12-1978

Composition and Structure of Replacement Forest Stands Following Southern Pine Beetle Infestations as Related to Selected Site Variables in the Great Smoky Mountains

Nathaniel White Kuykendall III
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by Nathaniel White Kuykendall III entitled "Composition and Structure of Replacement Forest Stands Following Southern Pine Beetle Infestations as Related to Selected Site Variables in the Great Smoky Mountains." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Edward R. Buckner, Major Professor

We have read this thesis and recommend its acceptance:

Clifford Amundsen, Charles Pless

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a thesis written by Nathaniel White Kuykendall III entitled "Composition and Structure of Replacement Forest Stands Following Southern Pine Beetle Infestations as Related to Selected Site Variables in the Great Smoky Mountains." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Edward R. Buckner

Edward R. Buckner, Major Professor

We have read this thesis and recommend its acceptance:

Clifford C. Amundsen

Charles D. Plass

Accepted for the Council:

L. Evans Roth

Vice Chancellor
Graduate Studies and Research

COMPOSITION AND STRUCTURE OF REPLACEMENT FOREST STANDS FOLLOWING SOUTHERN PINE BEETLE INFESTATIONS AS RELATED TO SELECTED SITE VARIABLES IN THE GREAT SMOKY MOUNTAINS

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Nathaniel White Kuykendall III

December 1978

ACKNOWLEDGMENTS

I would like to express my sincere gratitude for the guidance and encouragement offered by Dr. Edward Buckner, Department of Forestry, who served as major professor. Thanks are also extended to Dr. Clifford Amundsen, Department of Botany, and Dr. Charles Pless, Department of Agricultural Biology, for their critical reading of the document and helpful suggestions.

Grateful appreciation is extended to Dr. Ross Hinkle for his generous assistance in the analysis of data and to Mr. Don Broach of the University of Tennessee Computer Center for his consulting services.

Appreciation is extended to the Graduate Program in Ecology and the Department of Forestry for providing financial assistance and material support. Thanks also go to the staff of Great Smoky Mountains National Park and the U.S. Forest Service's Forest Pest Management Lab for providing information and research materials.

For their time and assistance in collecting field data, I wish to thank Ms. Rebecca Blowers, Mr. Thomas Burst, Ms. Mary Gall, Mr. James Gates, and Mr. Robert Menard.

Thanks are extended to Mrs. Virginia Goolsby, Ms. Wendy Smith, and Mrs. Maxine Martin for their invaluable help in the preparation of the manuscript.

To my parents, Dr. and Mrs. N. W. Kuykendall, Jr., I am especially grateful for their encouragement and support throughout my graduate education.

I would like to acknowledge a very special indebtedness to Dr. A. Randolph Shields, recently retired professor of biology at Maryville College. Through his teaching and his personal character Dr. Shields instilled in his students a deep appreciation for the science of ecology and for the natural and human history of the Great Smoky Mountains. I am particularly grateful for this introduction to the field.

ABSTRACT

Stand composition and eleven site factors were sampled in 49 stands in the Great Smoky Mountains in which the pine overstory had been killed by the southern pine beetle. Replacement community types were determined using cluster analysis of relative densities for 21 common species. Absolute densities for total stems, total pine, total oak, and eight individual species in the overstory, understory, and reproduction strata were related to selected site and vegetation variables by correlation and stepwise multiple regression.

Infestations greatly reduced the importance of pine in all replacement stands, converting most pine dominated stands to mixed pine-hardwood. Pine reproduction was minimal in all cases. All stands appeared to be in early stages of recovery, and canopy closure was very low.

Six replacement types were derived. The red maple-dogwood type occupied low elevation, lower slope, old field sites. The red maple-sourwood type occurred on mid elevation broad ridgetops and protected upper slopes. The blackgum-mixed pine type occurred on mid elevation, mid to upper slope, exposed sites. The mixed pine-scarlet oak and the Virginia pine-blacgum types occupied exposed ridgetops and upper slopes at mid to low elevations. The table mountain pine-pitch pine type occupied high elevation kills on steep, exposed, upper slope positions.

Important environmental factors influencing replacement stand composition and dynamics appeared to be elevation, incident solar radiation, topographic position, and soil nutrient availability.

