The sprouts of pitch pine, shortleaf pine, scarlet oak, blackjack oak, and blackgum were initiated below the wound callus tissue. These observations indicated sprouts on these species formed from dormant buds. Species which were not observed for these relationships may have formed sprouts from adventitious buds on wound callus tissue. Sprouts on injured trees may have also formed by root suckering.

Most individuals between 1 and 10 cm dbh were observed to sprout, whereas trees above 40 cm dbh commonly did not sprout. These observations indicated that the effect fire disturbance had on the reorganization phase was a function of species and size structure. Severe fire in a forest with small sprouting species will probably lead to a

predominance of sprout reproduction while severe fire in a large or very mature stand of either sprout or non-sprout producing species may lead to a predominance of seedling reproduction.

Red maple, pignut, blackgum, sourwood, chestnut oak and black oak had a significant increase in the number of sprouts per sprout clump as dbh increased. This trend occurred both 1 and 2 years after fire disturbance (Appendix, Tables 10 and 11). In contrast, the number of scarlet oak and blackjack oak sprouts per sprout clump did not increase with dbh, but did increase significantly with decreased litter (Figure 13). The number of sassafras sprouts per sprout clump also did not increase with dbh, but increased significantly as canopy closure decreased. Multivariable regression models using dbh and canopy closure were significant for red maple, blackgum, sourwood, and black oak. Regression models for these species indicated an increase in the number of sprouts per sprout clump with increased size and decreased canopy closure. The increase in sprout numbers observed in this study was partially an artifact of the sizes examined (see Discussion, page 75). Canopy openness may have increased the survival rate of emerging buds because of higher photosynthetic rates. The observed increase in sprout number with decreased litter may have no physiological interpretation, unless fewer buds were buried and this increased survival.

The mortality of sprouts between year 1 and year 2 ranged between 42% for pignut and 11% for red maple and sourwood (Table 4). The decrease in sprouts between years 1 and 2 was also reflected by the lower regression coefficients of regression models for sprouts 2 years after fire. However, the decreases in these coefficients were not

Figure 13. The change in numbers of sprouts per sprout clump as a function of diameter at breast height (dbh) of the parent tree and species.

The horizontal lines indicate the mean number of sprouts per sprout clump for each size class, and the vertical lines represent ± the standard deviation. Dots represent size classes where only 1 observation was available. The curves were fitted using semilogarithmic regression analysis.

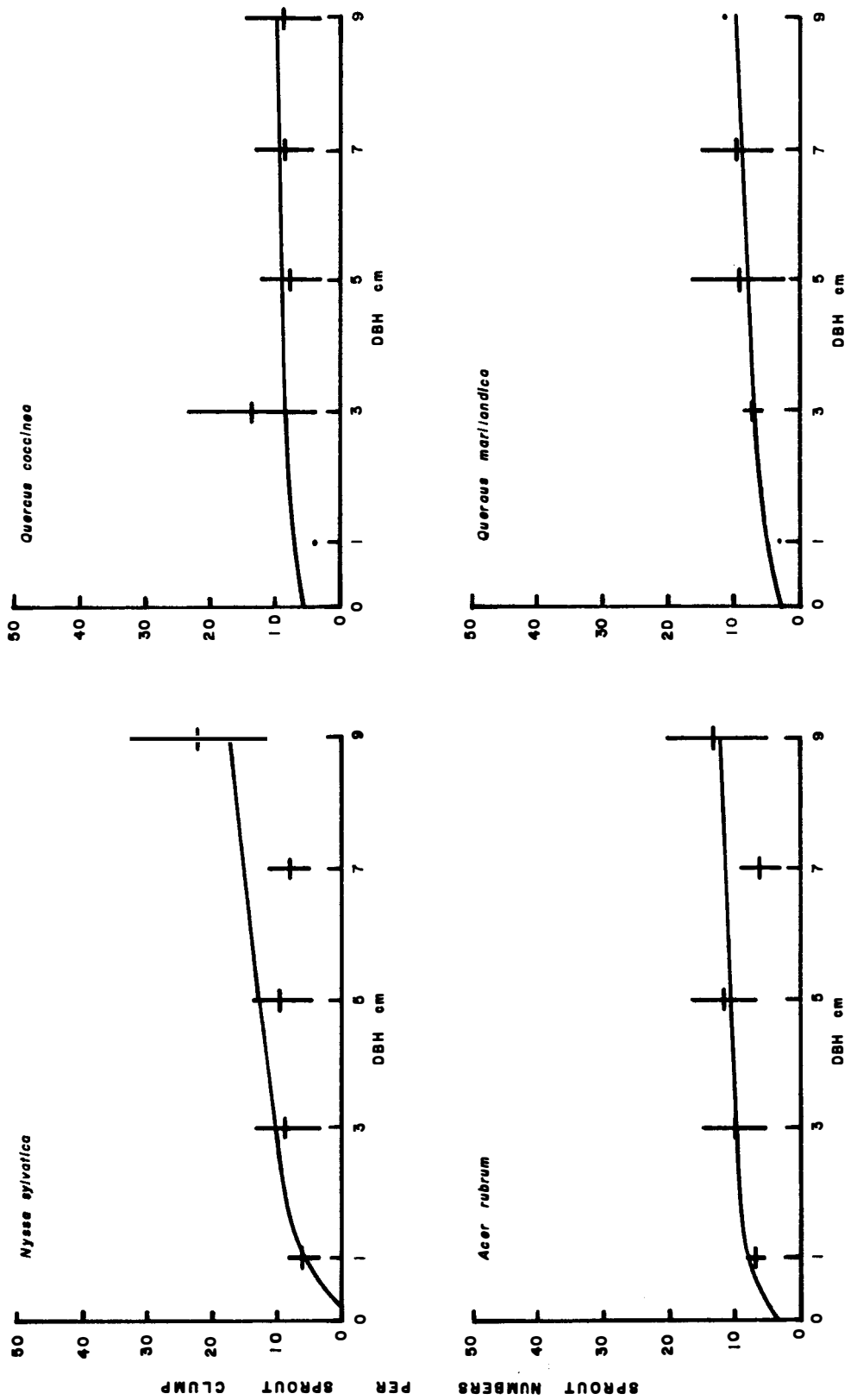

Quercus coccinea
Quercus marilandica
Nyssa sylvatica
Acer rubrum
DBH cm
SPROUT NUMBERS PER SPROUT CLUMP

Figure 13

Table 4. Survivorship of Sprouts of Trees Less Than 10 cm dbh.[a]

Species	Mean Sprouts Clump^{-1} Year 1	Year 2	Survivorship %
Acer rubrum	9.6	8.5	89
Carya glabra	5.2	3.0	58
Nyssa sylvatica	10.6	8.8	84
Oxydendrum arboreum	13.3	11.8	89
Quercus coccinea	9.8	7.3	74
Quercus marilandica	8.9	7.3	82
Quercus prinus	12.4	9.5	76
Quercus velutina	5.0	4.0	80
Sassafras albidum	10.0	7.3	74

[a]Survivorship was calculated for period 1 and 2 years after fire.

significant when examined with the t-test. After initial formation, one would expect sprout mortality as one or more sprouts assumed dominance.

The height of the tallest sprout in each clump increased significantly with diameter in blackgum, sourwood and blackjack oak. Height might be expected to increase initially with size since stored reserves are increased. As canopy openness increased the height of the tallest sprout in each clump increased significantly for blackgum, scarlet oak, and chestnut oak (Appendix, Table 12). The increase in light and hence photosynthetic rates probably explains the positive correlation of canopy openness and sprout height.

North facing slopes tended to have taller sprouts 2 years after fire than south facing slopes. Increased moisture on northern slopes should lead to an increase in sprout growth. However, Wendel (1975) found no correlation of sprout height to site index.

Seedling reproduction. Two years after fire there was a significant ($.05>_p>.01$) increase in pine seedling density as canopy opening increased and litter depth decreased (Table 5). One year after fire the same relationship between pine seedling density, canopy openness and residual litter depth was apparent but not significant. Mortality between year 1 and year 2 averaged 73% when canopy closure was greater than 50%. During the same period there was a slight increase in pine seedling density on sites with over 50% canopy openness.

After 2 years of growth, pine seedlings on open sites reached a maximum height of approximately 0.5 m. Under closed forests, pine

Table 5. Relationship of Residual Litter Depth, Canopy Openness and Pine Seedling Density and Survivorship Between 1 and 2 Years After Fire.

Litter Depth mm	Canopy Openness Index Percent	Seedlings m^{-2} Year 1	Year 2[a]	Survivorship Percent
0.9	82	1.48	1.50	101
4.7	77	0.96	0.93	97
8.2	75	0.55	0.73	133
5.8	50	0.50	0.11	20
0.6	14	0.06	--	-
1.0	15	0.00	0.00	0
9.0	33	0.52	0.14	27
10.2	19	0.79	0.42	53
17.0	23	0.18	0.07	38
27.0	14	0.21	0.11	52
29.8	37	0.33	0.12	36
26.7	89	0.00	0.00	0

[a]The relationship at year 2 can be expressed by the formula: Seedlings m^{-2} = -0.318 + 0.340 ln (Canopy Open + 1) - 0.243 in (litter depth + 1) $F_{2,8} = 4.56$, $.05>p>.01$.

seedlings were of smaller stature. Where hardwood sprouts were dense, they cast shade on pine seedlings and appeared to reduce pine height growth. Pine seedling diameters 5 cm above the ground were greatest on open sites. After 2 years of growth the ratio of stems 0-2 mm to stems >2 mm in diameter in open sites was 0.99. Under closed canopies the ratio was 4.27 and indicated the greater number of small stems.

As fire severity and canopy openness increased the density of yellow poplar, sourwood, black locust and winged sumac seedlings increased in oak forest (Appendix, Tables 13 and 14). All other species had observed densities that could be accounted for by root collar sprouts or seedling sprouts. Cool fires in oak forest produced few new seedlings.

Winged sumac and pine were the only species with many seedlings in burned pine forest plots (Appendix, Tables 15 and 16). Dense patches of sourwood stems were observed, and these were of seedling origin. Seedlings of princess tree, devil's walking stick and smooth sumac grew in both severely burned pine and oak forests. Sassafras and persimmon probably also reproduced by seed after fire. However, only a seedling inventory before fire will establish the proportion of stems originating after fire from seed.

The overall survival of woody reproduction in severely burned forests was lower than in forests with cool fires (Table 6). Hickories had higher survivorship on open sites while the other species examined had higher survival under closed canopies.

Recovery of community structure after fire. Shrub basal area was significantly influenced ($0.05>_p>0.01$ for 2-way ANOVA) by the

Table 6. Survivorship of Woody Stems Less Than 1 cm dbh Between 1 and 2 Years After Fire.

Species	Stem Survivorship			
	Mild Fires		Severe Fires	
	Percent	Stems	Percent	Stems
Acer rubrum	100	63	60	20
Carya spp.	33	6	50	2
Kalmia latifolia	81	450	57	879
Nyssa sylvatica	98	367	64	514
Oxydendrum arboreum	100	17	63	62
Quercus spp.	96	205	78	227
Sassafras albidum	95	556	43	1238
Total	92	1664	52	2942

severity and time since disturbance. There was no significant difference in basal area between forest cover types. One year after cool and hot fires in pine forest shrub basal areas were 0.38 m^2 ha^{-1} and 0.55 m^2 ha^{-1}, respectively. The higher shrub basal area on severely disturbed sites was caused by the abundance of sprouts and seedlings. Severely disturbed stands also had greater basal area increments than mild fires. The time required for a disturbed forest to regain the shrub basal area present before fire was short. After 2 years, cool fire basal areas were 51% of the pine and 100% of the oak pre-fire values. Two years after severe fire in oak and pine forests, shrub basal areas exceeded values before fire by as much as 130%.

Shrub species richness* after fire in pine forests was 1 to 5 species lower than the mean of unburned pine forests. The missing species usually represented seedlings of hemlock, beech, Fraser magnolia and red oak. The increase in species richness between year 1 and year 2 was highest after mild disturbance (+1 to +5) and lowest after severe fire (-3 to -6). The increase in light and water stress on open sites may have increased species turnover. After 2 years the number of shrub species in mildly burned oak forest was similar to unburned oak forest (23 versus 24). A severely disturbed oak forest had 30 species 2 years after fire.

Discussion

Reproductive and growth strategies of trees after disturbance can be divided into outgrowth of previously existing vegetation and

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*Shrub species richness is defined here as the number of woody species per 0.1 ha that are less than 0.5 cm diameter at breast height.

upgrowth from seedlings, and sprouts (Bormann and Likens 1979). Although Bormann and Likens used this classification in northern hardwood forests, it is also applicable to Southern Appalachian forests. Trees which maintain their original stratal position may close canopy openings by outgrowth after cool surface fires. As fire intensity increases upgrowth should become increasingly important in terms of canopy replacement.

Seedling reproduction. Seedlings established after fire arise from seeds stored in soil, from individuals on the disturbed site, and from individuals outside the site. The origin of seedlings observed in this study was difficult to assess directly. However, hypotheses were erected based on seed characteristics, such as weight, and observations of potential source trees. Yellow poplar, sumac, hemlock, devil's walking stick and princess tree seeds probably came from outside of the disturbed sites. Of these species, princess tree, devil's walking stick and sumac appeared to travel the farthest from the seed source. Most of the other seedlings probably originated from individuals on or adjacent to the disturbed sites. Although no obvious effects were observed in this study, the season and severity of a fire may have affected the proportion of seeds colonizing from inside and outside the disturbance. Most species in the study area have seeds which ripen and disperse during fall and winter. Severe fires during late winter, spring and early summer would consume seeds on the ground and kill mature trees before seed ripening. Once the internal seed source is removed, seeds from outside the stand would dominate the seed rain. Serotinous cones in table mountain pine enable this species to release a great deal of stored

seed after severe fires (Barden 1979). Since the release of seeds in serotinous cones is related to fire severity, table mountain pine may colonize severely burned stands during any season. Another strategy of site colonization involves the germination of buried seeds (Marks 1974). Observations indicated that black locust, the sumacs, sassafras, yellow poplar and mountain holly may have germinated from buried seed. It should be noted, however, that each of these species except the sumacs was also observed to generate seedling and root collar sprouts. Seed source and mode of transport are important factors in determining whether fire suppression has caused local extinctions of short lived canopy species dependent on mineral soil and direct sunlight for seedling establishment. As seed weight and distance from the source tree increase, the ability to colonize a burned site should decrease. Storage of seed in soil horizons or in parent trees would enable species to colonize sites without transport after a fire.

Species which reproduced mainly by seed on severely disturbed sites in this study are usually considered shade-intolerant (Fenton and Bond 1964, Trimble 1975, Wilson and McQuilkin 1963). The increase of light in severely disturbed stands may have selected against mesic species such as red oak (Smith et al. 1976). Topographic position and aspect also influenced seedling establishment. Yellow poplar was observed here to grow slowest on south facing upper slopes. Minckler and Jensen (1959) observed that yellow poplar seedlings were most dense on north facing lower slopes and least dense on south facing upper slopes. As litter depth decreased on severely burned sites in the present study, there were more pine seedlings. This was consistent

with the previous observations of many investigators that pines germinated best on mineral soil and grew fastest in direct sunlight (Ahlgren 1960, Jackson 1959, Fenton and Bond 1964, Wilson and McQuilkin 1963). Except on extremely xeric, exposed, rocky sites, disturbances such as fire and windthrow may be needed to provide natural seedbeds for pines (Barden 1979). Aside from the pines, no correlation between seedling density and litter depth was revealed. However, Minckler and Jensen (1959) observed correlations between seedling density and litter depth in their studies on hardwoods.

Seedling sprout reproduction. The density of seedling sprout reproduction was estimated from unburned stand data. This technique has definite disadvantages and ideally inventories of seedlings should be made before a fire.

Observations on burned plots indicated many species were capable of generating seedling sprouts. Since most seedlings were killed above the ground by both mild and severe fires, the absolute importance of seedling sprouts in upgrowth probably did not change a great deal with fire severity. McQuilkin (1975) and Sander (1971) observed that oak seedling sprouts had greater height growth rates than seedlings.

Root collar sprouts. As fire severity increased, the importance of root collar sprouts increased. Changes in the density of root collar sprouts were also dependent on the species composition, size and age of the individuals killed above the ground by fire. The ability of species to form sprouts observed in this study was consistent with observations of other investigators. Averell (1929), Grano (1955), Perala (1974)

and Soloman and Blum (1974) demonstrated that hardwoods range considerably in their ability to form sprouts. Stone and Stone (1954) observed that many species of pine form sprouts (especially shortleaf and pitch pines). In general trees greater than 40 cm dbh were not observed to sprout in the present study. Other authors reported that trees above 50 to 65 cm dbh rarely sprouted (Johnson 1975, Roth and Hepting 1943, Solomon and Blum 1975, Wendel 1975). Trees examined for sprouts in the present study were too small or young to show a decrease in the number of sprouts per clump with respect to either size or age. Other investigators reported that the number of sprouts per clump initially increased with size and age. However, when trees became very large or old the number of sprouts per clump declined (Johnson 1975, Roth and Hepting 1943, Sander 1971, Woods and Cassady 1960).

The height of the tallest sprout in each clump increased, with dbh for blackgum, sourwood and blackjack oak. Since the quantity of resources stored in the root system was probably a function of size, other species might have exhibited this trend. Sander (1971) observed sprout height growth increased as the diameter of the parent stem of oaks increased. In contrast to these findings, Wendel (1975) found no increase in the height growth of the dominant sprout was associated with parent stem diameter. However, trees in Wendel's study exceeded 10 cm dbh whereas Sander's parent stems were seedlings or seedling sprouts.

Species were observed in the present study to differ in sprout survival 1 and 2 years after fire. Older sprout clumps would have been more useful in determining persistence of sprouts of the various species examined. Theoretically, increased shading by sprouts should lead to the

suppression of shade intolerant species and may dramatically alter successional trends after fire.

Summary

Factors determining the relative importance of seedling, seedling sprout and root collar sprouts to upgrowth were quite complex and interrelated. Most species were probably able to exploit each reproductive mechanism to some degree. The importance of root collar sprouts and new seedlings increased as fire severity increased. Conversely, seedling sprouts were most important on sites with little canopy disturbance. The proportion of sprouting species in the forest before fire was also an important determinant of tree sprout density. Yellow pine forests had one-third the tree sprouts of oak forests after severe fires. Trees of intermediate age and size had the highest probability of sprouting and also developed the most sprouts. Hence, the importance of tree sprouts was probably at a maximum for younger and smaller forests. Seedling sprout reproduction remained constant, in absolute terms, for both mild and severe fires. However, the chances of an individual of the same species reaching dominance during upgrowth were probably higher for seedling sprouts than for new seedlings. Extremely rapid growth of some species (e.g., yellow poplar) from seed may compensate for the initial competitive advantage of sprouts. Persistence of sprouts may reduce the importance of shade-intolerant seedling reproduction. Pine seedlings germinated best on the thinnest litter layers. Other species such as yellow poplar, sourwood, devil's walking stick, princess tree and sumac may have also reproduced better when fires consume a majority of the litter. The importance of seedling

reproduction increased as fire severity increased. Seedlings tended to be relatively more important in yellow pine forest than in oak forest for a given fire severity.