Future composition of replacement types was projected based on present composition and site conditions. The red maple-dogwood type will succeed to stands dominated by mixed hardwoods and white pine. In the red maple-sourwood type, the blackgum-mixed pine type, and the Virginia pine-blackgum type, chestnut oak will eventually dominate with scarlet oak and scattered pines in the canopy. The mixed pine-scarlet oak type will succeed to stands dominated by scarlet oak with residual pines as associates. Canopy closure will remain very open in the table mountain pine-pitch pine type due to the suppression of regeneration by dense mountain laurel, and the overstory will consist of widely spaced scarlet oaks and residual pines.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

INTRODUCTION

In the past twenty-five years there have been two outbreaks of the southern pine beetle (Dendroctonus frontalis Zimm.) in the Great Smoky Mountains National Park in Tennessee and North Carolina. The first of these lasted from 1954 to the winter of 1957-1958, and the second more extensive outbreak began in the fall of 1967 and continued at varying intensity through the winter of 1976-1977. Patches of dead pines from the last epidemic can be seen throughout the western half of the Smokies evincing the intensity of the outbreak. At its height in the late 60's and early 70's the U.S. Forest Service reported the brood densities in the Smokies were among the highest on record for the south (Ward et al., 1971b).

National Park Service policy for dealing with pine beetle outbreaks in the Smokies has varied. Between 1954 and 1955, 13,295 trees were cut and treated at a total cost of over $28,000 in an effort to control the epidemic (National Park Service, 1955a; 1955b). During the last outbreak, however, no control methods were initiated, and the infestations were allowed to run their course. This passive management policy is in keeping with the long-term goal of reinstating natural processes with minimal human interference on National Park lands.

Although the National Park Service currently accepts periodic outbreaks of the southern pine beetle (Wiggens, 1969), the impact of infestations on the vegetation of the Smokies has not been investigated.

Disturbance to forest stands by pine beetles is discriminating and concentrated. Because of the aggregate attack behavior of the beetle, individual infestations are highly localized, killing from one to several hundred trees in easily defined clusters. Within a cluster, or "hot spot," the beetles kill primarily yellow pines (i.e., in the study area pitch, table mountain, Virginia, and shortleaf pines) and occasionally white pine while leaving associated species undamaged and soil litter in place. Such infestations are intensive, often completely eliminating pine from the canopy.

Factors determining the occurrence of southern pine beetle infestations are complicated. Diversity in soils, elevation, topography, land-use patterns, and disturbance to the forest, both natural and artificial, have created a complex distribution of yellow pines in the southern Appalachian region. Many of these same variables interact with southern pine beetle populations to influence the severity and duration of the attack.

In order to evaluate the effects of the southern pine beetle in the Smokies, the objectives of this study were (1) to characterize the present composition and seral position of replacement stands following beetle-kills in the Smokies, (2) to describe selected site variables and to relate these to vegetation, and (3) to project potential forest cover on beetle-killed sites in the absence of further disturbance.

CHAPTER II

THE STUDY AREA

A. PHYSICAL FEATURES

The Great Smoky Mountains are a segment of the Unaka Mountains, a major unit of the Blue Ridge Province (Fenneman, 1938). The 114 km (71 mile) range borders eastern Tennessee and western North Carolina and is encompassed in the Great Smoky Mountains National Park. Maximum topographic relief is 1768 meters (5802 feet) ranging from 256 meters (840 feet) to 2024 meters (6642 feet).

The sampling sites for this study were located in the northwestern quarter of Great Smoky Mountain National Park in Blount and Sevier County, Tennessee (Figure 1). Plots were in former pine stands killed by southern pine beetles and were on outlier ridges and ravines away from the central crest of the Smokies.

Within the sample, maximum topographic relief was 942 meters (3090 feet) and ranged from 338 to 1280 meters (1110-4200 feet) with a mean elevation of 713 meters (2339 feet). The majority of beetle kills encountered were on upper ridge and ridgetop positions, although the few kills found at lower slope and draw sites were also included in the sample. Slope angle varied from level ridgetop to over 60% slope. Aspects were wide ranging, but were primarily southwest to southeast.

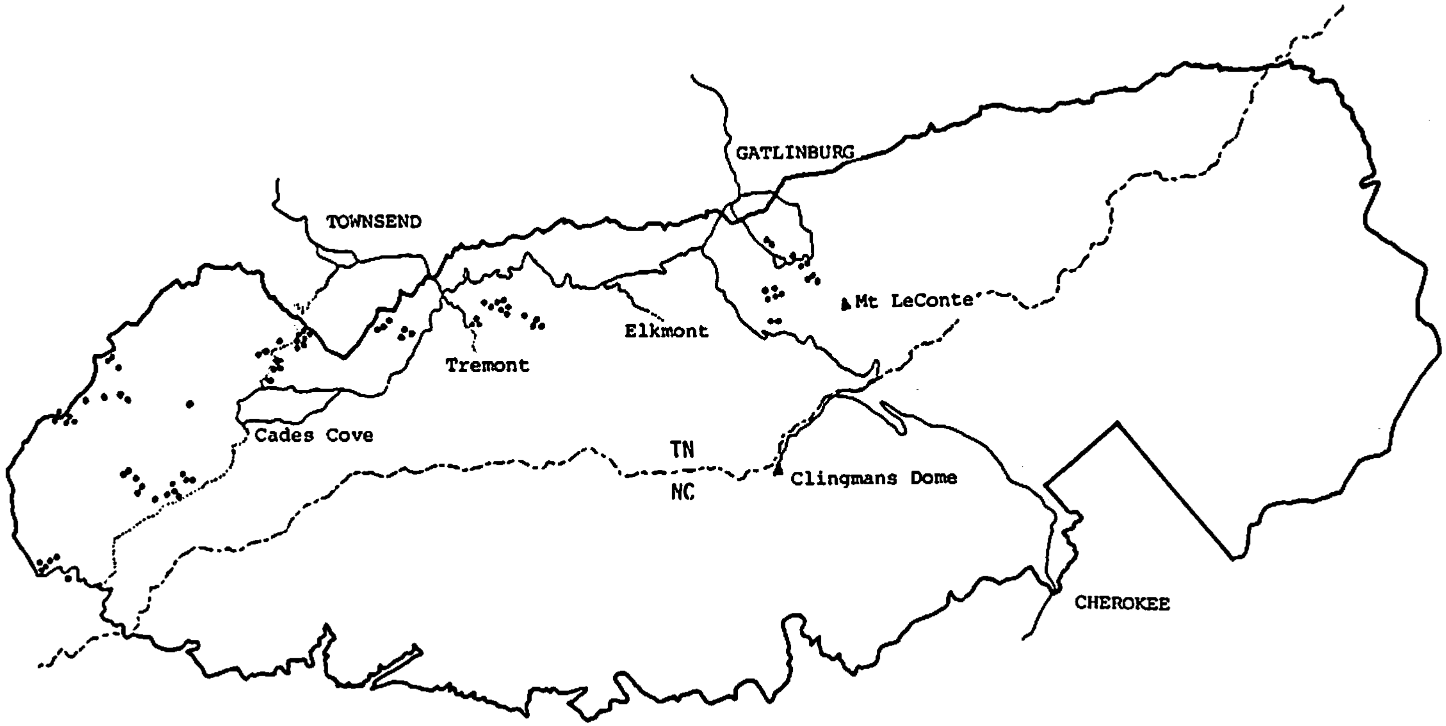

Figure 1. Locations of sample plots in the Great Smoky Mountains National Park.

B. SUBSTRATE

The geology of the Great Smoky Mountains is ancient and complex. Rocks are predominantly Precambrian and have been greatly affected by folding, faulting, metamorphorism, and weathering (King et al., 1968).

Geologic substrates for all sampled sites were later Precambrian sedimentary rocks of the Ocoee Series. Most low elevation plots were overlain by the Wilhite Formation of the Walden Creek Group. Rocks in this formation are mostly siltstone with some conglomerate and quartzite and with occasional limestone and dolomite lenses (King et al., 1968).

Sampled sites at higher elevations were on Elkmont and Thunderhead Sandstones of the Great Smoky Group. Both sandstones are somber grey, and are principally composed of quartz and potassic feldspar grains (King et al., 1968).

The majority of mid elevation sites were on Cades Sandstone, an unassigned formation of the Ocoee Series. Rocks are thick-bedded, light-colored feldspathic sandstones with occasional agrillaceous interbedding. Other mid elevation sites were underlain by the Snowbird Group consisting of the Roaring Fork Sandstone and the Metcalf Phyllite formations. Roaring Fork Sandstone is feldspathic quartzite interbedded with phyllitic agrillaceous and silty rocks. Metcalf Phyllite rocks are similar but show less sedimentary structures (King et al., 1968).