VII. PRESENT VEGETATIONAL PATTERN

Introduction

Vegetation varies along spatial and temporal gradients. The establishment of permanent plots allows examination of temporal patterns under a wide variety of environmental conditions. The vegetation description presented here represents the initial forest composition of the permanent plot system. Spatial differences in forest composition and internal stand structure were used to pose hypotheses concerning successional processes. Future studies may reveal the true nature of temporal changes in this forested ecosystem.

Results

Indirect canopy ordination. One hundred sample stands with a total of 89 species were ordinated by the Bray-Curtis polar ordination method (BC). Relative basal area and relative stem density were the values used in these ordinations.

Almost all species exhibited a continuous distribution on both the stem density and the basal area BC ordinations. Both ordinations were interpreted by examining the distribution of dominant species. The basal area ordination was dominated by yellow pines, white pine, oaks, hemlock and yellow poplar. When stem density was used, a new suite of species dominated the ordination and this included: blackgum, mountain laurel, dogwood and silverbell.

Yellow pines composed over 60% of the basal area in the most xeric position of the basal area ordination (Figure 14). Yellow pine

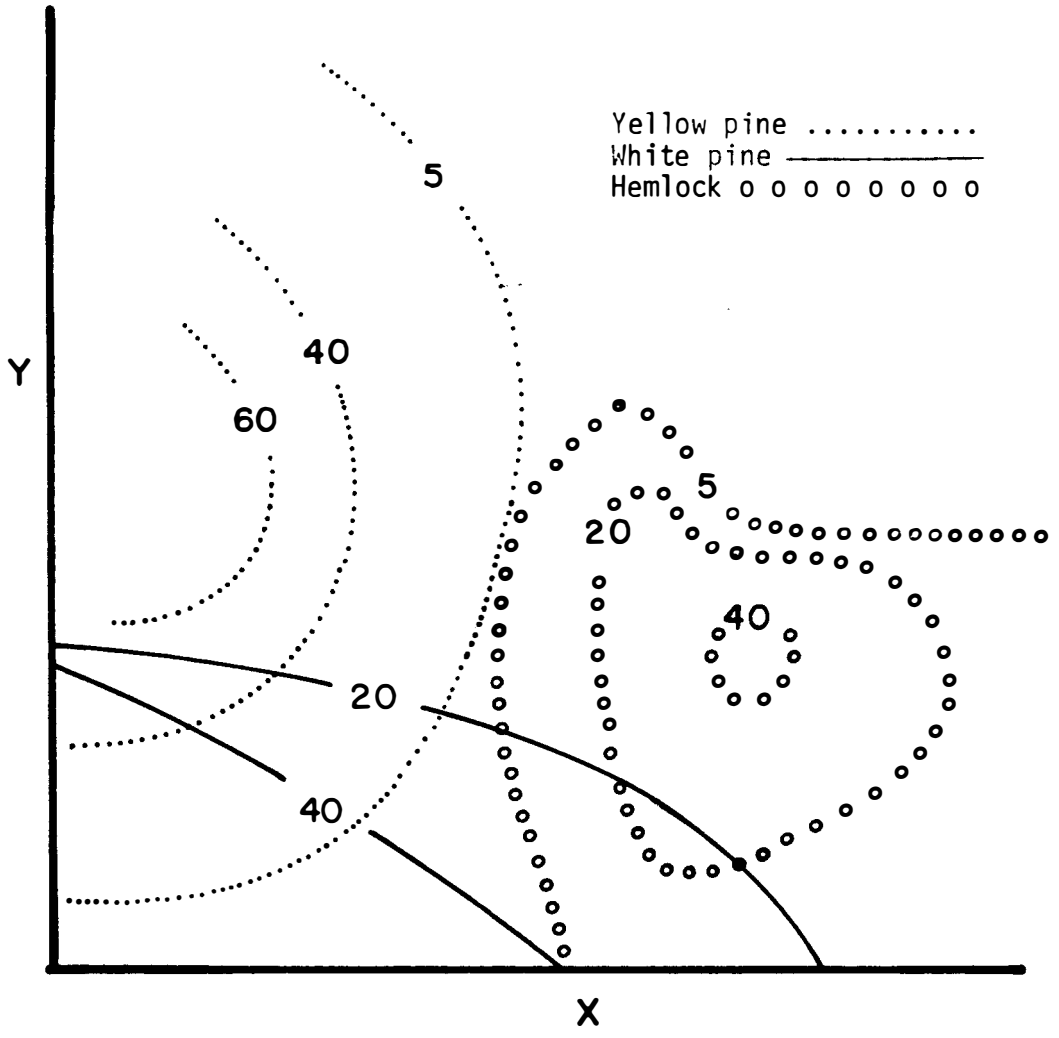


Figure 14. Distribution of yellow pine, white pine and hemlock relative basal area on Bray-Curtis ordination of basal area composition.

Lines indicate areas of equal relative basal area.

importance decreased as mixing with white pine, chestnut oak and black oak occurred. Yellow pine forests on xeric sites and on former agricultural lands occupied similar positions on the basal area ordination, although the understory compositions were quite distinct. White pine was very common throughout the study area and occurred in 82% of the inventoried stands. White pine and oak mixed with hemlock on relatively mesic sites.

The distribution of oaks in the ordination model was quite complex. Nonetheless, each species had a distinct maximum as well as a zone of overlap with neighboring species (Figure 15). Chestnut oak was the most common oak, occurred in 77% of the examined stands, and was usually absent from the most mesic sites. The other oak distributions were ranked by a hypothetical moisture preference. The most xeric oak species were scarlet oak and blackjack oak. As moisture increased chestnut oak, black oak, red oak and white oak appeared. The maximum overlap in oak species occurred on sites with intermediate moisture conditions where a mixed oak community occurred.

Yellow poplar occurred in 45% of the examined stands and composed a large portion of the basal area on mesic sites (Figure 16). Yellow poplar occurred with hemlock and oaks on these sites. Chestnut was once very common in the study area. Evidence of former chestnut remains occurred in 70% of the stands. Downed chestnut log occurrence and abundance was used to assess the importance of chestnut blight on the indirect ordination model (Figure 17). Chestnut logs were most abundant on sites where red oak and oak mixtures occurred. In addition to oak mixtures these stands had pignut hickory, mockernut hickory, black locust,

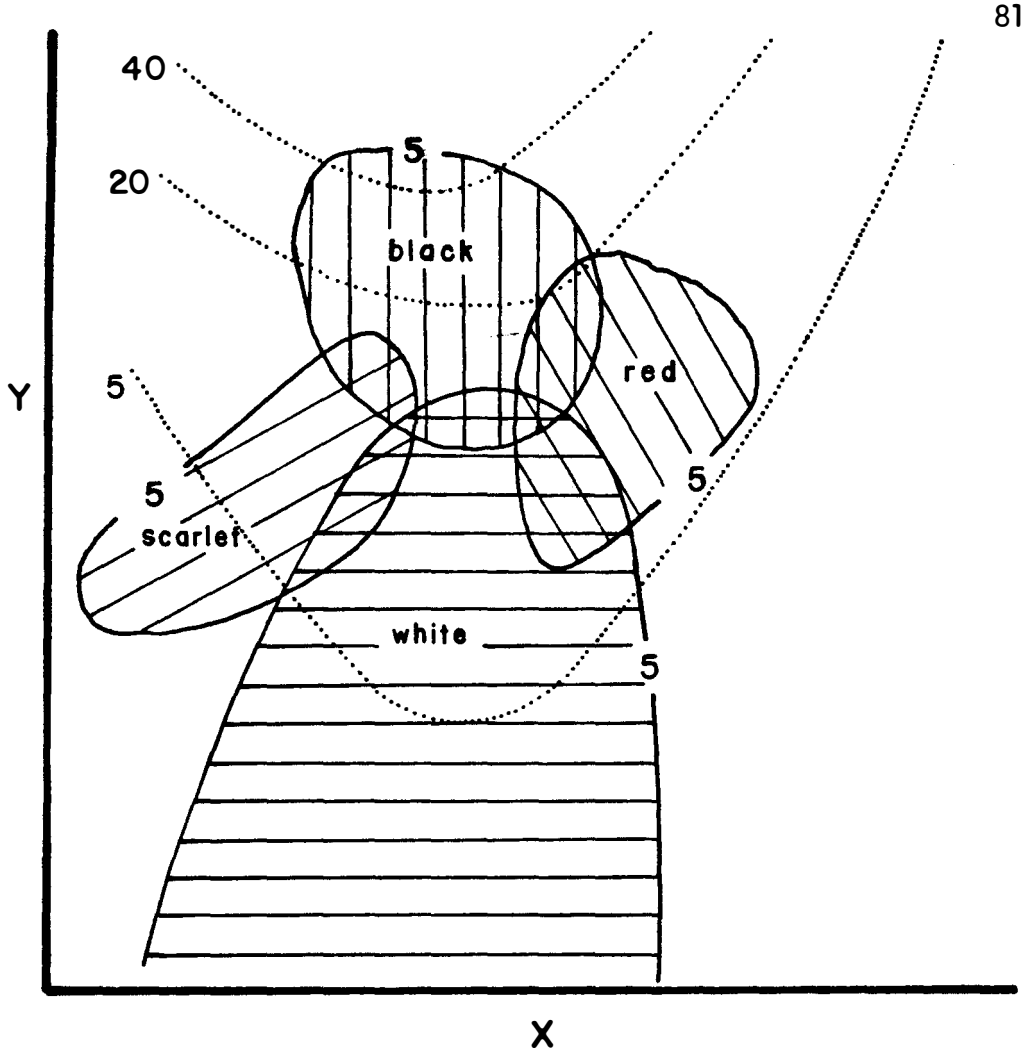


Figure 15. Distribution of oak relative basal area on Bray-Curtis ordination of basal area composition.

The contour lines indicate relative basal area of white, scarlet, chestnut, red and black oak. Cross-hatching represents greater than 5% basal area. The dotted lines indicate contour lines of chestnut oak relative basal area.

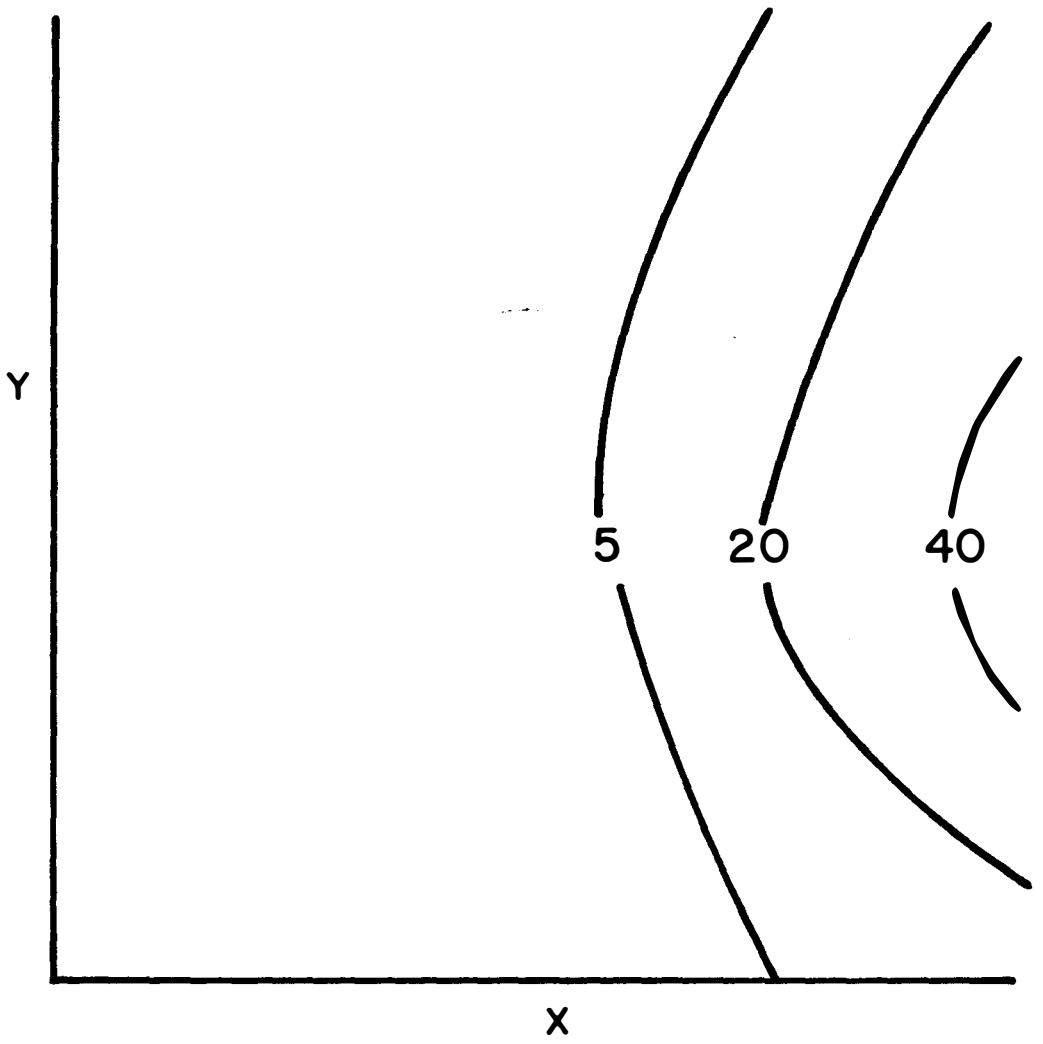


Figure 16. Distribution of yellow poplar relative basal area on Bray-Curtis ordination of basal area composition.

Lines indicate areas of equal relative basal area.

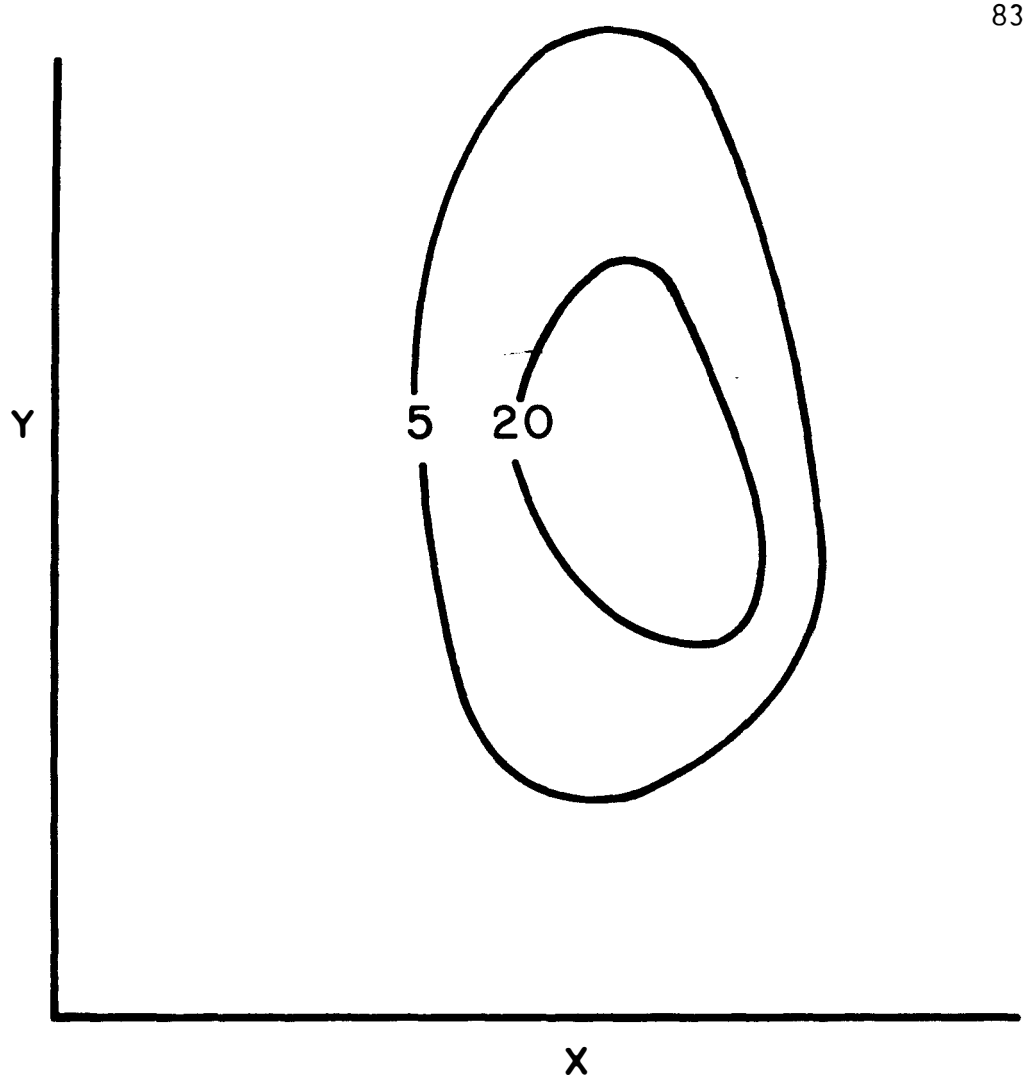


Figure 17. Distribution of percent canopy opening caused by chestnut mortality on Bray-Curtis basal area ordination.

yellow poplar, red maple, silverbell and Fraser magnolia. This species assemblage was similar to that described by Shanks and Woods (1959) in their study of chestnut replacement and indicated that chestnut was most abundant in the transition between oak and cove hardwood communities. Except for a reduction in total stand basal area, it was difficult to determine the exact influence of chestnut blight on stand structure. Small trees of black locust, yellow poplar, sassafras and sourwood have probably grown in gaps formed by the demise of mature chestnuts.

Yellow pines also dominated the stem density ordination on the most xeric sites (Figure 18). Hemlock stem dominance occurred on drier sites than basal area dominance, and may have represented an expansion of this species onto more xeric sites. This expansion may have been caused by fire suppression, since frequent surface fires would have eliminated seedlings and small trees. Evidence of multiple fires was common on oaks and hickories growing on these sites.