Soils in the Smokies have been generally mapped, but detailed information is limited. Below 305 meters (1000 feet) in elevation Hapludults of the Ultisol order are common on exposed sites, and Inceptisols, mainly Dystrocrepts, are prevalent at higher elevations

(Springer et al., 1975; M. Springer, Personal Communication). Golden (1974) found Typic or Lithic Dystrocrepts under his high elevation pine types in the central Smokies.

Deep soils are common in coves and on protected sites while soils are generally thin on steep slopes and exposed sites. For this study soil depths were defined as follows: deep > 2 meters, moderate < 2 meters > 85 cm, and thin < 85 cm.

The U.S. Soil Conservation Service survey maps for Blount and Sevier counties include all of the sampled areas in the Ramsey soil series (Elder, 1959; Hubbard, 1956). Ramsey soils are generally described as thin, poorly developed, strongly acid, and low in fertility. They are derived from sandstones, quartzites, shales, slates, and conglomerates and are residual lithosols commonly on steep to very steep slopes (Elder, 1959).

Within the Ramsey series, survey maps showed the sample plots to be on four soil types. Seventy-six percent of the plots were on Ramsey slaty silt loam steep or very steep phases. All plots within this map unit were at low to mid elevations. Ramsey slaty silt loam has a rapid percolation rate and low water-holding capacity, and it is moderately fertile and of medium acidity (Elder, 1959).

Plots above 915 meters (3000 feet) in elevation (15% of the total sample) were within the general map unit named Rough-mountainous land (Ramsey soil material). This is a miscellaneous land type and is characteristically very steep and extremely stony. Over most of the map unit 20 to 70% of the land surface is estimated to be outcrops or boulders

with Ramsey soil material in the intervening spaces. Other soil characteristics can vary considerably within this unit depending on topography, elevation, and vegetation (Hubbard, 1956).

Four plots (5% of the total sample) were mapped as steep phase Ramsey stony fine sandy loam. This soil is medium to strongly acid, moderately low in plant nutrients, excessively drained, and low in water-holding capacity. Three plots (4% of the total sample) were on the very steep phase of the Ramsey shaley silt loam soil. This soil is thin, excessively drained, low in water-holding capacity, and low in fertility (Hubbard, 1956).

Limited soil data collected at sampling sites suggested that the soils were generally xeric and infertile. Fifty-nine percent of the plots had soils less than 85 cm deep. A horizons averaged 2.6 kg/hectare phosphorus and 108.4 kg/hectare potassium, and pH ranged from 4.2 to 5.2. Organic horizons were mostly thin (1-5 cm) at low and middle elevations and fit McGinnis' (1958) thin duff mull type. At high elevations O horizons were much thicker (8-12 cm) and were a crusted mor (Shanks, 1954b).

C. CLIMATE

Due to elevational and topographic diversity the climate and microclimates of the Great Smoky Mountains are quite variable. Shanks (1954a) used Thornthwaite's (1948) classification system to describe climatic conditions measured at four stations at different elevations in the central Smokies. The resulting classes were humid mesothermal at

445 m (1460 ft), perhumid mesothermal at 1158 m (3800 ft) and at 1524 m (5000 ft), and climatic conditions at the 1920 m (6300 ft) station were more humid than Thornthwaite's perhumid microthermal class.

Mean maximum temperatures in the Smokies occur in June, July, and August, and mean minimums come in December and January. Mean annual temperature at Gatlinburg, Tennessee (elevation = 443 m, 1454 ft) is 13.7° Celsius (56.7°F) with a mean maximum of 21.4°C (70.5°F) and mean minimum of 63.6°C (43.3°F) (U.S. Dept. of Commerce, 1969).

Shanks (1954a) found that temperatures decreased with increased elevation at an average rate of 2.23° Fahrenheit per 1000 feet, or 1.24° Celsius per 305 m. During the growing season, this causes a 5.5° to 8.3° Celsius (10°-15°F) difference in temperatures between the base of the mountains and the highest peaks.

Precipitation maxima occur in March and in July and August, and minima occur in May and in September and October (U.S. Dept. of Commerce, 1973). September is the only month when potential evapotranspiration values at low elevations exceed precipitations (Shanks, 1954a). Elevation affects precipitation as well as temperature. Thirty-year records show that Gatlinburg averaged 141.1 cm (55.54 inches) per year while precipitation at Clingmans Dome averaged 208.9 cm (82.26 inches), an increase of 48% over a 1581 m (5188 ft) rise in elevation (Tennessee Valley Authority, 1968).