Blackgum (Figure 19) dominated stem densities with yellow pines on xeric sites and mixed with dogwood and mountain laurel on slightly less xeric sites. Mountain laurel distribution on the indirect ordination model was bimodal (Figure 20). A possible explanation of this phenomenon may arise from interactions between dogwood and mountain laurel. The ability of dogwoods to concentrate calcium and the acidic soil requirement of mountain laurel are well known. Perhaps these two properties caused the observed bimodal distribution of mountain laurel. Silverbell occurred on sites that appear similar to those occupied by dogwood, but the two species tended to dominate on opposite ends of the ordination model. Rhododendron dominated stem composition on the most

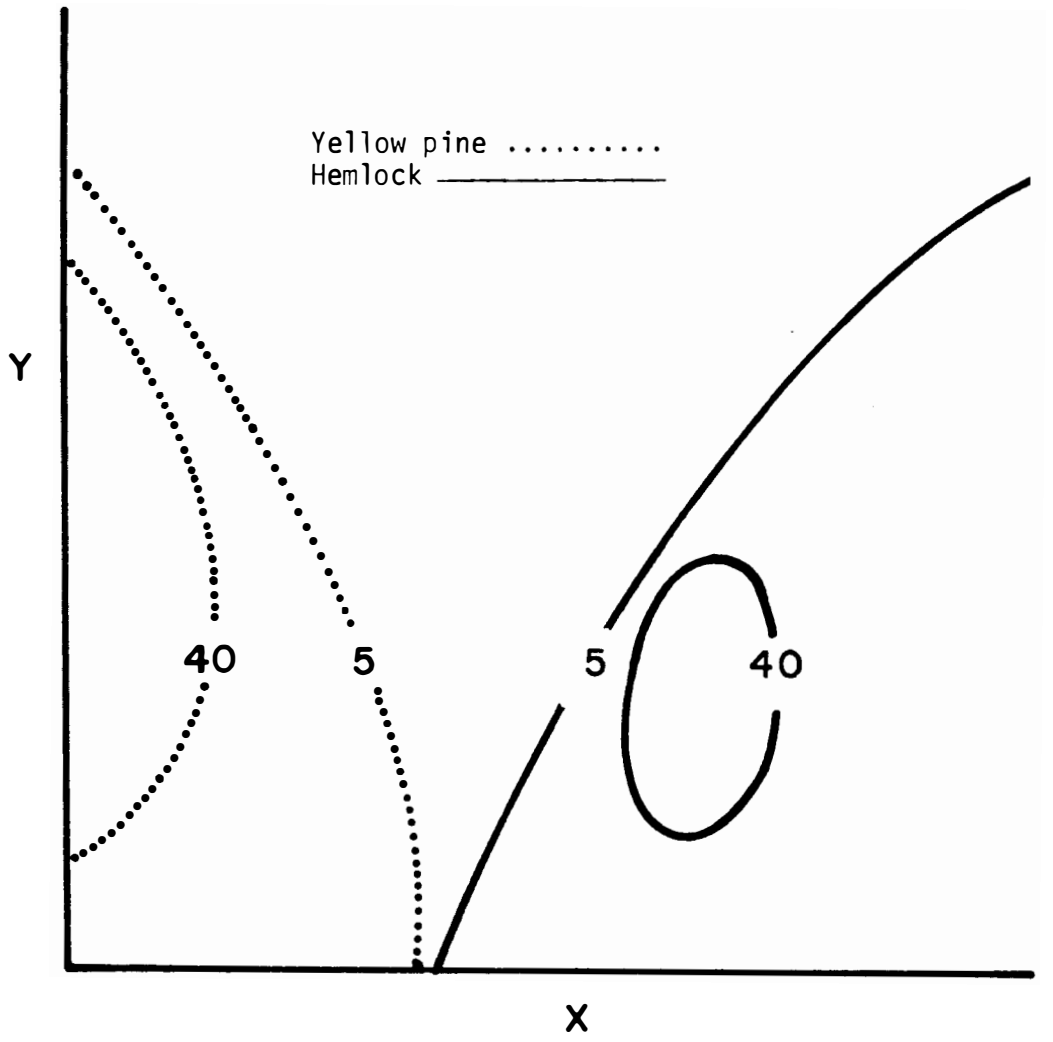


Figure 18. Distribution of yellow pine and hemlock relative density on Bray-Curtis ordination of canopy stem composition.

Lines indicate areas of equal relative stem density.

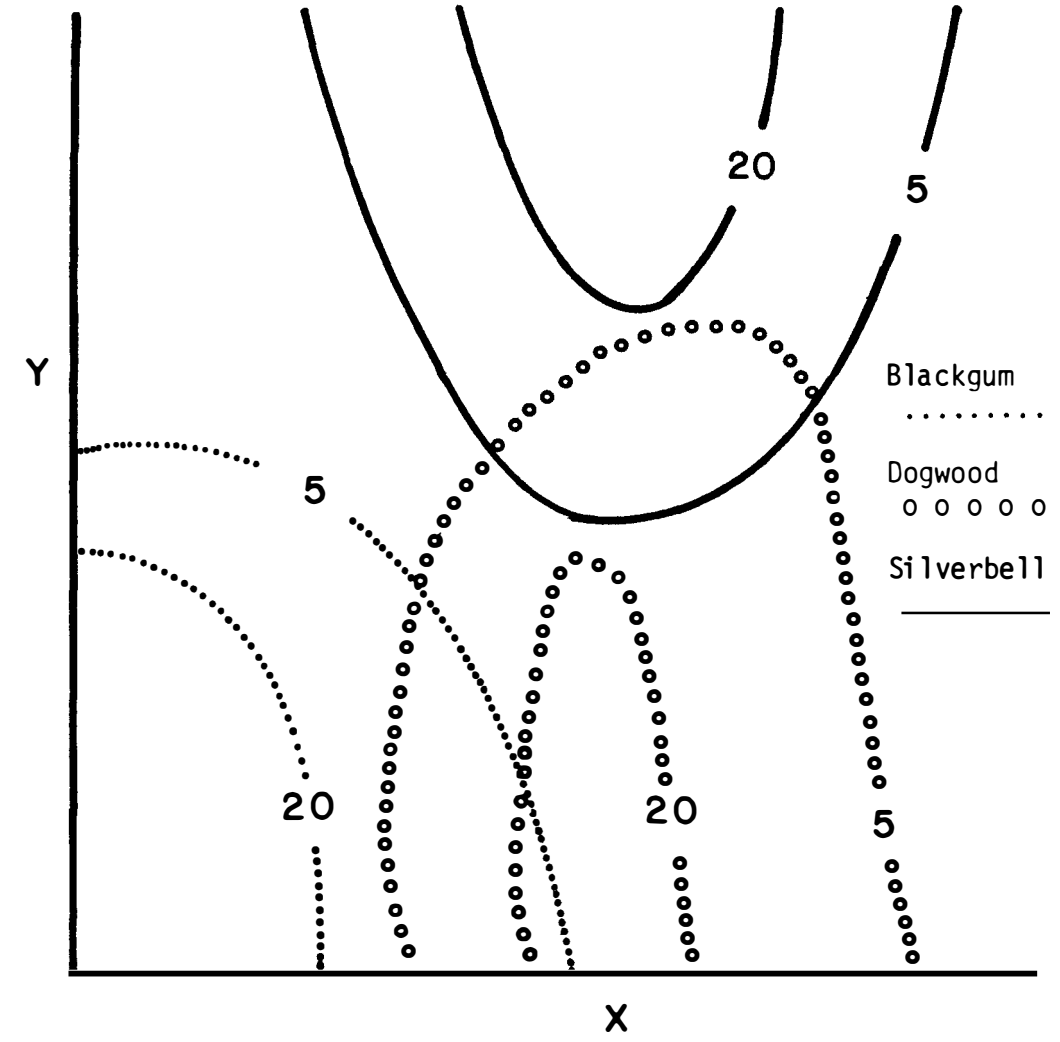


Figure 19. Distribution of blackgum, dogwood and silverbell relative density on Bray-Curtis ordination of stem composition.

Lines indicate areas of equal relative stem density.

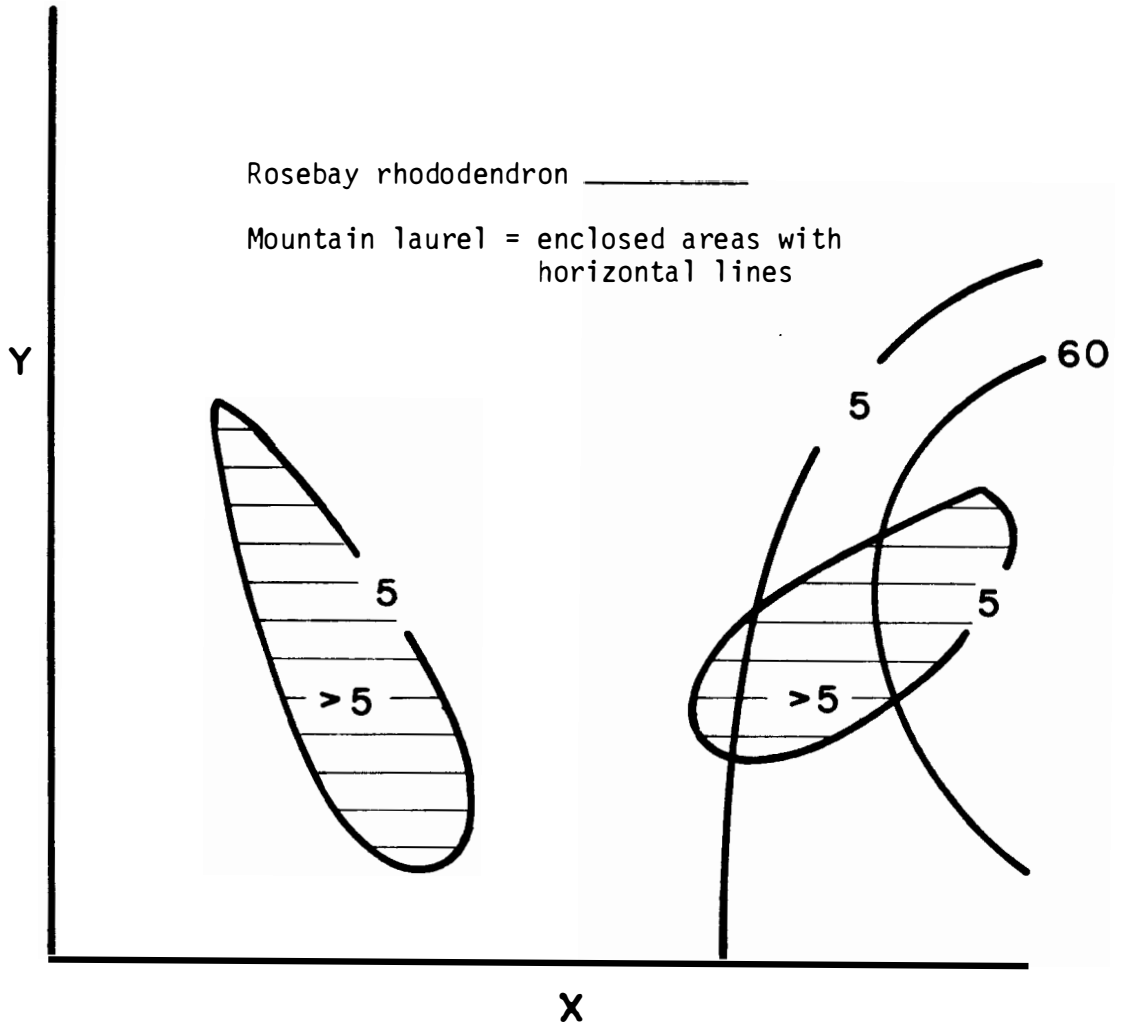


Figure 20. Distribution of mountain laurel and rosebay rhododendron relative density on Bray-Curtis ordination of stem composition.

Lines indicate areas with equal relative stem density.

mesic sites. These were often sites where hemlock and yellow poplar dominated in terms of basal area.

A gradient of moisture corresponded well with both indirect ordination models (Figures 21-22). However, the relationship of vegetation to site variables was complex. Many different site types (based on slope position, aspect, and concavity) had equivalent vegetational composition. For example, south facing draws had vegetation similar to that on north facing upper slopes. Disturbance gradients also interacted with moisture gradients. South facing upper slopes burned frequently, whereas north facing lower slopes burned less frequently and probably with less severity. Clearing by man confounded the correspondence of moisture and vegetation even further. In the stem density ordination a gradient of soil nutrient richness may also be important in determining species distributions.

Direct canopy ordination. Simple linear correlation coefficients were used to assess the degree to which complex gradients covaried (Table 7). In the case of chestnut blight the positive correlation with elevation was supported by Whittaker's (1956) observation that dead chestnut stems increased with elevation up to 1400 m. The negative correlations of chestnut blight to aspect and SBI also corresponded to the reported importance of chestnut in submesic forests (Whittaker 1956, Woods and Shanks 1959). Since slope was used to calculate SBI the negative correlation was expected. The lack of correlation of aspect and SBI probably was explained by their nonlinear relationship; aspect x aspect had a significant negative correlation ($r = -0.315$, $p<.01$) with SBI. The positive correlation of elevation and slope position was also

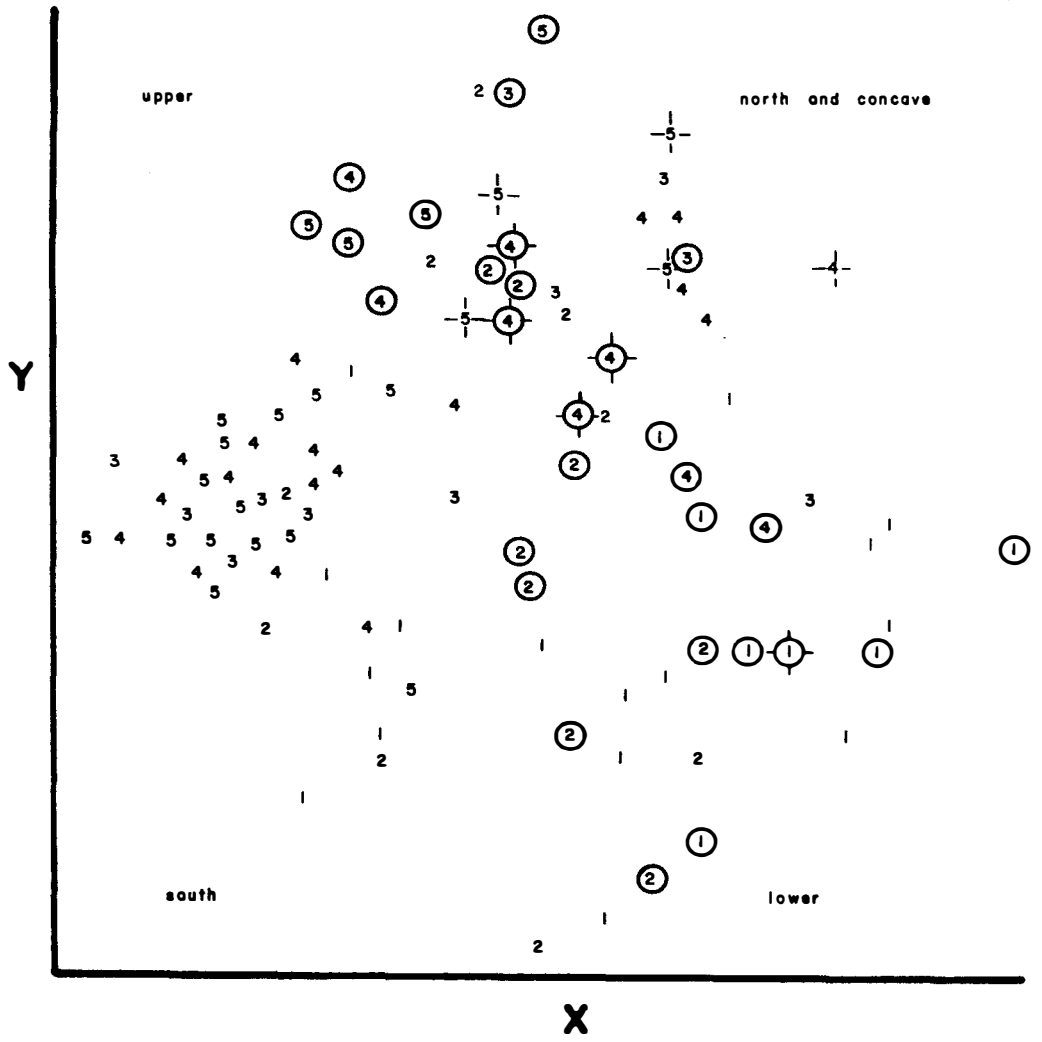


Figure 21. Relationship of topographic variables to Bray-Curtis ordination of canopy basal area.

The numbers represent percent slope position in 20% increments where 1 is the lowest slope position and 5 is the highest slope position. Numbers with circles indicate north facing slopes, and numbers without circles are south facing slopes. Crosses represent concave slope shapes.

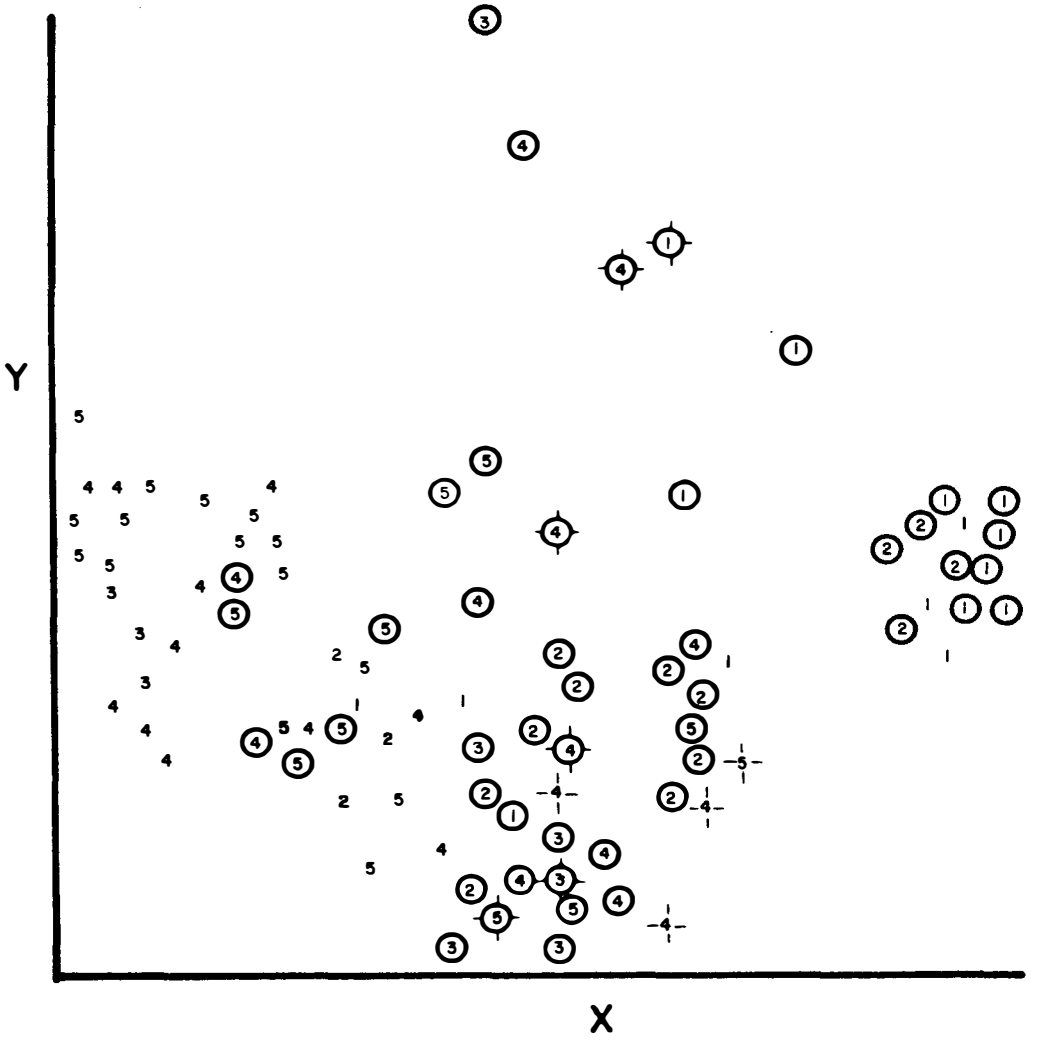


Figure 22. Relationship of topographic variables to Bray-Curtis ordination of canopy stem composition.

Numbers represent percent slope position in 20% increments where 1 is the lowest slope position and 5 is the highest slope position. Numbers with circles indicate north facing slopes and numbers without circles are south facing slopes. Crosses represent concave slope shapes.