Although the climate of the Smokies is generally temperate and humid, microclimatic conditions on the majority of the sites sampled were probably much warmer and less humid than the norm due to topographic

exposure and a comcomitant increase in potential evapotranspiration. Annual potential solar beam irradiation at sample sites was roughly estimated based on azimuth and percent slope measurements (Frank and Lee, 1966). The average estimate was 290.21×10^3 Langleys per year and estimates were as high as 316.9×10^3 Langleys per year as compared with 265.8×10^3 Langleys per year for level surfaces and lower values for northeast trending slopes. Beetle kills at upper slope and ridgetop positions were also more exposed to desiccating winds, further increasing potential evapotranspiration. Such conditions in combination with universally low soil water-holding capacity made most sampled sites very xeric. In a study of pine site characteristics on the Blue Ridge Escarpment, an area of high annual precipitation much like the Smokies, Racine (1966) found ridge sites subject to regular microclimatic drought, and this was probably the case on many sites in this investigation also.

D. VEGETATION

The flora of the Great Smokies is remarkably rich and diverse. Herbarium collections from the area total approximately 1450 species of vascular plants representing 126 families and 531 genera (Hoffman, 1966). Of these 131 are tree species. Nonvascular forms total at least 2567 species (Hesler, 1962; King and Stupka, 1950).

Like the flora, complex vegetation patterns have evolved in the Smokies due to the mountains' ancient geologic stability and elevational, topographic, and microclimatic variety. Several authors have advanced different community type divisions to describe the vegetation (Cain,

1931; Miller, 1938; Shanks, 1954b; Whittaker, 1956; Golden, 1974). An excellent overview is provided by Shanks (1954b) who delineated six forest types: (1) cove hardwood forests which occupy coves and sheltered slopes below 1372 meters (4500 feet), (2) hemlock forests occurring both on sheltered sites along streams below 914 meters (3000 feet) and on exposed slopes and narrow ridges between 914 and 1372 meters (3000-4500 feet); (3) northern hardwood forests, deciduous forests within the spruce-fir altitudinal zone above 1372 meters; (4) spruce-fir forests which are boreal evergreen stands above 1372 meters; (5) closed oak forests occupying intermediate to dry slopes below 1372 meters; and (6) open oak and pine stands on dry ridges and exposed slopes below 1372 meters.

Prior to infestation the beetle killed stands sampled averaged over 80% pine. The original stands would have been included in Shanks (1954b) open oak and pine type, or, more specifically, in Whittaker's (1956) Virginia pine, pitch pine health, and table mountain heath types.

E. HUMAN INFLUENCES

Man has probably been a member of the ecosystems of the Great Smoky Mountains since the Pleistocene (Coe, 1974; Quentin Bass, Personal Communication). Even though human influence in the environment has varied from prehistoric times to the present, man has probably made significant modifications of the vegetation throughout his occupation.

Recent archeological surveys of the Great Smokies area have found evidence of aboriginal occupation dating to the Paleo-Indian period, and

artifacts from the Archaic, Woodland, Mississippian, and post-European contact periods were collected throughout the Great Smoky Mountains National Park (Bass et al., 1975). Archeological data suggest aboriginal use of the landscape became less extensive and more intensive as sedentary cultures developed around horticulture and agriculture during the Late Archaic and the Late Woodland and Mississippian periods. The greatest impact of prehistoric people on vegetation was probably from their use of fire for facilitating mast collecting, encouraging berry production, and for driving game while hunting (Kozlowski and Ahlgren, 1974; Quentin Bass, Personal Communication).

European settlement of the Smokies began in earnest in the early nineteenth century, and by the Civil War all prime agricultural land had been occupied by whites (Albright, 1974). As the population expanded, settlers were relegated to subsistence farming on steep valley slopes resulting in heavy localized soil erosion and necessitating periodic abandonment and re-clearing of small patches of forest (Kephart, 1922). Fires were regularly set on south facing slopes to encourage blueberries and to improve grazing for free ranging livestock (Shields, 1977; Lindsay, 1976).

About 1800 small-scale commercial lumbering began in the Smokies. Harvesting was selective and environmental impacts were limited. However, in the early 1900's large-scale, mechanized logging operations were moved into the mountains, and commercial clearcutting continued until 1938. Little discrimination was used in selecting timber, and harvesting methods often caused massive soil erosion and severe fires (McCracken,

1978). By 1940 only 200,000 acres of pristine forests, about 40% of the Great Smoky Mountains Park, remained (National Park Service, 1976).

Since the logging days human impacts on the environment have resulted more from protection rather than utilization. The Great Smoky Mountains National Park was established by Congress in 1934 (Campbell, 1960), and since that time the principal management goal of the National Park Service has been to return most of the area to its pre-European settlement state. With the exception of small developed areas, roads, and three historic districts, natural succession has been allowed to proceed, and active management of forest communities has been largely limited to fire suppression. Until recently, all fires have been extinguished as soon as possible, and 40 years of effective fire suppression has significantly affected vegetation. Currently, however, the role of fire is being investigated by the National Park Service in order to review fire management policies.

Another important European-cultural influence in the Smokies has been the introduction of exotic plants and animals. The most far-reaching impacts have been the elimination of mature chestnut trees by an exotic parasitic fungus (Woods and Shanks, 1959) and the decline and potential elimination of Fraser fir by the balsam-woolly aphid, an insect pest (Hay et al., 1976).

CHAPTER III

SELECTED LITERATURE

A. SOUTHERN PINE BEETLE OUTBREAK AND ATTACK CHARACTERISTICS

The southern pine bark beetle is native to the southeastern U.S. and is the most destructive forest insect in eastern America (Baker, 1972). Pine beetles attack all five pine species native to the study area although white pine is seldom infested. Death of infested trees is due to disruption of the cambial vascular system usually caused by a combination of mechanical injury from beetle gallery construction and from the introduction of the blue stain fungus Ceratocystis Minor (Dixon and Osgood, 1961).

Epidemic populations of the southern pine beetle occur periodically, and appear to be controlled most efficiently by climatic conditions. In North and South Carolina outbreaks have been linked to late summer and early fall rain deficiencies (Craighead, 1925; King, 1972). In the same area Beal (1933) reported that outbreaks occurred during a succession of mild winters and were terminated when winter temperatures dropped to 10°F or less for several days.

Outbreaks of the southern pine beetle, as with other species of Dendroctonus, characteristically display mass attacks on individuals or small groups of pines. This aggregate behavior results in hot spots, or spot infestations, which serve as epicenters for the spread of epidemic populations.

There is a definite pattern to the rise and eventual collapse of mass attacks. The sequence begins when newly emerged, unmated female beetles are attracted to the host tree by volatile terpenes emitted from the tree itself. Trees under water stress or injured trees may emit more of these attractants than vigorous trees and are more likely to be selected as hosts (Hodges and Pickard, 1971). However, without such strong host attractants and when beetle populations are at endemic levels, selection is more or less random (Gara, 1967).

Once the female has landed and begins boring into the bark, she releases the pheromone frontalin (3,5-dimethyl-6, 8-dioxabicyclo (3.2.1) octane) which in combination with the host terpene, alpha-pinene, triggers the mass attack. Though this aggregate pheromone is intraspecific, the sex ratio of arrested beetles is three males to every female. The sex ratio is soon balanced by the accumulation of the pheromone verbenone released by the males. Verbenone inhibits male beetle response to frontalin, but in low concentrations it does not inhibit female response (Renwick and Vite, 1970).

The mass attack is eventually halted when the host tree succumbs to the beetles. A healthy pine mechanically inhibits the boring activity of pine beetles by exuding resins into the inner bark. Ironically the resins are also the source of the alpha-pinene attractant. If the pine finally succumbs to the attack, resinosis ceases and the alpha-pinene component of the aggregate pheromone is no longer available. Simultaneously, frontalin production also decreases as the females engaged in gallery tunnelling. As a result the relative concentration of verbenone

from male beetles increases to the point of inhibiting further attraction of both sexes to the host and the infestation collapses (Renwick and Vite, 1970).

B. INFESTATIONS AND STAND CONDITIONS

Stand vigor is closely related to susceptibility to beetle attack. Severely stressed trees not only appear to attrack bark beetles but also are unable to resist attack by sustaining resinosis (Lorio and Hodges, 1977). On exposed, xeric sites, moisture-stress may occur regularly (Racine, 1966), but stress is intensified during periods of deficient rainfall which favor epidemic beetle populations. On less xeric sites overstocked, slow growing stands are often infested (Bennett, 1968). Trees injured from lightning or fire have been reported to act as attractants to beetles (Hodges and Pickard, 1971; Craighead and St. George, 1928).