Table 7. Pearson Product Moment Correlation Coefficients Among Environmental Gradients Used in Direct Gradient Analysis (N=88).

	Elevation	Aspect	Slope	Slope Position	Concavity	Chestnut Blight	Beetle Kill	SBI
Elevation								
Aspect								
Slope								
Slope Position	0.418**							
Concavity			-0.206[a]					
Chestnut Blight	0.271*	-0.244*						
Beetle Kill								
SBI			-0.251*			-0.342**		

[a] p = 0.054.

*.05>p>.01.

**.01>p.

expected given the pattern of topography in the study area. The highest elevation plots were placed on Mount Lanier which was high above all local ravines and draws. The negative correlation between slope angle and concavity was probably an actual relationship. Draws became steeper and less concave toward ridge-tops. Since fire histories could not be determined for all sites, the correlation between this disturbance and other variables was not calculated.

Total canopy stem density including evergreen heaths significantly decreased as slope position increased and reached a maximum at 650 m elevation ($p < .01$, $r^2 = 0.14$). When evergreen heaths (rosebay rhododendron and mountain laurel) were excluded from canopy stems, the relationships between density, slope position and elevation remained similar. Stem densities in ravines and lower slopes ranged between 329 and 822 stems per 0.1 ha when evergreen heaths were included. When evergreen heaths were excluded stem densities decreased to a range of 86 to 292 stems per 0.1 ha. Middle and upper slopes had stem densities ranging between 162 and 441 and 111 and 469 stems per 0.1 ha, respectively. Basal area significantly decreased curvilinearly as slope position increased ($p < .01$, $r^2 = 0.26$). In ravines and on lower slopes basal area ranged between 28 and 63 $m^2\ ha^{-1}$. Basal areas on middle and upper slope positions were similar and ranged from 19 to 37 $m^2\ ha^{-1}$. Canopy richness (species per 0.1 ha) decreased significantly ($p<.01$, $r^2 = 0.14$) with elevation at a rate of 1 species per 100 m (Figure 23). Canopy richness also tended to increase on mid-slope positions with SBI ranging between 270 and 300 (west, east and south facing slopes). Also, as slope position was increased, the species richness maximum was displaced onto

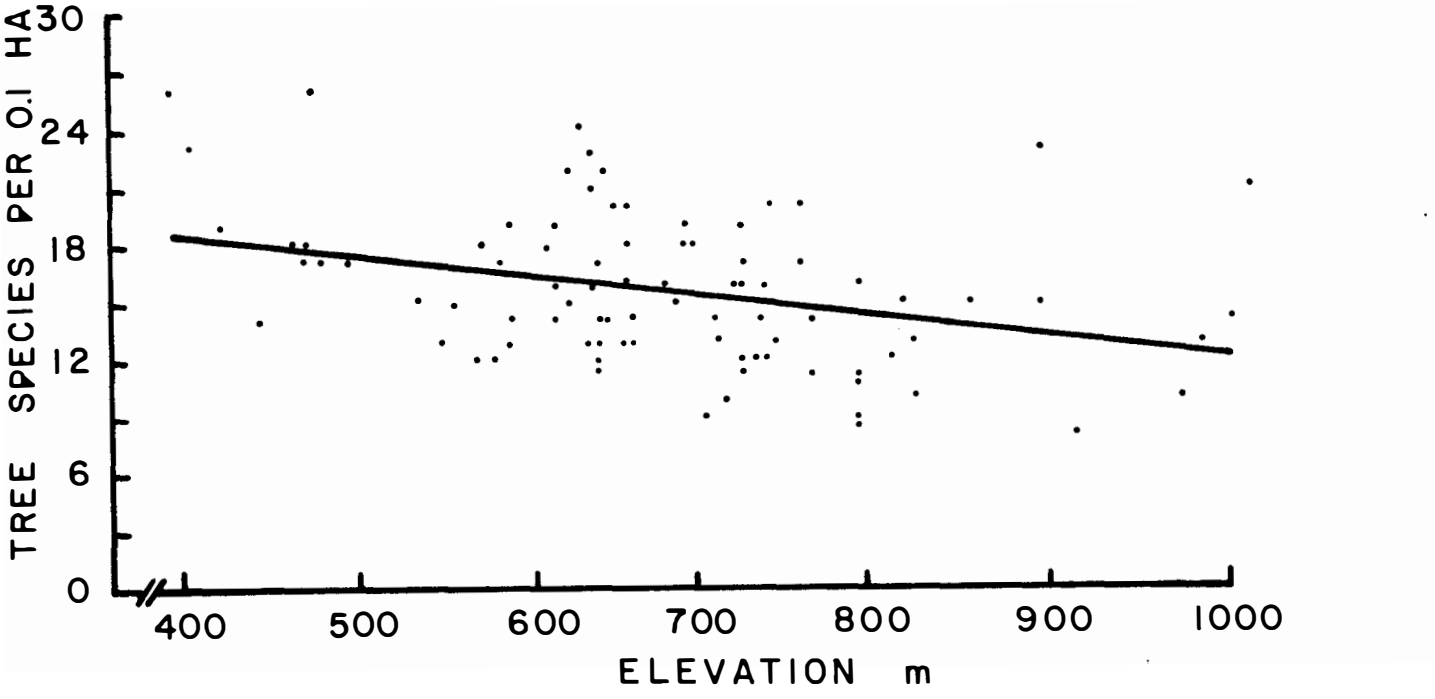


Figure 23. Decrease in tree species per 0.1 ha as a linear function of increasing elevation.

TSR is the number of tree species per 0.1 ha.

sites with lower SBI. Thus, forests with intermediate moisture were richest in canopy species.

Lower slopes and ravines had dense thickets of rhododendron+ and mountain laurel. Both species decreased in abundance as slope position increased, although mountain laurel progressed farther up slopes than rhododendron. Mountain laurel also increased with SBI*, whereas rhododendron tended to decrease. Sweet pepper bush and witch hazel composed a small but consistent portion of the thickets in ravines and on lower slopes. Witch hazel and sweet pepper bush appeared to increase with SBI and were similar to mountain laurel in distribution.

Hemlock consistently composed a large portion of ravine and lower slope basal area. Although hemlock occurred in many sites, basal area decreased with slope position* and SBI*. As slope position increased both stem density and basal area maxima of hemlock shifted onto sites with lower SBI. The absolute maximum for hemlock stem density occurred on middle slopes, and increased as concavity* increased.

Yellow poplar, Fraser magnolia, American holly and sweet birch exhibited their highest basal area and stem density importance in ravine and lower slope positions. Although all species tended to decrease as slope position increased, yellow poplar increased on middle and upper slope positions as concavity increased. As elevation* increased, the

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+At elevations below 500 m piedmont rhododendron occurred with rosebay rhododendron, especially along Panther Creek.

*Within this section the * symbol appearing after an independent variable denotes a statistically significant regression relationship. The regression equations are presented in the Appendix, Tables 18 and 19.

basal area of sweet birch decreased. Yellow poplar importance increased on middle and upper slope positions as elevation increased. One would also expect yellow poplar to increase after disturbances (e.g., wind-throw).

White pine was very common on all types of sites, but basal area decreased with slope position* and elevation*. Mosaic charts indicated white pine importance shifted to sites with lower SBI as slope position increased. Disturbance events on all but southern upper slopes may lead to an increase in white pine importance.

Beech, white ash, green ash, basswood, buckeye, sweet gum, sugar maple, black cherry, cucumber tree and umbrella tree occurred in ravines and lower slopes but were fairly uncommon and localized. Most of these species increased as SBI decreased. In very sheltered north facing ravines these species increased in importance as hemlock importance decreased. Umbrella tree and sweet gum importance decreased with elevation, while the other species probably increased or remained constant.

White oak occurred on many sites, but consistently occurred on south facing lower slopes. Regression models indicated that white oak increased with SBI*, and decreased with slope position*, concavity* and elevation*. White oak has been observed on broad ridge-tops above 610 m. Since chestnut oak also occurred on these ridge-top sites, but not on south facing lower slopes, this would indicate moisture, disturbance conditions, etc., were not similar and that white oak had two population centers. Whittaker (1956) proposed that white oak was composed of two population centers which were separated along the

elevation gradient. It was possible there was some genetic basis for the occurrence of population centers. The white oak on ridge-tops observed here may have represented a low elevation extension of Whittaker's high elevation ridge-top population.

Middle slopes had a large number of species, but few species exhibited a maximum on these sites. Striped maple occurred on lower and upper slopes but had a relative density maximum on middle slopes. The importance of striped maple decreased as SBI* increased and is highest at 610 m elevation*. Dogwood also had a stem density and basal area maximum on middle slopes and decreased as SBI* increased. Dogwood was more common than striped maple. Both species shifted onto sites with a lower SBI as slope position increased. Dogwood showed a significant increase in abundance as concavity* increased.

Mockernut hickory occurred on upper, middle and south facing lower slopes but displayed a maximum on middle slopes with an intermediate SBI (210-270). A statistical model indicated that mockernut had a basal area maximum on middle slopes* (60%) and at 825 m elevation. As concavity increased the importance of mockernut also increased*.

Black locust and red oak were most abundant on middle slopes, decreased with increased SBI* and increased with elevation*. As slope position increased red oak was shifted onto sites with lower SBI. Numerous dead stems of black locust indicated this species was a more important component earlier. Black locust was often very important on sites where chestnut stumps and logs were common, and where fire removed a large fraction of the canopy. If major exogenous disturbances are excluded, the occurrence of black locust should be restricted to sites

where windthrow and endogenous disturbances allow full sunlight to reach the forest floor.

Black oak tended to occur on upper and middle slope positions more than red oak. Moreover, black oak basal area was highest on middle slopes* with intermediate SBI*.

Black oak density decreased with increased concavity*. Red maple was very common and present in all but the most xeric and mesic sites. Regression models indicated red maple basal area was highest on upper slopes*, decreased with SBI*, increased with concavity* and had an elevational maximum of 730 m.

Pignut hickory decreased with SBI*, and slope position* and increased with elevation*. A mosaic chart, however, indicated that pignut was most important on upper slopes above 610 m. At lower elevations pignut was more important on middle slope positions, but did not compose as large a portion of the relative density. Perhaps the complex nature of pignut distribution could not be fit with a polynomial model.

Silverbell increased with elevation* and was most important on northern aspects*. Mosaic charts indicated that silverbell stem and basal area density was highest on upper slopes above 760 m with low SBI (less than 210). Silverbell was similar to white ash, buckeye, basswood and bitternut hickory in the relationship between SBI, slope position and elevation. All these species occurred in ravines below 760 m and tended to occur on north facing concave middle and upper slopes above this elevation.

Chestnut oak had a maximum of basal area and stem density on north facing upper slopes. Regression models indicated that chestnut oak decreased with SBI*, increased with slope position* and exhibited a maximum at 700 m. Chestnut oak distribution along the elevation gradient was consistent with Whittaker's (1956) observed maximum at 760 m. On south facing slopes, chestnut oak increased as concavity increased although concavity was not significant in the regression models.

Sassafras basal area increased with elevation above 610 m, and stem density increased with slope position* and decreased with concavity*. Although sassafras was less common on lower slope positions, the largest individuals occurred on those sites.

Sourwood occurred in stands ranging from mesic to xeric but tended to be most abundant on upper slopes with intermediate SBI. Regression models indicated a maximum when SBI was approximately 210 for all sites.

The yellow pines, blackjack oak, scarlet oak and blackgum had maxima on upper slopes and increased as SBI increased. These species differed in their distribution along gradients of elevation, concavity and slope position.

Virginia pine and shortleaf pine decreased with elevation*, while table mountain pine increased with elevation*. Pitch pine showed no significant change with elevation, although there appeared to be an increase with elevation above 450 m. Shortleaf pine did not occur above 670 m, while Virginia pine dominated most often on sites between 370 m to 825 m. Table mountain pine occurred as low as 550 m but usually became most important above 730 m.

Blackgum stem density and basal area increased with SBI* but were highest on slope positions ranging between 70-85%. As concavity* increased blackgum decreased. This response to concavity was similar to that of the yellow pines.

Scarlet oak increased with slope position*, and SBI* and decreased with concavity*. Both scarlet oak and blackjack oak occurred on sites with lower SBI as slope position increased. Scarlet oak tended to extend onto sites with lower SBI than blackjack oak. Although the regression models for scarlet oak did not include elevation, there appeared to be an increase with elevation. In contrast, blackjack oak decreased with elevation and was usually not found above 825 m. Post oak and southern red oak occurred in the study area but were very localized and occurred below 550 m on sites similar to scarlet oak.

The time elapsed since fire disturbance appeared to be less important in determining canopy composition than gradients of topographic-moisture and elevation. Two factors accounted for this pattern. First, successional changes were not observed directly and were constructed by assembling plots from different sites along a temporal gradient. Therefore, differences in composition were attributable to spatial and/or temporal gradients. The second factor was that most stands were burned within 20 years of one another. This time period may have been too short to reveal temporal changes when confounded with site differences.

After surface fires there appeared to be little difference in the proportions of pine, oak, and other hardwoods on upper south facing slopes (Appendix, Table 19). Immediately after fires the proportion of pine increased slightly, but after 10 to 20 years the growth of oak and hardwood sprouts combined with pine mortality lead to a decrease in

relative density of pine stems. The forest with the oldest fire scar on a south facing upper slope (70 years) did not have a dramatic increase in oaks or hardwoods. The transition from yellow pine to oak and hardwood dominance upper slopes probably occurs after 100 years of succession unless a disturbance (e.g., southern pine bark beetle) removes the pines before senescence. The rate at which hardwoods and oaks replaced yellow pines was also dependent on the position along the topographic-moisture gradient. For example, lower slope positions, cleared for agriculture, were losing yellow pines in large numbers after 50 years of succession.

On north facing upper slopes long-term changes after surface fire were also slight. There appeared to be a slight decrease in the number of oak and yellow pine stems; the latter often became uncommon after 60 years without fire. Hardwoods and hemlock on the other hand tended to increase after 50 years.

The most dramatic changes after fire occurred after severe fires on both north and south facing slopes (Table 8). Severe fires have been uncommon in GRSM and only 2 stands were found with recent fires. Stem densities of both sites were 2-3 times higher than expected. On the north facing slope there was an increase in yellow poplar, black locust, devil's walking stick, sassafras, red maple, and a decrease in oaks and hickories. On south facing slopes, the importance of oaks (mostly blackjack oak) increased via sprouting. Southern winged sumac, devil's walking stick and black locust also increased after severe fire on south facing slopes.

Table 8. Relative Stem Density of Species Groups After Severe Fire on North and South Facing Slopes.

Species Group	Relative Density North Facing Slope 1000 m Elevation 7 Years Since Fire	 South Facing Slope 567 m Elevation 21 Years Since Fire
White Pine	+[a]	+
Hemlock	0	0
Yellow Pine	0	46
Mixed Hardwood	91	17
Oak	7	27
Hickory	1	3
Other	1	7
Total Stems	848	755

[a]Denotes less than 1%.

Direct ordination of canopy reproduction. The distribution and abundance of canopy reproduction gives a general indication whether a species will change in abundance given a continuation of present conditions. Species with an abundance of reproduction may be replacing themselves or expanding their range on environmental gradients. However, the presence of reproduction does not indicate these individuals will become canopy dominants. An alternative hypothesis states that if growth rates are very slow then a subcanopy status might be the endpoint for most individuals. Thus, mesic species invading a xeric site might be able to reproduce successfully even though the maximum size attained keeps these individuals in the shrub or subcanopy strata. Another limitation to using reproductive abundance as an indicator of long-term trends occurs when a species has low density but high survivorship. In this case a few seedlings might in fact become members of the canopy. In contrast, a species with low survivorship may not attain canopy status before death. Given the limitations of canopy reproduction as an indicator of long-term successional trends, it seems best to use a cautious approach. Long-term trends based on these data are, therefore, stated as hypotheses to be tested. The permanent plot system should serve as a baseline to test the validity of the projected trends.

Canopy reproduction on lower slopes and in ravines was very sporadic. The dense cover of rhododendron, mountain laurel and doghobble reduced the amount of sunlight reaching the forest floor considerably. In many of these sites a very thick carpet of organic matter covered the forest floor (Harmon 1980). Both shading and thick organic horizons, alone or in combination, may have led to the paucity of canopy

reproduction. Seedlings of red maple, sassafras, American holly, shadbush, hemlock, sweet birch, dogwood, Fraser magnolia, sourwood, yellow poplar, white pine, red oak, black oak and white oak were observed. Most were of very small size or still retained their cotyledons. Hemlock and American holly were the only species which seemed to have individuals in most size classes of shrubs and trees. It, therefore, seems likely other species reproduce successfully either when mineral soil is exposed or when a rotting stump or log is available and/or when an opening allows sufficient sunlight to reach the forest floor.

Regression equations indicated that hemlock stem density decreased with slope position, but increased with concavity. However, observations indicated hemlock density can be just as high on middle slopes with SBI less than 300. Hemlock occurred on burned sites as soon as 2 years after fire, but appeared to rarely grow into the canopy layer on southern middle and upper slopes.

Silverbell, dogwood, American holly, Fraser magnolia, yellow poplar, striped maple, pignut hickory, mockernut hickory, white oak and red oak were densest on middle slopes. Silverbell and dogwood reproduction distributions were similar to canopy distributions. American holly occurred on both xeric and mesic sites, but regression models indicated a significant decrease in stem density with slope position. Fraser magnolia also occurred on xeric and mesic sites although this species appeared to be most abundant on middle slopes with SBI ranging between 210 and 300. There was a significant increase in Fraser magnolia stem density as elevation decreased and as SBI and years since burn (YSB)

increased. New Fraser magnolia seedlings have been observed on fires after only 2 years. Yellow poplar had the greatest stem density when slope positions were near 40% and increased with elevation and decreased with slope steepness. Although yellow poplar seedlings were common, very few trees less than 10 cm dbh were found, which indicated yellow poplar may have had low reproductive success. Two years after a severe fire in oak forest there were 600 yellow poplar seedlings per hectare, and some individuals were already over 1 meter in height. Fire may, therefore, play an important role in increasing successful yellow poplar reproduction on mesic sites. Other disturbances such as chestnut blight, windthrow and agricultural clearing have also led to successful establishment of yellow poplar, but only windthrow and fire will be important in future reproduction dynamics. Striped maple reproduction was more widespread than canopy stems and occurred on xeric as well as mesic sites. Regression models indicated that the basal area of striped maple reproduction was highest on middle slopes, increased with aspect, and decreased with SBI. Pignut hickory appeared to occur in stands that were slightly less mesic than mockernut. Regression models of basal area indicated pignut has a maximum at slope position 67%, whereas the maximum for mockernut was 58%. The two hickory species also responded differently to the elevational gradient; pignut increased above 300 m and mockernut decreased.

American chestnut was once a prominent canopy species on middle slopes with low SBI. Chestnut reproduction in this study was most dense on upper slopes with intermediate to high SBI. The presence of chestnut sprouts in the present study did not indicate where this

species reached its biomass maximum. Keever (1953) noted that chestnut sprouts from seedling reproduction were more profuse and vigorous than sprouts from larger trees. Moreover, seedling reproduction was observed by Keever to be most common on south facing slopes.

Black locust, red maple, sourwood, chestnut, blackgum, scarlet oak, chestnut oak, blackjack oak, black oak, mountain holly, sassafras, white pine, pitch pine, and Virginia pine all had their highest stem density on upper slopes. Sourwood, red maple and sassafras reproduction occurred on sites ranging from the most mesic to xeric. Regression analysis indicated sourwood density decreased with increasing SBI and slope steepness; however, a mosaic chart revealed sourwood was most abundant on upper slopes, but as elevation increased the maximum was shifted to sites with a higher SBI. Red maple exhibited its highest density at a slope position of 65-70 and increased with SBI, but decreased with slope steepness and concavity. White pine had the widest distribution of all the pines and occurred at all elevations and on sites ranging from mesic to xeric. As slope position increased white pine moved onto sites with lower SBI, but an increase in elevation had the opposite effect and caused a contraction onto sites with higher SBI. White pine regression models suggested density increased with SBI and decreased with elevation and concavity. The basal area of white pine reproduction decreased with slope, elevation and years since fire disturbance.

Chestnut oak and black oak seedlings had similar distributions on environmental gradients. Both species increased on sites with intermediate SBI and as slope position increased. Thus, upper east and west

facing slopes had a maximum of black oak and chestnut oak reproduction. Blackjack oak and scarlet oak seedlings were restricted to more xeric sites than black oak and chestnut oak. Blackjack oak occurred on upper slopes below 800 m with SBI over 300. Scarlet oak occurred on middle and upper slopes and increased with SBI and years since burn.

Black locust density tended to be highest on upper slopes. Regression models indicated black locust density increased with slope position, decreased with years since burn and had a maximum on slightly concave sites. After fire black locust sprouts and seedlings were often very dense and on open sites grew over 2 m tall in 2 years. On sites where chestnut blight opened the canopy black locust trees often filled the gaps. Aside from pine, black locust was the most common dead tree recorded. Black locust will probably decrease in importance throughout the forest. Localized stands may continue to develop in windthrows and on severely burned sites.

Blackgum density increased significantly with SBI and had a maximum on a slope position of 70%. In contrast sassafras density significantly increased with elevation above 800 m, and increased with slope position and slope steepness. Therefore, sassafras appeared less restricted to south facing slopes than blackgum. Sassafras increased with elevation in both the canopy and shrub layer.

Virginia pine was the most common species of yellow pine in reproduction. Although regression models indicated Virginia pine density increased only with slope position, there also appeared to be a decrease with elevation and an increase with SBI. Pitch pine density also increased with SBI and slope position but tended to increase with

elevation. Table mountain pine and short leaf pine seedlings were occasionally observed in the field but were not as abundant as Virginia pine or pitch pine seedlings.

Canopy cover types. The classification procedure separated 94 plots into 9 cover types. The remaining 6 plots were transitional and could be classified into more than one cover type. The unlogged cover types included from xeric to mesic: (1) yellow pine, (2) chestnut oak-scarlet oak, (3) white pine, (4) mixed oak, (5) mixed hardwood, (6) hemlock and (7) cove hardwood. Two cover types were separated by dominance as well as man-caused disturbance history: (1) old-field pine and (2) successional hardwoods.

The yellow pine cover type (Appendix, Table 20) included 26 plots of which 3 plots were transitional to the chestnut oak-scarlet oak cover type and 2 plots transitional to the mixed oak cover type. The yellow pine mean basal area was 25.9 m^2 ha^{-1} and the mean stem density was 409 stems per 0.1 ha. Dominant trees of this cover type included Virginia pine, pitch pine, table mountain pine, scarlet oak and blackgum. Elevation, in part, controlled the dominance of individual pine species. Table mountain pine tended to increase with elevation whereas Virginia pine tended to decrease. However, this trend was by no means absolute and Virginia pine dominance occurred as high as 1000 m. Two variants of the yellow pine cover type were also recognized depending upon the understory presence of mountain

laurel. Plots without mountain laurel had a thick cover of low bush blueberry and black huckleberry.

The chestnut oak-scarlet oak cover type (Appendix, Table 21) included 14 plots with a mean basal area of 26.9 m^2 ha^{-1} and a mean stem density of 264 stems per 0.1 ha. Basal area dominants within this cover type included red maple, Virginia pine, scarlet oak and chestnut oak. Although chestnut oak dominated the basal area in most plots, scarlet oak was important locally. The understory layers of this cover type were most often dominated by bear huckleberry.

The white pine cover type (Appendix, Table 22) included 5 plots with a mean basal area of 34.9 m^2 ha^{-1} and a stem density of 498 stems per 0.1 ha. Basal area dominance was mainly by white pine although red maple, Virginia pine, white oak and hemlock were also important. Mountain laurel often formed a dense understory layer in this cover type. The white pine cover type was highly variable in composition because of its juxtaposition with the yellow pine, mixed oak, chestnut oak-scarlet oak, hemlock and mixed hardwood cover types. Slight variations in slope position, concavity and aspect shifted the white pine cover type from mesic associates (e.g., hemlock) to more xeric associates (e.g., Virginia pine).

The mixed oak cover type was very complex and was dominated by one of 5 oaks (Appendix, Table 24). Ten plots were included in this classification with a mean basal area of 26.9 m^2 ha^{-1} and a mean

density of 249 stems per 0.1 ha. Oaks which assumed dominance in this cover type were white oak, scarlet oak, chestnut oak, red oak and black oak. Chestnut oak was the only oak species to occur in all the plots of this type. The distributions of the other oak species were determined by the moisture gradient as well as local geographical differences. Red and white oak dominance usually increased in the more mesic sites, whereas chestnut oak and scarlet oak increased as sites became more xeric. Species associated with the mixed oak cover type included white pine, red maple and pignut hickory.

The mixed hardwood cover type (Appendix, Table 29) included 16 plots with a mean basal area of 23.8 m^2 ha^{-1} and a mean density of 222 stems per 0.1 ha. The composition of this cover type was also quite variable and included 47 species. Dominant species included red maple, dogwood, pignut hickory, mockernut hickory, silverbell, yellow poplar, chestnut oak, red oak, black oak and black locust. This cover type once contained a great deal of American chestnut. The demise of this species may account for the relatively low basal area and high compositional variability of this cover type. The increase in the occurrence of grape vines was another notable feature of this cover type. Understories were dominated by herbaceous cover in contrast to the predominance of ericads in the other cover types.

The hemlock cover type (Appendix, Table 25) included 7 plots but was subdivided further based on the presence of a rosebay rhododendron

understory. When rosebay rhododendron was absent, a rich and dense cover of herbs and woody vegetation occurred. Stands with rosebay rhododendron were more common than those without this species. This cover type had the highest mean basal area (42.9 m^2 ha^{-1}) and a mean density of 377 stems per 0.1 ha. Dominant species of this cover type were yellow poplar, white pine, rosebay rhododendron and hemlock. Red maple and sweet birch were of lesser dominance but occurred in all plots of this cover type.

The last cover type without recent man-caused clearing was the cove hardwood (Appendix, Table 26). Seven plots were included with a mean basal area of 37.9 m^2 ha^{-1} and a density of 574 stems per 0.1 ha. The dominants of this cover type were variable but included red maple, buckeye, sweet birch, beech, yellow poplar, white pine, rosebay rhododendron, and hemlock. The abundance of rosebay rhododendron, hemlock, buckeye, and beech gave this cover type a very different appearance than the mixed hardwood cover type.

The old-field pine cover type (Appendix, Table 27) was cleared by man for agricultural purposes and had very different associated species than the yellow pine cover type. Virginia pine, white pine, pitch pine and shortleaf pine mixtures dominated the basal area. However, the stem density of dogwood, sweet gum, yellow poplar, and hemlock reflected the mesic nature of these sites. The old-field pine cover type included 5 plots with a mean basal area of 26.5 m^2 ha^{-1} and a mean density of 413 stems per 0.1 ha. Although dominated by yellow pines the understory of the old-field pine cover type was quite distinct from the yellow pine cover type. In the former, seedlings of

hemlock, dogwood and other hardwoods were dominant in contrast to the ericad dominated understory of the yellow pine cover type.

The successional hardwoods cover type (Appendix, Table 28) included only 3 plots with a mean basal area of 24.2 m^2 ha^{-1} and a mean density of 341 stems per 0.1 ha. The great compositional variability and low sample size made the description of this community tentative at best. The successional hardwood cover type was found on north facing slopes and in sheltered ravines which have been cleared for agriculture and homesites. As with the old-field pine cover type, it was usually restricted to portions of the study area which were outside the Morton Butler Tract (Figure 1, page 5). The major canopy dominants were red maple, mockernut hickory, dogwood, sweet gum, yellow poplar, white pine and hemlock. Sweet gum and yellow poplar mixtures composed over 40% of the basal area. Hemlock became more important in terms of stems and basal area as stand age increased.

The compositional relationships of the classified plots were examined by superimposing them on the basal area canopy ordination (Figure 24). The yellow pine, white pine and chestnut oak-scarlet oak cover types appeared to be most distinct, while the other cover types intermingled. The hemlock and cove hardwood cover types were especially mixed. The old-field pine cover type appeared to intermediate in composition between the yellow pine, white pine, hemlock and mixed hardwood cover types. The successional hardwood cover type had less of a central position in the ordination and was intermediate between the mixed hardwood, hemlock and cove hardwoods cover types.

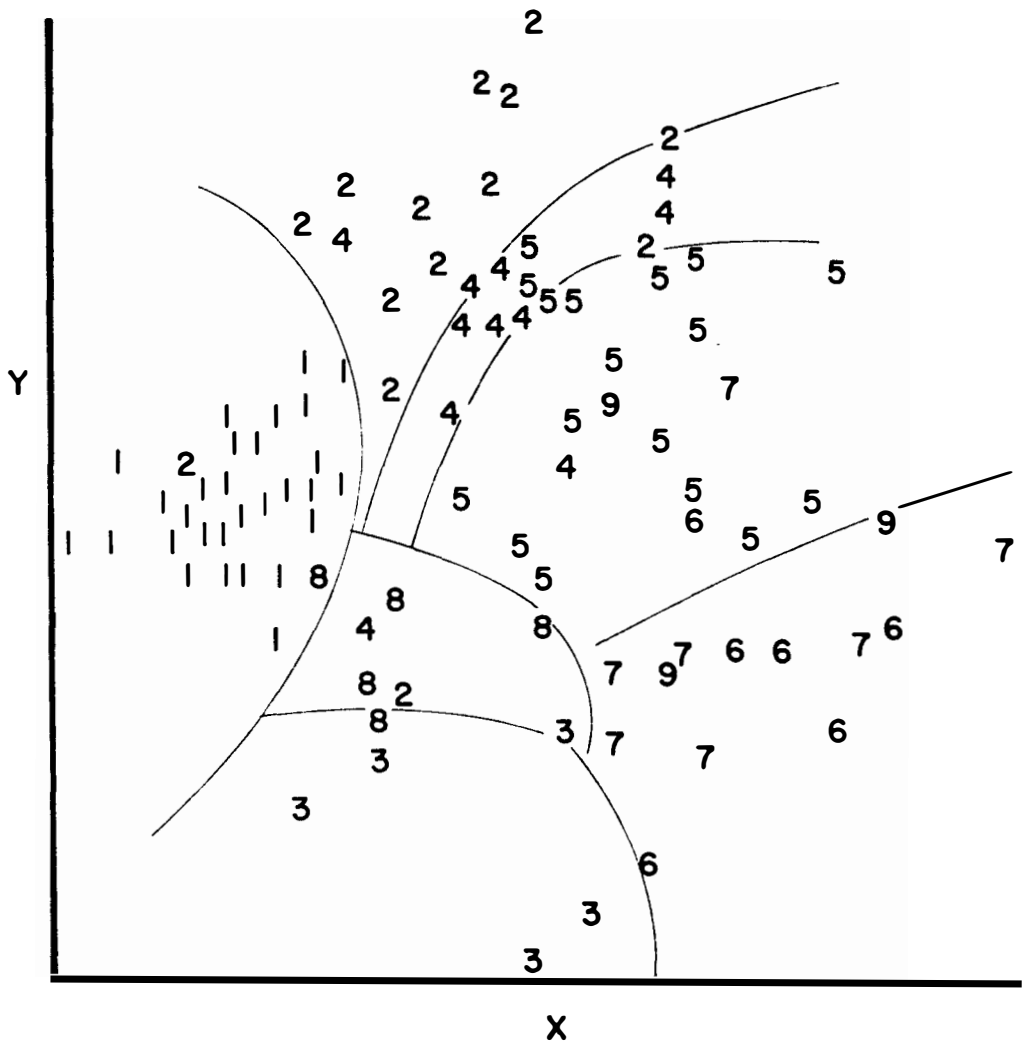


Figure 24. Distribution of canopy cover types on Bray-Curtis ordination of basal area composition.

The canopy cover types are (1) yellow pine, (2) chestnut-scarlet oak, (3) white pine, (4) mixed oaks, (5) mixed hardwoods, (6) hemlock, (7) cove hardwoods, (8) old-field pine and (9) successional hardwoods.

When slope position, convexity and SBI were used to array the cover types, a pattern quite similar to the indirect ordination emerged (Figures 25 and 26). On flat to convex sites the yellow pine cover type occurred on lower to upper slopes with high SBI. However, on concave sites the yellow pine cover type only occurred on ridge tops with the highest SBI. This shift to sites with higher slope position and SBI as concavity increased occurred for most cover types. A paucity of data for hemlock and cove hardwood cover types on concave sites may explain why this was not apparent on lower slope positions. As in the indirect ordination case, hemlock and cove hardwood cover types did not form distinct groups on the direct ordination. Moreover, the distinction between white pine, hemlock and cove hardwood cover types on lower slopes was less clear. These cover types may separate on successional as well as topographic gradients. White pine should be found on the more exposed xeric lower slopes, hemlock on intermediate moisture conditions and cove hardwoods on the most sheltered and mesic lower slopes. Disturbance by windthrow or perhaps fire would increase white pine, yellow poplar, sweet birch and sweetgum. Thus, one would expect the white pine and cove hardwood cover types to dominate early in succession.

Discussion

Canopy species richness. Whittaker (1956) found the highest within site diversity in stands transitional between oak and cove forests. In the western portion of GRSM, the richest forests occurred in the transition between oak and cove forests as well as the transition between yellow pine and hemlock-cove hardwood forests.

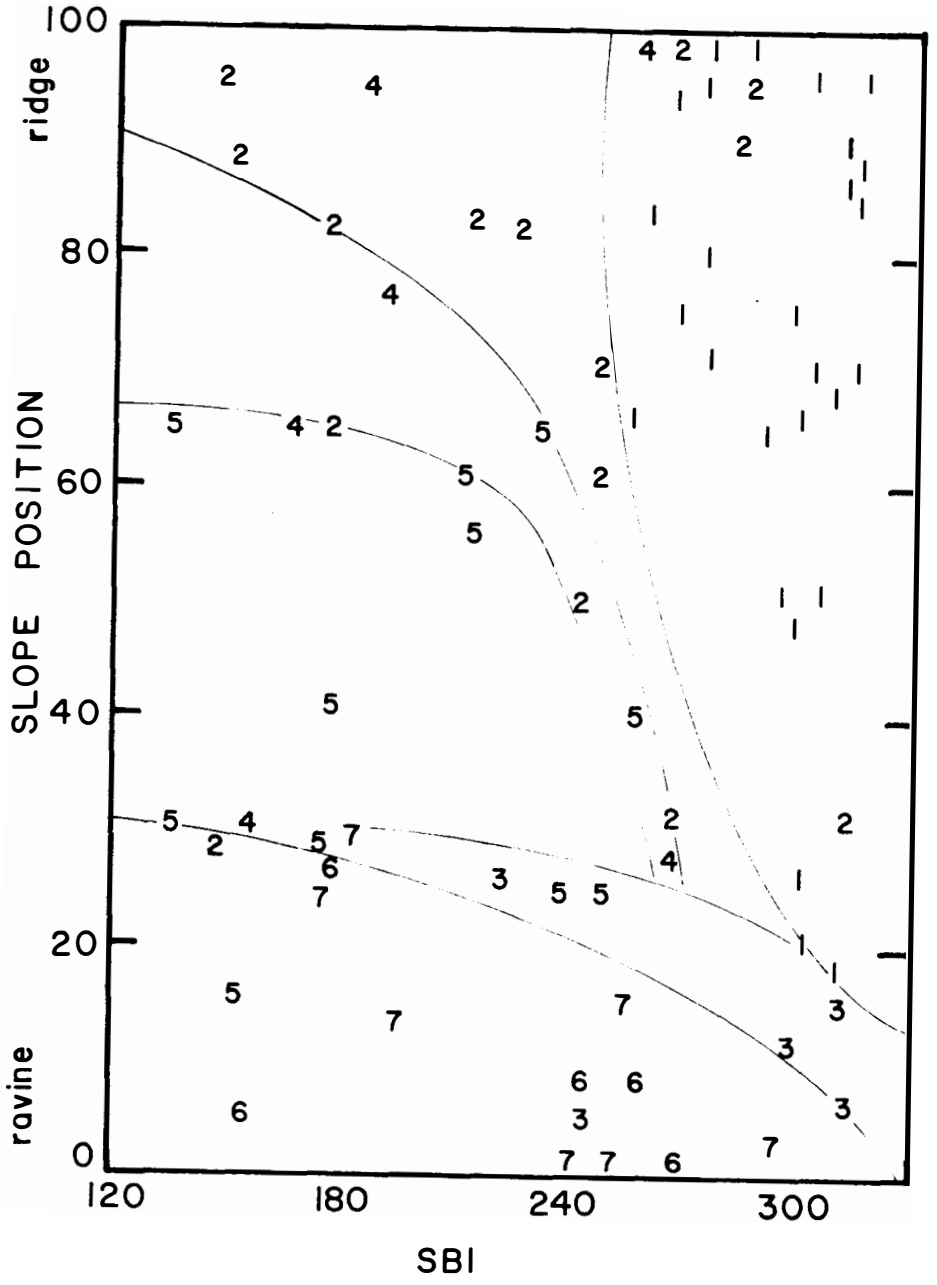


Figure 25. Distribution of canopy cover types on flat to convex sites as a function of solar beam irradiation (SBI) and slope position.

The canopy cover types are (1) yellow pine, (2) chestnut-scarlet oak, (3) white pine, (4) mixed oaks, (5) mixed hardwoods, (6) hemlock and (7) cove hardwoods.