In the Southern Appalachians pure pine stands appear to be more susceptible to infestations than mixed pine-hardwood stands (Hoffman and Anderson, 1945; Osgood, 1958), and two studies in the past have shown that infestations greatly reduce the importance of pine in such stands. Balch (1928) studied beetle kills in western North Carolina and projected future composition from advance regeneration. According to his prediction, beetle-kills would show a bimodal age distribution with an upper stratum of scattered pine and oak and a lower stratum containing 30% pine, 12% "desirable" hardwoods, and 58% "undesirable" hardwoods.

More detail is available from a study by Hoffman and Anderson (1945) of beetle kills at the U.S. Forest Service Bent Creek Experimental Forest near Asheville, North Carolina. Most of the sites in this study were low elevation old fields dominated by shortleaf and pitch pines. Only 3% of the infestations were larger than one acre; 59% were small kills averaging less than a tenth acre.

The beetles showed a definite preference for large trees. Seventy-five percent of the pines greater than 6 inches dbh were killed, but only 57% of the 4 inch size class and 19% of the 2 inch size class were killed (Hoffman and Anderson, 1945).

Canopy openings were found to favor hardwoods rather than pines. Pine basal area dropped from over 90% prior to the kill to 50% immediately afterward. Twenty years after the infestation pine regeneration was negligible, and only scattered residual pines remained in the canopy. Hardwoods replacing the pines were mostly "minor" and "less desirable" species including red maple, scarlet oak, post oak, black locust, blackgum, dogwood, sourwood, and others (Hoffman and Anderson, 1945).

Barden (1974) found that beetle infestations after lightning-caused surface fires in the Great Smoky Mountains reduced pine relative basal area from about 70% to 20-30%. Beetles killed approximately 80% of the original pine basal area and caused a more drastic change in stand composition than the earlier fire. Very little pine reproduction was found.

C. SOUTHERN PINE BEETLE EPIDEMICS IN THE SMOKIES

Specific reports of past outbreaks of the southern pine beetle in the Great Smoky Mountains are available only for the last 25 years, although periodic epidemics of this native species surely occurred earlier. The earliest record of an outbreak in the South was in 1842 (MacAndrews, 1926), and the first report of a beetle epidemic in the Southern Appalachians was in the 1890's (Hopkins, 1899) in West Virginia. An epidemic from 1913 to 1916 affected an estimated 200 square miles in Tennessee and Virginia (Thatcher, 1960).

The earliest available written document concerning southern pine beetle outbreak in the Great Smoky Mountains described the extent of the beetle damage and control measures for 1954 and 1955 (NPS, 1955a). According to the report, infestations were active throughout 1954 in the Smokemont, Deep Creek, Cataloochee, Cades Cove, and Big Creek sub-districts. In the 1954 calendar year 7318 trees were cut and treated at a total cost of $9,704.21.

A survey conducted in January of 1955 found a total of 25,350 trees infested in 219 separate infestations. In April of that year brood densities were reduced by a severe freeze. However, the population quickly rebounded and by September infestations were active at Eagle Creek, Abrams Creek, Sugarlands, Oconaluftee, Deep Creek, and scattered locations in the southwest section of the park. In 1955 $18,600 was allotted for sanitation operations, and by September of that year a 7-man crew had cut 5384 trees at a total cost of $13,205 (NPS, 1955a). By

November an additional 3746 trees were treated and an estimated 929 trees remained to be cut (National Park Service, 1955b).

In 1956 a memorandum from the assistant chief ranger listed infested tree estimates for the park based on known infestations and an aerial survey flown May 10 of that year. According to the memorandum Tremont district had 200 infested trees, Cades Cove 310, Abrams Creek 525, Twenty-mile 50, Hazel Creek 305, and Collins Creek 150. The estimated cost for control was $2,767.35 (Light, 1956).

No reports were available for 1957. A letter to park superintendent Hummel from E. J. Kowal, Chief of the Division of Forest Insect Research for the U.S. Forest Service Southeastern Forest Experiment Station, dated April 24, 1958, recommended curtailment of control operations in the Smokies based on a survey of brood trees in the Greenbriar area and other surveys in the Southern Appalachians. Kowal predicted that the epidemic had collapsed citing a general decrease in intensity since 1955, above normal rainfall in 1957, extremely low temperatures during the winter of 1957-1958 causing 90 to 100% brood mortality (exclusive of eggs), high survivalship of clerid beetles and other bark beetle predators, and other reasons. He cautioned against total abandonment of control efforts in case the population rebounded writing:

> We were a little fearful about applying our recommendation to the Greenbrier or other sections of the Park where there were very many infested trees. However, we are still convinced that natural mortality will likewise exert a strong effect in these areas. . . (Kowal, 1958).