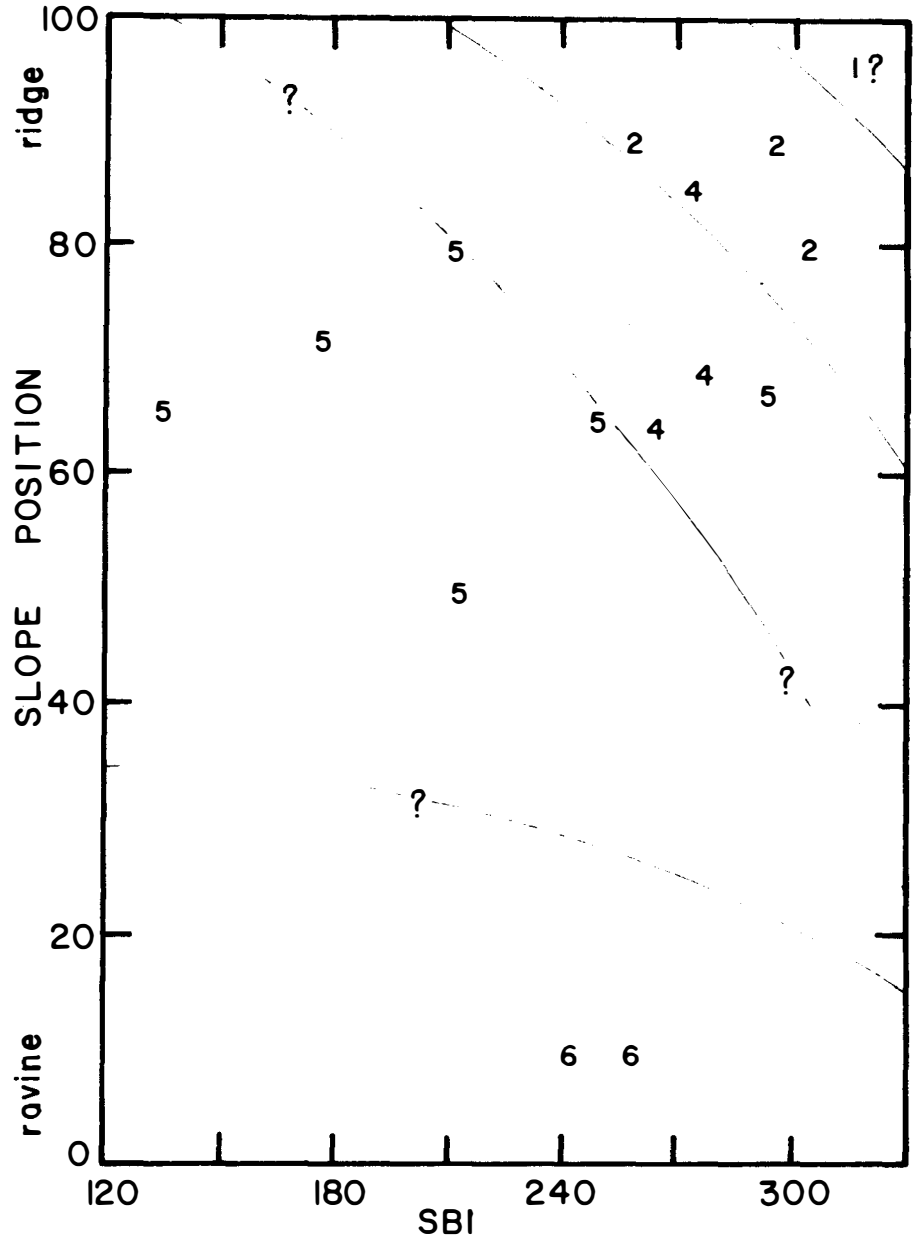


Figure 26. Distribution of canopy cover types on concave sites as a function of solar beam irradiation (SBI) and slope position.

The canopy cover types are (1) yellow pine, (2) chestnut-scarlet oak, (3) white pine, (4) mixed oaks, (5) mixed hardwoods, (6) hemlock and (7) cove hardwoods. Question marks indicate zones with no data other than field observations.

Fire disturbance initially tended to decrease canopy richness, especially as severity increases. Peet (1978) found an initial increase in total species richness* in severely burned Colorado conifer forests. After 50 years total species richness decreased as the tree crowns grew together. The break-up of the forest after 100 to 200 years led to an increase in diversity. Bormann and Likens (1979) examined the development of the northern hardwood community after clear-cutting. Species richness* was also found to be highest a few years after disturbance, lowest during maximum crown closure (50 years) and intermediate when an uneven aged forest developed (250 years). Bormann and Likens (1979) and Peet (1978) hypothesize that the final increase in species is attributable to the invasion of tolerant species and the occurrence of small disturbances such as tree gaps which create suitable habitat for intolerant species. It would appear many of the forests on middle to lower slopes in the western portion of GRSM were near a crown closure maximum and, therefore, a species richness minimum. One would anticipate that if fire disturbance continues to be excluded, species richness will remain at a minimum until even aged forests break up. Allowing forests to burn would probably increase the overall species richness of the landscape.

Canopy species distribution. Whittaker (1956) examined the distribution of canopy species along complex gradients of moisture and elevation. In constructing a moisture gradient, Whittaker considered

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*All vascular plants.

draws more mesic than sheltered slopes (lower slopes in this study) regardless of aspect and slope position. The present study demonstrated, however, that vegetational composition in draws changed dramatically with both aspect and slope position. Although reducing aspect, slope steepness, slope position and convexity to a one-dimensional moisture gradient is appealing, it is very difficult. The very similar patterns revealed in the direct and indirect ordination of cover types indicated that this procedure may even be inappropriate.

In spite of these differences, the overall correspondence between vegetation patterns described by Whittaker (1956) and those of the westernmost portion of GRSM was high. Since Whittaker only examined stem density, the discussion will exclude basal area. Another major difference in methodology was that Whittaker excluded mountain laurel and rhododendron from the sample. To minimize sampling differences these two species were excluded from the comparison.

Blackgum, hemlock, white pine, striped maple, dogwood, pignut hickory, silverbell and sassafras appeared to be more important in the western part of GRSM than the central part of GRSM. Of these species hemlock, striped maple, dogwood and silverbell may have represented ingrowth during the 20 year interlude. The remaining species differences may have represented geographical differences caused by overall topographic relationships, elevation, floristic relationships and disturbance histories.

Relative stem densities of hemlock found in the western part of GRSM were higher than Whittaker reported for middle (open) slopes.

Although geographic differences could not be discounted, the importance of hemlock as a small canopy component has apparently increased. The expansion of hemlock distribution may have been caused by fire suppression.

Scarlet oak, chestnut oak, chestnut, red oak, sourwood and witch hazel appeared to be less important in the western part of GRSM than the central part of GRSM. The decrease in stem importance may have been in part caused by ingrowth of hemlock, striped maple and dogwood. The decrease in chestnut was obviously caused by chestnut blight.

Canopy cover types. The canopy cover types presented in this study were very generalized and included finer subdivisions presented by Whittaker (1956), Golden (1974), DeYoung (1979) and Thomas (1966). In each of these studies, the importance of cove hardwoods, hemlock, submesic hardwoods, oaks and yellow pines shifted as one proceeded from mesic to xeric soil conditions. Elevational changes within cover types were also consistent with those presented by Golden (1974) and Whittaker (1956). The most significant changes with respect to elevation occur within the yellow pine cover type.

Kuykendall (1978) observed a number of hardwood and oak forests replacing yellow pine forests disturbed by southern pine bark beetle. Of particular relevance to the present study were the red maple-sourwood, blackgum-mixed pine, mixed pine-scarlet oak, and the Virginia pine-blackgum cover types. These represented forests dominated by subxeric to xeric hardwoods on sites formerly dominated by yellow pines.

As the yellow pine forests mature one would expect forests of compositions similar to those reported by Kuykendall (1978) to develop on middle to upper slopes with SBI in excess of 240.

Summary

Data gathered on forest canopies from 100 permanent plots were examined using indirect ordination, direct ordination and community classification. The three techniques were found to be complimentary.

Both the indirect and direct ordinations supported the hypothesis of continuous change in canopy composition. A gradient of slope position and aspect corresponded closely to the indirect ordination. Degree of concavity and disturbance history also influenced the pattern revealed by indirect ordination technique but were difficult to assess.

Mosaic charts and regression analysis indicated the importance of environmental gradients in influencing canopy species distributions. The most important factor appeared to be moisture as reflected by slope, slope position, aspect, solar beam irradiation (SBI) and concavity. Progressing along a moisture gradient from xeric, convex south facing upper slopes to mesic concave lower slopes and ravines the canopy vegetation changed in a very complex manner. Elevationally related changes were most important for the yellow pines and blackjack oak. Although no dramatic changes were observed for forests after 50 years of succession after surface fire, a decrease in yellow pines, blackjack oak, black locust, yellow poplar, sumac, devil's walking stick and persimmon is anticipated. After severe fire, stem density increased dramatically and the proportion of shade intolerant species increased.

Disturbance by man (e.g., agricultural clearing) increased the abundance of white pine, Virginia pine, yellow poplar and sweet gum.

Nine canopy cover types were presented. Forests which were not recently logged or cleared by man were divided into 7 canopy cover types. From xeric to mesic these included: yellow pine, chestnut oak-scarlet oak, white pine, mixed oak, mixed hardwood, hemlock and cove hardwood. Forests recently cleared by man had old-field pine or successional hardwood cover types depending on the position along the topographic-moisture gradient.

VIII. SUMMARY AND CONCLUSIONS

Fire History

(1) Present fire records and examination of fire scars indicated that man-caused fires were a more important influence on vegetation than lightning-caused fires during the last 150 years. The mean fire interval on south facing slopes for the period between 1855 to 1940 was 12.7 years. Historical records indicated aboriginal man-caused fires probably had a profound effect on vegetation patterns. More data are needed to determine the difference in fire regimes during aboriginal and Euro-American historical periods.

(2) Evidence of fire was found in all but the most mesic portions of the topographic-moisture gradient. Fires left scars on trees most frequently on southern upper slopes, and least frequently on northern lower slopes. Southern lower slopes and north facing upper slopes were intermediate in the occurrence of fire scars. In yellow pine forests, fires were more frequent below 600 m elevation.

(3) Fires in yellow pine forests were more frequent and/or larger during years with below normal rainfall.

(4) The majority of yellow pine forests examined for fire scars were burned last between 1910 and 1940. Only a few yellow pine forests in the entire study area had burned since 1940. Changes in land use, combined with active fire suppression have reduced the influence of fire considerably.

(5) Allowing lightning fires to burn unhindered will probably not maintain the fire regime responsible for the present or the

historical vegetation pattern. Lightning fires would have to be very large to maintain this regime. At present, little data exists on the size of unsuppressed lightning fires. Nonetheless, it appears lightning fires will only create small and scattered patches of disturbed habitat.

Initial Disturbance Effects

(1) Fire severity was found to be a function of topography, weather and fuel loadings. Based upon these criteria south facing upper slopes with pine forest will tend to have the severest fires. The presence of southern pine bark beetle kill dramatically increased the probability of severe fire.

(2) Fire prepared a complex array of habitats. Canopy opening increased as mortality in terms of stems or basal area increased. An increase in canopy opening was not always associated with an increase in organic horizon removal.

(3) Only extremely severe fires caused major changes in canopy species richness. Most changes in canopy species richness were probably only temporary. Canopy species richness will probably increase when sprouts from trees killed above the ground by fire and seedlings grow into the canopy strata.

(4) Fire was found to be both an endogenous and exogenous disturbance. Consistent shifts in forest composition immediately after fire indicated that the community itself controlled the direction of change. The magnitude of change was determined by both the community and the severity of the disturbance.

(5) Species had different abilities to survive fire, but fire severity and size must be considered before valid comparisons can be made. The probability of fire survivorship was modeled for ground fires as a function of species, stem size, height and bark thickness. Attributes allowing individual trees to survive fires included thick bark, epicormic branching, high branching habit, resistance to decay and pathogenic attack, and rapid growth rates.

(6) Fire regimes on upper slopes before the establishment of GRSM probably favored thick barked, fast growing species which possessed the ability to sprout. Fire suppression has allowed thin barked and/or slow growing species to enter size classes that are resistant to ground fire. Thus, the basic dynamics of fire disturbance have changed with fire suppression. Allowing lightning-caused fires to burn will probably not exclude species with thin bark and slow growth rates from most positions along the topographic-moisture gradient.

Early Response to Fire Disturbance

(1) Seedlings, seedling sprouts and tree root collar sprouts all contributed to the initial response after fire disturbance. The importance of each reproductive form was dependent upon community composition prior to disturbance, age and size structure, fire severity, position along the topographic moisture gradient, and litter depth. The relationship between dependent and independent variables was quite complex and further work is needed before the exact relationships are clear.

(2) On south facing slopes, seedlings of yellow pines, sourwood, devil's walking stick, sumac and princess tree became established after severe fires. Density of yellow pine seedlings increased with increased

canopy opening and decreased litter depth. On north facing slopes yellow poplar, black locust, sourwood, yellow pine, white pine, devil's walking stick, sumac, and princess tree became established after severe fires. Although some seedlings were established on north and south facing slopes after mild fire, growth rates and densities were both low.

(3) Seedling sprout densities remained relatively constant as fire severity increased. Tree root collar sprout density generally increased as fire severity increased. Root collar sprout density was lowest in pine dominated forests. In oak dominated forests, tree root collar sprouts should theoretically be densest in severely burned young forests and sparsest in very mature large forests.

(4) Fire suppression has reduced the habitat many seedlings require for successful reproduction. Short lived species (e.g., sumac) have probably already become very uncommon within the study area. These species were observed in very rocky exposed habitats or on very recent burns. Long lived species will take longer to decline in importance.

Present Vegetational Pattern

(1) The present vegetation pattern reflected complex responses to site factors such as the topographic-moisture gradient and elevation as well as the fire disturbance regime. Fire disturbance and site factors did not operate independently from one another.

(2) After 50 years of fire suppression no dramatic changes in vegetation composition were detected using the zonal approach. However, a major decrease in yellow pines, blackjack oak, black locust, yellow poplar, sumac, devil's walking stick, and persimmon is anticipated.

It was hypothesized that an initial decline in some of these species had already occurred but remains undetected. Hemlock has generally increased in the study area since fire suppression was initiated.

(3) Nine canopy cover types were presented and were based on basal area dominance by a species or species group and the degree of anthropogenic disturbance. Cover types not cleared by man for agricultural use included from mesic to xeric: cove hardwoods, hemlock, mixed hardwoods, mixed oak, white pine, chestnut oak-scarlet oak, and yellow pine. Forests once cleared by man for agriculture included old-field pine and successional hardwcods. The most future compositional change is anticipated to be in the old-field pine, successional hardwood and the yellow pine cover types. With continued fire suppression the areal extent of the yellow pine cover type should decrease substantially in the next 50 years.

Conclusions

When the results of the five studies are viewed as a whole, the role of fire in determining vegetation pattern becomes apparent. Fire does not act independently of other disturbances, man, climate, vegetation or environmental gradients. Rather, fire interacts with these factors to establish a complex mosaic. When all these factors remain constant the overall composition of the mosaic pattern will remain in steady state even though the vegetation at any one site may be constantly changing (Bormann and Likens 1979). By changing the fire disturbance regime man has changed the vegetational pattern in the westernmost portion of GRSM. At the present time the vegetational pattern in the westernmost portion of GRSM is in a state of flux from a

regime with frequent, widespread fire to a regime with very little fire disturbance. The final vegetation pattern and the processes which maintain it will depend on the management policies the National Park Service adopts.

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APPENDIX

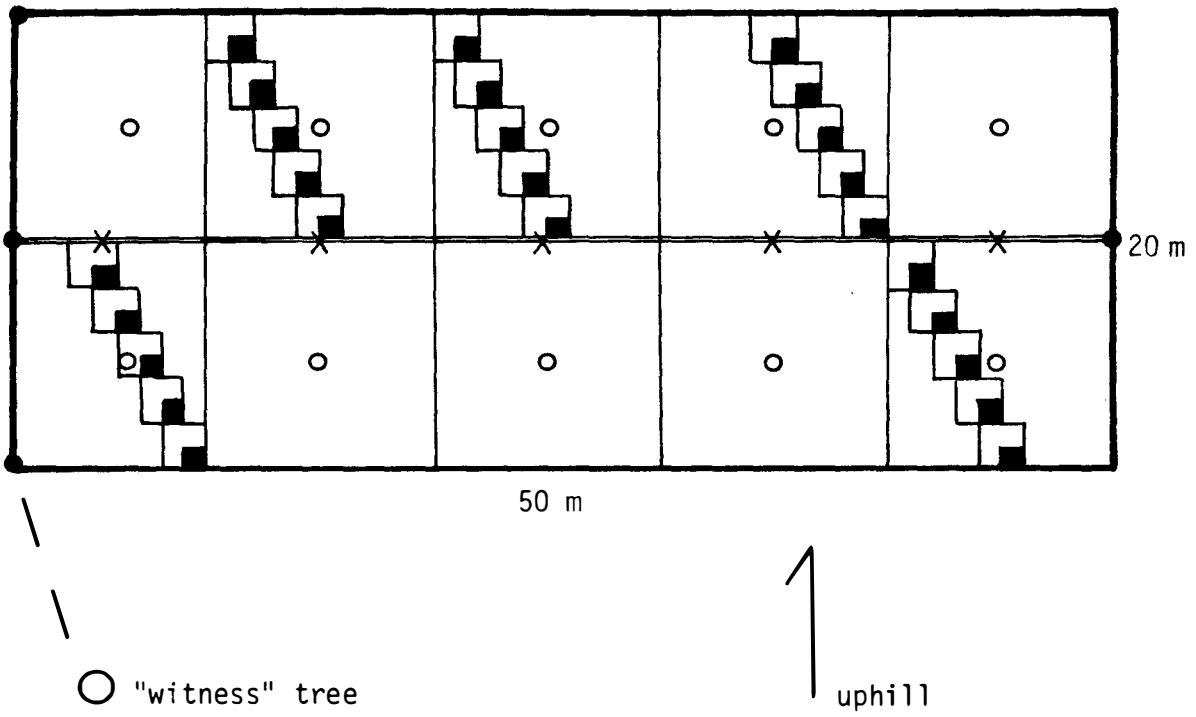


Figure 27. Plot design used in sampling

Table 9. Non-linear Regression Statistics for the Relationship of Diameter at Breast Height and Individual Survivorship Probabilities $P(S) = [1 + \text{Exp}\ (B_0 + B_1\ (\text{dbh}))]^{-1}$.

Species	B_0	B_1	R^2	X^2[a]
Acer rubrum	2.868	-0.518	0.966	11.69
Cornus florida	3.000	-0.500	0.825	4.47
Carya spp.	0.964	-0.256	0.886	6.88
Kalmia latifolia	3.000	-1.000	0.976	0.77
Nyssa sylvatica	2.000	-0.750	0.982	8.53
Oxydendrum arboreum	1.991	-0.753	0.989	1.69
Pinus spp.	3.733	-0.789	0.904	--
Pinus rigida	3.910	-0.765	0.978	3.50
Pinus strobus	2.000	-0.500	0.935	4.57
Pinus virginiana	4.000	-0.750	0.990	6.42
Quercus spp.	2.000	-0.500	0.872	--
Quercus prinus	5.000	-1.250	0.974	4.90
Quercus velutina	0.650	-0.228	0.956	4.68
Sassafras albidum	3.000	-0.750	0.954	6.07

[a]Chi-square was used to test the goodness of fit of regression predictions to the observed number of survivors. When X^2 is significant the observed number of survivors was not predicted by the regression model. X^2 (.0578) = 15.51. Chi-square tests were not performed for Pinus spp. and Quercus spp.

Table 10. Regression Statistics for the Number of Sprouts Per Sprout Clump from Trees Less Than 10 cm dbh 1 Year After Fire.[a]

Species	B_0	B_1	$\hat{s}_{B_1}$	B_2	$\hat{s}_{B_2}$	B_3	$\hat{s}_{B_3}$	R^2	N
Acer rubrum	-0.04	6.40	2.360	17.77	4.800			0.56**	26
Carya glabra	-6.00	10.82	5.816					0.63^{ns}	4
Nyssa sylvatica	-3.46	8.50	2.744	11.04	4.489			0.28**	56
Oxydendrum arboreum	-14.35	15.23	5.817	24.40	10.155			0.84*	7
Quercus coccinea	32.95					-7.29	2.245	0.23**	36
Quercus marilandica	34.39					-8.53	1.518	0.62**	21
Quercus prinus	-4.46	15.03	4.727					0.63*	8
Quercus velutina	-13.09	8.07	1.878	16.079	5.353			0.86*	6
Sassafras albidum	3.50			20.220	7.529			0.30*	19

[a]The independent variables are X_1, dead tree dbh (cm), X_2, canopy opening index (percent) and X_3, residual litter weight (kgm^{-2}). All equations are of the form $Y=B_0 + B_1 \ln (X_1 + 1)$.

^{ns} = Not significant.

* = $0.05>p>0.01$.

** = $0.01>p$.

Table 11. Regression Statistics for the Number of Sprouts Per Sprout Clump from Trees Less Than 10 cm dbh 2 Years After Fire.[a]

Species	B_0	B_1	$\hat{S}_{B_1}$	B_2	$\hat{S}_{B_2}$	B_3	$\hat{S}_{B_3}$	R^2
Acer rubrum	4.18	3.65	1.910					0.13[ns]
Carya glabra	-1.50	4.33	1.020					0.90*
Nyssa sylvatica	-3.80	8.14	2.351	8.81	3.847			0.29**
Oxydendrum arboreum	-11.76	13.12	4.995	20.69	8.720			0.83*
Quercus coccinea	25.56					-5.73	1.680	0.25**
Quercus marilandica	30.17					-7.65	1.046	0.74**
Quercus prinus	-4.60	12.59	3.035					0.74**
Quercus velutina	-12.65	6.43	0.732	16.70	2.087			0.97**
Sassafras albidum	2.52			17.30	5.941			0.33**

[a]The independent variables are X_1, dead tree dbh (cm), X_2, canopy opening index (percent) and X_3, residual litter weight (kgm^{-2}). Equations are of the form $Y = B_0 + B_1 \ln (X_1 + 1)$.

ns = Not significant.

* = $0.05>p>0.01$.

** = $0.01>p$.

Table 12. Regression Statistics for the Height of the Dominant Sprout from Trees Less Than 10 cm dbh 2 Years After Fire.[a]

Species	B_0	B_1	$\hat{S}_{B_1}$	B_2	$\hat{S}_{B_2}$	B_3	$\hat{S}_{B_3}$	R^2
Acer rubrum	4.75	4.18	2.375					0.11[ns]
Carya glabra	5.00	-1.44	2.040					0.20[ns]
Nyssa sylvatica	2.04	2.50	1.434	12.14	2.347			0.40**
Oxydendrum arboreum	-1.52	11.39	3.086					0.73*
Quercus coccinea	6.44			5.89	2.352			0.15*
Quercus marilandica	0.77	5.55	2.449					0.21*
Quercus prinus	14.13			47.32	3.489	-8.62	1.379	0.97**
Quercus velutina	12.93	-3.58	3.305					0.23[ns]
Sassafras albidum	4.09	2.06	2.317					0.04[ns]

[a]The independent variables are X_1, dead tree dbh (cm), X_2, canopy openness index (percent), and X_3, residual litter weight (kgm^{-2}). All equations are of the form $Y = B_0 + B_1 \ln (X_1) + B_2 \ln (X_2) + B_3 \ln X_3$. The sprout height (Y) is in dm.

[ns] = Not significant.

*0.05>p>.01.

**0.01>p.

Table 13. Woody Reproduction Stem Densities of 4 Chestnut Oak Forests with Mild Ground Fire.

Species	Stems 1000 m^{-2}		
	Stump Sprouts[a] Mean	Seedling Sprouts[b] Range	Quadrat Estimate Mean
Acer rubrum	124	30-700	487
Carya spp.	20	10-90	102
Cornus florida	17	0-100	253
Liriodendron tulipifera	5	0	10
Nyssa sylvatica	278	30-600	260
Oxydendrum arboreum	30	20-40	53
Pinus spp.	0	0	105
Quercus spp.	185	200-830	398
Robinia pseudoacacia	15	20-60	85
Sassafras albidum	64	80-2870	1120

[a]Calculated using number of top-killed trees and mean number of sprouts.

[b]Calculated by assuming each seedling would produce 1 sprout. Pre-fire seedlings estimated from similar unburned forests.

Table 14. Woody Reproduction Stem Densities of 1 Scarlet Oak Forest with Severe Fire.

Species	Stems 1000 m^{-2}		
	Stump Sprouts[a] Mean	Seedling Sprouts[b] Range	Quadrat Estimate Mean
Acer rubrum	17	30-690	135
Carya spp.	125	10-90	243
Cornus florida	100	0-100	164
Liriodendron tulipifera	10	0-10	661
Nyssa sylvatica	16	30-600	70
Oxydendrum arboreum	22	20-40	271
Pinus spp.	0	0	220
Quercus spp.	4000	200-830	7630
Robinia pseudoacacia	0	20-60	221
Rhus copallina	0	0	110
Sassafras albidum	24	80-2870	730

[a]Calculated using the number of top-killed trees and mean numbers of sprouts per clump.

[b]Calculated by assuming each seedling before fire produces 1 sprout. Pre-fire seedling density estimated from similar unburned forests.

Table 15. Woody Reproduction Stem Densities of 4 Pine Forests with Mild Ground Fire.

Species	Stems 1000 m^{-2}		
	Stump Sprouts[a] Mean	Seedling Sprouts[b] Range	Quadrat Estimate Mean
Acer rubrum	153	70-560	159
Carya spp.	1	0-40	3
Diospyros virginiana	0	0-20	29
Nyssa sylvatica	264	110-530	467
Oxydendrum arboreum	25	0-20	45
Pinus spp.	0	0	119
Quercus spp.	110	150-460	316
Sassafras albidum	47	540-7130	715

[a]Calculated using the number of top-killed trees and mean number of sprouts per clump.

[b]Calculated by assuming each seedling before fire produces 1 sprout. Pre-fire seedling density estimated from similar unburned forest.

Table 16. Woody Reproduction Stem Densities of 4 Pine Forests with Severe Fire.

Species	Stems 1000 m^{-2}		
	Stump Sprouts[a] Mean	Seedling Sprouts[b] Range	Quadrat Estimate Mean
Acer rubrum	135	70-560	43
Carya spp.	0	0-40	0
Diospyros virginiana	0	0-20	15
Nyssa sylvatica	664	110-530	685
Oxydendrum arboreum	75	0-20	98
Pinus spp.	0	0	435
Quercus spp.	383	150-460	348
Rhus copallina	0	0	62
Robinia pseudoacacia	3	0-10	8
Sassafras albidum	34	540-7130	1508
Ilex montana	3	0-540	108

[a]Calculated using number of top-killed trees and mean number of sprouts.

[b]Calculated by assuming each seedling would produce 1 sprout. Pre-fire seedling density estimated from similar unburned forests.

Table 17. Polynomial Regression Equations for Tree Stem Density (Number Per Hectare).[a]

Species[b]	INT	SBI	SBI^{2c}	POS	POS^{2c}	ELEV	ELEV^{2c}	ASP	ASP^{2c}	CON	CON^{2c}	R^2
ACRPNS	-2.541		-.0185		-.0574	.0046	-.0011					0.29
BTLLNT	1.675			-.0481	.3501							0.37
CRNFLR	5.842		-.0287		-.1274					-.0608	.2806	0.36
CRYGLB[d]	4.359		-.0165		-.0512	-.0024	.0007					0.21
CRYTMN[d]	8.982			.0294	-.2490	-.0049	.0009			-.0332	.1050	0.28
HLSCRL	6.370					-.0047	.0012	-.0199	0511			0.31
KLMLTF	5.938	-.0554	.1538	-.0149								0.23
LRDTLP	-1.884	.0350	-.0844	-.0071						-.0157	.0741	0.31
NYSSYL	-3.760		.0290	.0600	-.3519					.0532	-.2164	0.47
OXYARB	6.294	-.0442	.1036									0.10
PNSECH	3.266	-.0205	.0504		.0876	-.0007						0.28
PNSPNG	-3.396		.0141			.0009				.0248	-.1041	0.25
PNSRGD	-3.014		.0324	.0186						.0494	-.2299	0.47
PNSVRG	6.726	-.0601	.1645	.0268		-.0010				.0475	-.2612	0.50
QRCALB[d]	5.796	.0067			-.0544	-.0031	.0006	.0063		-.0176		0.36

Table 17 (Continued)

Species[b]	INT	SBI	SBI^{2c}	POS	POS^{2c}	ELEV	ELEV^{2c}	ASP	ASP^{2c}	CON	CON^{2c}	R^2
QRCCCC	0.263	.0093		.0152							-.0671	0.43
QRCPRN	-3.026	-.0050		.0106		.0050	-.0011					0.20
QRCRBR	1.621	-.0045		-.0044			.0001	-.0016				0.21
QRCVLT	0.822			.0354	-.2756			.0078	-.0171		-.0361	0.21
RBNPSD	0.589		-.0077				.0001	-.0016				0.24
SSSALB	0.172				.1387					.0248	-.1185	0.16
TSGCND	-0.023		-.0180	-.0746	.4717	.0051	-.0013			-.0293	.1831	0.48

[a]All equations are highly significant ($P<.01$) and are of the form log (stems + 1) = $B + B_1X_1 + B_2X_2 \ldots + B_nX_n$. Coefficients correspond to the following independent variables and units: INT intercept, SBI solar beam irradiation in 10^3 ly year^{-1}, POS slope position from ravine in percent, ELEV elevation in feet, ASP aspect in degrees azimuth, and CON concavity index.

[b]Species names which correspond to codes presented here appear in Appendix, Table 29.

[c]For ease of presentation all 2nd order coefficients have been multiplied by 10^3.

[d]An equation of the form stems = $B_0 + B_1X_1 + B_2X_2 \ldots + B_nX_n$ gave a higher value of R^2 but logarithmic transform was used for consistency.

Table 18. Polynomial Regression Equations for Tree Basal Areas (m^2 Per Hectare).[a]

Species[b]	INT	SBI	SBI^{2c}	POS	POS^{2c}	ELEV	ELEV^{2c}	ASP	ASP^{2c}	CON	CON^{2c}	R^2
ACRPNS	0.298	-.0008		-.0008								0.23
ACRRBR	-3.060		-.0068	-.0188	.0988	.0038	-.0008				.0282	0.32
BTLLNT	-1.239	.0102	-.0228	-.0244	.1767	.0009	-.0002					0.41
CRNFLR	-0.283	.0109	-.0284			-.0002						0.22
CRYGLB	0.769		-.0098		-.0352		.0001					0.23
HLSCRL	1.286					-.0010	.0003	-.0051	.0132			0.20
KLMLTF	-0.092		.0029	-.0038		.0001						0.18
LRDTLP	-4.643	.0532	-.1200	-.0091						-.0152	.0894	0.34
NYSSYL	-0.305			.0110	-.0768			.0066	-.0169			0.30
PNSECH	0.392		.0023		.0283	-.0003						0.20
PNSPNG	-1.303		.0069				.0001			.0128	-.0539	0.23
PNSRGD	-2.043		.0184	.0088						.0315	-.1375	0.39
PNSSTB	1.457			-.0067			-.0001					0.19
PNSVRG	4.020	-.0317	.0860	.0134		-.0009				.0229	-.1198	0.49
QRCALB	1.465	.0031			-.0438	-.0002			.0041	-.0081		0.26
QRCCCC	0.596	.0032			.0944						-.0360	0.35

Table 18 (Continued)

Species[b]	INT	SBI	SBI^{2c}	POS	POS^{2c}	ELEV	ELEV^{2c}	ASP	ASP^{2c}	CON	CON^{2c}	R^2
QRCPRN	-3.029		-.0128	.0068		.0042	-.0095					0.23
QRCRBR	0.531		-.0067	-.0038			.0001		-.0023			0.22
QRCVLT	-2.798	.0249	-.0549	.0188	-.1697			.0017				0.16
RBNPSD	0.322		-.0059			.0002		-.0014				0.27
SSSALB	0.808					-.0008	.0002					0.10
TSGCND	-0.881	.0286	-.0647	-.0515	.3450							0.42

[a]All equations are highly significant ($P<.01$) and of the form $\log (BA + 1) = B_0 + B_1 X_1 + B_2X_2 \ldots + B_nX_n$ coefficients correspond to the following independent variables: INT intercept, SBI solar beam irradiation in 10^3 ly year^{-1}, POS slope position from ravine in percent, ELEV elevation in feet, ASP aspect in degrees aximuth and CON concavity index.

[b]Species names which correspond to codes are presented in Appendix, Table 29.

[c]For ease of presentation all 2nd order coefficients have been multiplied by 10^3.

Table 19. Change in Stand Composition Along the Time Since Burn Gradient.[a]

N	YSB	Yellow Pine		Oak		Mixed Hardwood		Total	Stems
		% BA	% STEMS	% BA	% STEMS	% BA	% STEMS	$BA_{m^2ha^{-1}}$	No. ha^{-1}
2	21	88[b] (85-91)[c]	49 (35-63)	7 (5-9)	13 (8-17)	5 (3-6)	38 (28-48)	24 (23-25)	395 (320-469)
1	32	68	21	22	31	6	30	21	302
1	40	75	31	18	22	5	42	24	198
9	45	78 (63-94)	52 (31-74)	12 (1-29)	9 (4-17)	8 (2-16)	35 (22-48)	28 (23-37)	345 (208-422)
6	55	66 (46-88)	33 (14-55)	18 (3-30)	8 (2-16)	13 (11-21)	54 (41-71)	31 (27-37)	348 (299-427)
1	65	78	58	16	7	6	34	29	370

[a]When more than one sample was available, a mean value and the range are presented. There are no significant differences between stands along time since burn. BA is basal area.

[b]Mean.

[c]Range.

Table 20. Canopy Composition of the Yellow Pine Cover Type (N=26).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer rubrum	2.1	8.1	88.5
Amelanchier laevis	0.2	+[c]	30.7
Aralia spinosa	+	+	3.8
Calycanthus floridus	+	+	3.8
Carya glabra	+	0.2	15.4
Carya tomentosa[b]	0.2	0.8	30.8
Cornus florida	+	0.2	11.5
Diospyros virginiana	+	+	3.8
Halesia carolina	+	+	7.6
Hamamelis virginiana	+	+	11.5
Ilex montana	+	+	15.4
Ilex opaca	+	+	3.8
Kalmia latifolia	0.5	10.9	57.6
Liriodendron tulipifera	+	+	3.8
Magnolia fraseri	+	+	3.8
Nyssa sylvatica	4.8	17.2	100.0
Oxydendrum arboreum	1.5	3.1	92.3
Pinus echinata	1.7	0.9	34.6
Pinus pungens	11.4	4.4	53.8
Pinus rigida	27.8	11.5	100.0
Pinus strobus	1.4	2.4	61.5
Pinus virginiana	34.3	24.1	92.3

Table 20 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Pyrularia pubera	+	+	15.4
Quercus alba	0.6	0.4	23.1
Quercus coccinea	6.9	5.0	96.1
Quercus falcata	0.1	0.1	3.8
Quercus marilandica	2.1	2.9	57.7
Quercus prinus	3.6	1.2	69.2
Quercus rubra	0.1	0.1	19.2
Quercus stellata	+	+	3.8
Quercus velutina	1.2	1.4	69.2
Rhododendron calendulaceum	+	+	3.8
Rhododendron maximum	+	0.2	3.8
Rhus copollina	+	+	3.8
Robinia pseudoacacia	+	+	7.7
Sassafras albidum	0.4	4.0	88.5
Stewardia ovata	+	+	7.6
Tsuga canadensis	0.1	0.3	30.8
Vaccinium stamineum	+	+	23.1

[a]The mean basal area ± sd is 25.9 ± 6.8 m^2 ha^{-1} and the mean stem density ± sd is 409 ± 154.4 stems per 0.1 ha.

[b]May include Carya pallida.

[c]Denotes less than 0.1%.

Table 21. Canopy Composition of the Chestnut Oak-Scarlet Oak Cover Type (N=14).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer pensylvanicum	0.1	3.3	21.4
Acer rubrum	9.6	22.2	100.0
Amelanchier laevis	0.1	0.3	21.4
Betula lenta	0.1	0.3	14.3
Betula lutea	+[b]	+	14.3
Carya glabra	2.4	2.8	78.6
Carya tomentosa	1.0	1.4	50.0
Carya species	+	0.2	
Castanea dentata	0.1	0.1	21.4
Cornus florida	1.4	8.0	92.8
Halesia carolina	+	0.2	14.3
Hamamelis virginiana	0.1	0.9	7.1
Kalmia latifolia	+	0.6	14.3
Liriodendron tulipifera	3.2	0.4	42.8
Magnolia fraseri	+	+	7.1
Nyssa sylvatica	3.0	10.6	100.0
Oxydendrum arboreum	3.1	5.1	92.8
Pinus echinata	+	0.2	7.1
Pinus pungens	+	+	14.3
Pinus rigida	2.7	2.3	50.0
Pinus strobus	3.8	6.0	100.0
Pinus virginiana	6.2	4.8	57.1

Table 21 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Quercus alba	2.7	2.7	42.8
Quercus coccinea	10.5	2.9	64.2
Quercus marilandica	0.8	0.4	7.1
Quercus prinus	41.0	8.4	100.0
Quercus rubra	1.3	0.5	28.6
Quercus velutina	3.2	1.8	71.4
Rhododendron calendulaceum	+	+	7.1
Rhododendron minus	+	0.6	7.1
Rhododendron maximum	0.1	0.1	14.3
Robinia pseudoacacia	0.5	0.1	21.4
Sassafras albidum	0.1	1.5	50.0
Stewartia ovata	+	0.2	14.3
Tsuga canadensis	2.7	10.9	78.6
Vaccinium stamineum	+	+	7.1
Vitis aestivalis	+	+	14.3

[a]The mean basal area ± sd is 26.9 ± 7.27 and the mean stem density ± sd is 264 ± 73.5 stems per 0.1 ha.

[b]Denotes less than 0.1%.

Table 22. Canopy Composition of the White Pine Cover Type (N=5).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer pensylvanicum	0.3	1.2	20.0
Acer rubrum	10.1	12.7	100.0
Alnus serrulata	+[b]	+	20.0
Amelanchier laevis	0.1	.5	40.0
Betula lenta	0.3	0.1	60.0
Calycanthus floridus	+	0.2	20.0
Carya glabra	3.4	0.6	100.0
Carya tomentosa	1.3	0.9	80.0
Castanea dentata	+	+	20.0
Clethra acuminata	+	0.2	40.0
Cornus florida	0.6	3.8	80.0
Halesia carolina	+	0.2	40.0
Hamamelis virginiana	+	0.4	20.0
Ilex opaca	+	+	60.0
Kalmia latifolia	1.8	21.8	80.0
Liriodendron tulipifera	0.9	0.1	40.0
Magnolia fraseri	0.4	0.2	40.0
Nyssa sylvatica	1.3	1.9	80.0
Oxydendrum arboreum	2.5	4.5	100.0
Pinus echinata	0.7	0.1	40.0
Pinus pungens	0.1	0.1	20.0
Pinus rigida	3.8	0.4	40.0

Table 22 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Pinus strobus	38.5	12.5	100.0
Pinus virginiana	6.0	2.8	60.0
Pyrularia pubera	+	0.2	60.0
Quercus alba	7.6	1.0	80.0
Quercus coccinea	1.0	0.4	60.0
Quercus marilandica	+	+	20.0
Quercus prinus	3.1	1.1	80.0
Quercus rubra	0.8	0.2	40.0
Quercus velutina	2.7	0.5	60.0
Rhododendron maximum	3.0	13.2	60.0
Robinia pseudoacacia	0.1	0.1	20.0
Sassafras albidum	0.3	0.9	100.0
Stewartia ovata	0.1	0.3	40.0
Tsuga canadensis	9.1	15.5	100.0

[a]The mean basal area ± sd is 34.9 ± 9.82 m^2 ha^{-1} and the mean stem density ± sd is 498 ± 178 stems per 0.1 ha.

[b]Denotes less than 0.1%.

Table 23. Canopy Composition of the Mixed Oak Cover Type (N=10).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer pensylvanicum	0.3	1.8	50.0
Acer rubrum	11.1	16.9	90.0
Amelanchier laevis	+[b]	+	10.0
Betula lenta	0.3	0.3	30.0
Carya glabra	9.5	5.1	100.0
Carya ovata	0.1	0.1	10.0
Carya tomentosa	2.3	1.1	60.0
Castanea dentata	+	0.8	10.0
Clethra acuminata	+	+	10.0
Cornus florida	1.6	15.4	90.0
Fagus grandifolia	+	+	10.0
Fraxinus americana	+	+	10.0
Halesia carolina	0.1	1.1	40.0
Hamamelis virginiana	0.2	1.6	20.0
Ilex opaca	+	0.2	10.0
Kalmia latifolia	0.4	3.2	20.0
Liriodendron tulipifera	4.0	0.8	80.0
Magnolia fraseri	+	0.2	20.0
Nyssa sylvatica	2.0	5.8	90.0
Oxydendrum arboreum	3.6	4.6	90.0
Pinus echinata	0.3	3.3	10.0
Pinus rigida	1.2	0.6	30.0

Table 23 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Pinus strobus	2.5	5.1	100.0
Pinus virginiana	1.3	1.3	50.0
Quercus alba	3.5	0.7	30.0
Quercus coccinea	4.7	0.5	60.0
Quercus prinus	25.7	8.7	100.0
Quercus rubra	5.9	2.3	70.0
Quercus velutina	14.7	3.3	90.0
Rhododendron calendulaceum	+	0.6	30.0
Rhododendron maximum	0.5	1.9	20.0
Robinia pseudoacacia	1.3	0.7	60.0
Sassafras albidum	0.9	5.1	70.0
Tsuga canadensis	1.7	9.3	90.0
Vaccinium sp.[c]	+	+	10.0
Vitis aestivalis	+	0.4	20.0

[a]The mean basal ± sd is 26.9 ± 5.46 m^2 ha^{-1} and the mean stem density ± sd is 249 ± 88.8 stems per 0.1 ha.

[b]Denotes less than 0.1%.

[c]Possibly *Vaccinium constablaei*.

Table 24. Canopy Composition of the Mixed Hardwood Cover Type (N=16).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer pensylvanicum	0.2	1.4	50.0
Acer rubrum	9.4	9.8	87.5
Acer saccharum	0.5	0.5	18.7
Aesculus octandra	0.2	0.8	12.5
Amelanchier laevis	+[b]	0.2	18.7
Aristolochia durior	+	0.2	12.5
Betula lenta	0.2	0.4	12.5
Betula lutea	+	+	6.2
Carpinus caroliniana	+	0.2	6.2
Carya cordiformis	0.5	0.5	6.2
Carya glabra	11.6	6.4	100.0
Carya ovata	0.1	0.1	12.5
Carya tomentosa	10.7	4.5	87.5
Castanea dentata	+	0.4	18.7
Cercis canadensis	+	0.2	12.5
Cornus florida	5.1	26.7	93.7
Fagus grandifolia	+	0.2	12.5
Fraxinus americana	1.8	2.4	31.2
Halesia carolina	5.3	8.3	75.0
Hamamelis virginiana	+	0.2	6.2
Ilex opaca	+	+	6.2
Juglans nigra	0.1	+	6.2
Kalmia latifolia	+	+	6.2
Liriodendron tulipifera	12.3	1.9	81.2
Magnolia fraseri	0.8	0.8	43.7

Table 24 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Nyssa sylvatica	0.5	1.5	62.5
Ostra virginiana	0.1	0.5	12.5
Oxydendrum arboreum	2.3	1.9	81.2
Pinus echinata	0.1	0.1	6.2
Pinus rigida	0.2	+	6.2
Pinus strobus	1.8	1.8	81.2
Pinus virginiana	0.3	0.1	6.2
Pyrularia pubera	+	0.4	18.7
Quercus alba	3.0	1.2	31.2
Quercus coccinea	0.1	0.1	12.5
Quercus prinus	8.5	5.2	81.2
Quercus rubra	5.8	1.6	75.0
Quercus velutina	6.0	1.0	68.7
Rhododendron maximum	+	+	12.5
Robinia pseudoacacia	6.1	1.5	50.0
Sassafras albidum	0.6	1.8	68.7
Stewartia ovata	+	0.2	12.5
Tilia heterophylla	1.1	1.1	6.2
Tsuga canadensis	3.9	12.9	75.0
Ulmus americana	0.1	0.3	6.2
Vitis aestivalis	0.1	2.9	62.5
Vitis rotundifolia	+	+	6.2

[a]The mean basal area ± sd is 23.8 ± 5.46 m^2 ha^{-1} and the mean stem density ± sd is 222 ± 91.9 stems per 0.1 ha.

[b]Denotes less than 0.01%.

Table 25. Canopy Composition of the Hemlock Cover Type (N=7).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer pensylvanicum	0.3	1.5	83.3
Acer rubrum	3.4	3.8	100.0
Acer saccharum	+[b]	0.4	16.6
Amelanchier laevis	+	+	16.6
Aesculus octandra	+	0.4	16.6
Betula lenta	3.8	2.6	100.0
Carpinus caroliniana	+	+	16.6
Carya glabra	0.1	0.3	50.0
Carya tomentosa	1.3	0.5	50.0
Castanea dentata	+	+	16.6
Cercis canadensis	+	+	16.6
Clethra acuminata	0.2	1.2	33.3
Cornus florida	0.9	3.9	83.3
Fagus grandifolia	+	0.6	33.3
Fraxinus americana	0.1	0.2	50.0
Halesia carolina	1.0	13.2	50.0
Hamamelis virginiana	0.2	1.0	66.6
Ilex opaca	0.9	1.7	83.3
Kalmia latifolia	0.4	0.4	16.6
Leucothoë fontanesiana	+	0.4	33.3
Lindera benzoin	+	1.5	16.6
Liquidambar styraciflua	4.7	3.2	16.6

Table 25 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Liriodendron tulipifera	17.6	1.4	83.3
Magnolia fraseri	0.6	0.6	66.6
Nyssa sylvatica	0.1	0.1	33.3
Oxydendrum arboreum	1.5	2.1	83.3
Pinus strobus	5.8	1.2	66.6
Pinus virginiana	+	0.2	16.6
Pyrularia pubera	+	+	16.6
Quercus falcata	+	+	16.6
Quercus prinus	2.7	0.1	16.6
Quercus rubra	+	0.2	33.3
Rhododendron maximum	8.6	38.4	50.0
Tilia heterophylla	1.7	0.7	16.6
Tsuga canadensis	43.3	17.3	100.0
Ulmus americana	+	+	16.6
Vitis aestivalis	+	0.8	16.6
Vitis rotundifolia	+	0.2	16.6

[a]The mean basal area ± sd is 42.9 ± 10.31 m^2 ha^{-1} and the mean stem density ± sd is 377 ± 249.4 stems per 0.1 ha.

[b]Denotes less than 0.1%.

Table 26. Canopy Composition of the Cove Hardwood Cover Type (N=7).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer pensylvanicum	0.7	0.8	57.1
Acer rubrum	9.0	1.6	85.7
Acer saccharum	+[b]	+	14.2
Amelanchier laevis	0.6	0.4	28.6
Aesculus octandra	3.0	0.2	14.2
Betula lenta	4.3	1.3	100.0
Calycanthus floridus	+	+	14.2
Carya glabra	0.4	0.4	71.4
Carya tomentosa	+	0.2	42.8
Clethra acuminata	0.3	1.7	57.1
Cornus florida	0.6	0.6	100.0
Fagus grandifolia	5.5	0.3	42.8
Fraxinus americana	+	+	14.2
Halesia carolina	0.3	0.3	42.8
Hamamelis virginiana	0.2	0.6	71.4
Ilex opaca	0.7	0.3	42.8
Kalmia latifolia	2.6	5.4	71.4
Leucothoë fontanesiana	+	0.8	57.1
Liriodendron tulipifera	13.1	0.7	71.4
Magnolia fraseri	1.8	0.6	71.4
Nyssa sylvatica	+	+	14.2
Oxydendrum arboreum	1.8	1.0	71.4

Table 26 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Pinus strobus	8.6	0.8	71.4
Pyrularia pubera	+	0.2	14.2
Quercus alba	3.2	0.6	42.8
Quercus coccinea	0.3	0.1	14.2
Quercus prinus	0.9	0.1	42.8
Quercus rubra	1.4	+	42.8
Quercus velutina	3.3	0.1	42.8
Rhododendron maximum	15.9	68.7	100.0
Robinia pseudoacacia	0.1	0.1	14.2
Sassafras albidum	0.9	0.3	42.8
Tilia heterophylla	3.2	0.4	14.2
Tsuga canadensis	16.9	10.7	100.0
Vitis aestivalis	+	0.2	42.8

[a]The mean basal area ± sd is 37.9 ± 11.95 $m^2 ha^{-1}$ and the mean stem density ± sd is 574 ± 152.0 stems per 0.1 ha.

[b]Denotes less than 0.1%.

Table 27. Canopy Composition of the Old-Field Pine Cover Type (N=5).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer negundo	0.1	0.3	20.0
Acer pensylvanicum	+[b]	0.2	20.0
Acer rubrum	3.1	19.9	100.0
Alnus serrulata	0.1	0.9	40.0
Amelanchier laevis	+	+	40.0
Aesculus octandra	+	0.6	20.0
Betula lenta	+	0.2	20.0
Calycanthus floridus	+	0.2	20.0
Carpinus caroliniana	0.3	1.5	60.0
Carya glabra	0.4	0.2	40.0
Carya tomentosa	0.3	0.3	20.0
Catalpa speciosa	+	+	20.0
Cercis canadensis	0.1	0.7	40.0
Cornus florida	2.3	10.9	100.0
Diospyros virginiana	+	0.2	20.0
Fagus grandifolia	+	+	20.0
Fraxinus americana	+	0.2	20.0
Halesia carolina	0.3	1.1	40.0
Ilex opaca	0.3	2.5	40.0
Juniperus virginiana	+	0.2	40.0
Kalmia latifolia	+	0.2	20.0
Liquidambar styraciflua	3.3	2.3	60.0
Liriodendron tulipifera	6.5	5.9	100.0
Magnolia fraseri	+	+	20.0
Nyssa sylvatica	0.2	0.4	60.0
Oxydendrum arboreum	2.7	6.3	100.0

Table 27 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Platanus occidentalis	0.2	0.2	40.0
Pinus echinata	2.3	0.5	60.0
Pinus pungens	0.1	0.1	20.0
Pinus rigida	7.7	1.5	100.0
Pinus strobus	7.7	10.5	100.0
Pinus virginiana	50.3	12.5	100.0
Prunus serotina	1.1	1.9	80.0
Quercus alba	6.3	3.9	40.0
Quercus coccinea	0.2	+	20.0
Quercus falcata	0.9	1.3	20.0
Quercus imbricaria	1.0	1.6	20.0
Quercus rubra	+	0.2	20.0
Quercus stellata	0.5	0.9	40.0
Quercus velutina	0.3	0.3	40.0
Rhamnus caroliniana	+	0.6	20.0
Rhus copollina	0.2	1.2	40.0
Sassafras albidum	0.2	0.4	40.0
Tsuga canadensis	0.5	3.5	60.0
Vaccinium arboreum	+	0.2	20.0
Vaccinium stamineum	+	0.8	40.0
Vitis aestivalis	+	0.4	40.0
Vitis rotundifolia	+	0.6	40.0

[a]The mean basal area ± sd is 26.5 ± 8.45 m^2 ha^{-1} and the mean stem density ± sd is 413 ± 173.1 stems per 0.1 ha.

[b]Denotes less than 0.1%.

Table 28. Canopy Composition of the Successional Hardwood Cover Type (N=3).[a]

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Acer rubrum	5.2	13.0	100.0
Acer saccharum	0.1	0.8	33.0
Alnus serrulata	0.3	3.9	33.0
Amelchanier laevis	+[b]	0.3	33.0
Asimina triloba	+	1.2	33.0
Betula lenta	1.2	1.6	100.0
Betula lutea	+	0.2	33.0
Carpinus caroliniana	2.1	4.5	100.0
Carya glabra	0.5	0.9	67.0
Carya tomentosa	5.9	2.3	33.0
Cercis canadensis	0.1	0.2	67.0
Cornus florida	4.8	24.5	100.0
Fagus grandifolia	0.1	0.4	67.0
Fraxinus americana	0.1	0.6	100.0
Halesia carolina	0.1	0.4	33.0
Hamamelis virginiana	0.1	1.0	33.0
Ilex opaca	0.1	1.6	33.0
Juglans nigra	1.1	0.1	33.0
Juniperus virginiana	+	0.1	33.0
Lindera benzoin	+	0.3	33.0
Liquidambar styraciflua	16.3	4.8	100.0
Liriodendron tulipifera	29.4	5.6	100.0

Table 28 (Continued)

Species	Relative Basal Area	Relative Density	Frequency of Occurrence in Plots
Magnolia tripetala	+	0.2	33.0
Nyssa sylvatica	0.4	1.5	67.0
Ostrya virginiana	0.8	1.0	67.0
Oxydendrum arboreum	2.0	3.0	67.0
Pinus echinata	0.6	0.1	33.0
Pinus strobus	5.1	4.0	67.0
Pinus virginiana	2.1	0.4	67.0
Prunus serotina	1.2	0.5	33.0
Pyrularia pubera	+	0.2	33.0
Quercus alba	0.5	0.2	33.0
Quercus falcata	0.1	0.2	67.0
Quercus prinus	0.1	0.1	33.0
Quercus rubra	0.9	0.1	67.0
Quercus velutina	0.6	0.2	67.0
Sassafras albidum	0.7	0.4	67.0
Tilia heterophylla	0.1	0.1	33.0
Tsuga canadensis	16.3	16.2	100.0
Ulmus alata	0.1	0.3	67.0
Ulmus americana	0.4	0.1	67.0
Vitis aestivalis	0.1	1.4	67.0
Vitis rotundifolia	0.1	1.5	100.0

[a]The mean basal area ± sd is 24.2 ± 6.27 m^2 ha^{-1} and the mean stem density ± sd is 341 ± 104.5 stems per 0.1 ha.

[b]Denotes less than 0.1%.

Table 29. Scientific Names, Common Names and Codes for Species in the Text.

Scientific Name	Common Name	Code
Acer negundo	boxelder	
A. pensylvanicum	striped maple	ACRPNS
A. rubrum	red maple	ACRRBR
A. saccharum	sugar maple	
Aesculus octandra	buckeye	
Alnus serrulata	hazel alder	
Amelanchier laevis	shadbush	
Aralia spinosa	devil's walking stick	
Aristolochia durior	dutchman's pipe	
Asimina triloba	pawpaw	
Betula lenta	sweet birch	BTLLNT
B. lutea	yellow birch	
Calycanthus floridus	sweetshrub	
Carpinus caroliniana	ironwood	
Carya cordiformis	bitternut hickory	
C. glabra	pignut hickory	CRYGLB
C. ovata	shagbark hickory	
C. pallida	sand hickory	
C. tomentosa	mockernut hickory	CRYTMN
Castanea dentata	American chestnut	CSTDNT
Catalpa speciosa	catalpa	
Celtis occidentalis	hackberry	
Cercis canadensis	redbud	
Clethera acuminata	sweet pepperbush	
Cornus florida	dogwood	CRNFLR
Diospyros virginiana	persimmon	
Fagus grandifolia	beech	
Fraxinus americana	American ash	
F. pennsylvanica	green ash	
Gaylussacia baccata	black huckleberry	
G. ursina	bear huckleberry	
Halesia carolina	silverbell	HLSCRL
Hamamelis virginiana	witchhazel	
Ilex montana	mountain holly	
I. opaca	American holly	
Juglans nigra	black walnut	
Juniperus virginiana	eastern red cedar	
Kalmia latifolia	mountain laurel	KLMLTF
Leucothoe fontanesiana	doghobble	
Lindera benzoin	spicebush	
Liquidambar styraciflua	sweet gum	
Liriodendron tulipifera	yellow poplar	LRDTLP
Magnolia acuminata	cucumber tree	
M. fraseri	Fraser magnolia	
M. tripetala	umbrella tree	

Table 29 (Continued)

Scientific Name	Common Name	Code
Nyssa sylvatica	blackgum	NYSSYL
Ostrya virginiana	hophornbeam	
Oxydendrum arboreum	sourwood	OXYARB
Paulownia tomentosa	princess tree	
Pinus echinata	shortleaf pine	PNSECH
P. pungens	table mountain pine	PNSPNG
P. rigida	pitch pine	PNSRGD
P. strobus	white pine	PNSSTB
P. virginiana	Virginia pine	PNSVRG
Plantanus occidentalis	sycamore	
Prunus serotina	black cherry	
Pyrularia pubera	oilnut	
Quercus alba	white oak	QRCALB
Q. coccinea	scarlet oak	QRCCCC
Q. falcata	southern red oak	
Q. imbricaria	shingle oak	
Q. marilandica	blackjack oak	
Q. prinus	chestnut oak	QRCPRN
Q. rubra	red oak	QRCRBR
Q. stellata	post oak	
Q. velutina	black oak	QRCVLT
Rhamnus caroliniana	Carolina buckthorn	
Rhododendron calendulaceum	flame azalea	
R. maximum	rosebay rhododendron	RHDMXM
R. minus	piedmont rhododendron	
Rhus copallina	winged sumac	
R. typhina	staghorn sumac	
Robinia pseudoacacia	black locust	RBNPSD
Sassafras albidum	sassafras	SSSALB
Stewartia ovata	stewartia	
Tilia heterophylla	basswood	
Tsuga canadensis	hemlock	TSGCND
Ulmus alata	winged elm	
U. americana	American elm	
Vaccinium arboreum	sparkleberry	
V. constablaei	Constable's blueberry	
V. stamineum	deerberry	
V. vacillans	lowbush blueberry	
Vitis aestivalis	summer grape	
V. rotundifolia	muscadine	

VITA

Mark Edward Harmon was born in Waltham, Massachusetts on June 28, 1953. He attended elementary schools in Wayland, Massachusetts and was graduated from Wayland High School in June 1971. The following September he entered Amherst College and in June 1975 received a Bachelor of Arts degree with a major in Biology.

Between June and December of 1975 he worked as a technician for Gradient Modeling, Inc. in Glacier National Park, Montana. From June 1976 to October 1980 he worked as a technician at the Uplands Field Research Laboratory in the Great Smoky Mountains National Park.

After graduation Mr. Harmon will enter the Graduate School of Oregon State University and study toward a Doctor of Philosophy degree with a major in Botany.