Apparently Kowal's assessment was correct. A letter dated January 28, 1959, from Acting Superintendent Johnson to the Regional

Director reported aerial and ground surveys in the park found "virtually no insect activity." A letter the next month from the new Park Superintendent, Fred Overly, to the Regional Office confirmed the release of $1,260.00 originally allotted to beetle control, and reported that a build-up of beetle populations after the winter of 1957-1958 did not materialize (Overly, 1959).

Between 1959 and 1967 the only report found concerning southern pine beetle status in the Smokies was a reference in a 1965 general aerial survey of the park which found only scattered red-topped and fading pines indicating endemic beetle populations (Ciesla, 1965).

In the summer of 1967 infestations characteristic of epidemic beetle populations were reported in the Tusquitee Ranger District of Nantahala National Forest which adjoins the park in North Carolina. This was the first evidence of outbreak in the Southern Appalachians since the winter of 1959-1960. By late summer hot spots appeared in the Cades Cove district of the Smokies.

In December of 1967 the first of what was to become a series of aerial and ground surveys was initiated by the USFS Division of Forest Pest Management in cooperation with the National Park Service. The first sketch map flight estimated that 129 individual infestations containing 4279 fading or red-topped trees were active in the Cades Cove area. This averaged 8.4 trees per thousand acres of host type. Ground surveys showed a mean brood density of 493 live insects per square foot of infested bark, and the ratio of adult beetles to brood was 1:12.3, indicating a rapidly growing population. The U.S. Forest Service,

however, recommended no control action be initiated due to the remoteness of the kills and the high cost of control (Clerke et al., 1968a). Another aerial survey was flown in February, 1968, using infrared photography. It confirmed the outbreak status of the beetle in Cades Cove estimating 7.10 ± 2.50 spots with 38.59 ± 24.77 infested trees per thousand acres of host type (Clerke et al., 1968b).

An aerial photo survey flown in late August, 1968, indicated that infestations had enlarged and spread. There were an estimated 24.6 ± 7.2 spots with 495.4 ± 226.9 discolored trees per thousand acres of host type. Infestations were still limited to the Cades Cove district and were found between 457 and 762 meters (1500-2500 feet) in elevation. Sample bolts from infested trees were x-rayed and brood densities averaged lower than the previous year (Clerke et al., 1968c).

The infestation expanded from Cades Cove to the Fontana Lake area of the park and to adjoining National Forest land during the late summer and fall of 1968. The low temperatures during the winter of 1968-1969 caused high brood mortality, but surveys in April, 1969, still showed 18.0 ± 3.7 active spots with 387.6 ± 179.0 discolored trees per thousand acres of host type (Clerke and Bassett, 1969). Surveys in September indicated that even though the outbreak was expanding, the rate of expansion was slowing down. At that time the infestation level was 12 ± 5 spots with 385 ± 278 red and fading trees per thousand acres of host type. Brood densities were low and predators and parasites were numerous. No control operations were recommended (Ward et al., 1969).

In January of 1970 temperatures in the park dropped below 0° Fahrenheit for three consecutive days causing 99 to 100% brood mortality (Flavel et al., 1970). A subsequent aerial and ground survey indicated an infestation level of 16 ± 1 spots containing 247 ± 383 discolored trees per thousand acres host type. However, most of these trees were believed to have been infested prior to the cold snap, and it appeared that the outbreak had collapsed (Ward and McDowell, 1970).

In spite of the winter mortality, beetle populations resurged during the summer months of 1970. Surveys in the fall and winter of 1970 revealed that Cades Cove was free of infestations, but beetle populations were fairly heavy in the Fontana area. Brood levels were 227 insects per square foot of infested bark and there were an estimated 28 spots containing 2686 infested trees in the park with 31% of the trees supporting active broods (Barry and Wilson, 1971).

Winter brood mortality was again heavy during early 1971, and an April survey found beetle activity to be at low levels. There were an estimated 74 spots containing 716 infested trees with 18% of the trees supporting active broods within the park. The infestation continued in the Fontana area and had spread to Fighting Creek Gap near Park Headquarters (Barry et al., 1971).

The final aerial survey was conducted in September of 1971. Beetle populations had declined significantly in the Fontana area averaging 10 spots and 43.3 discolored trees per thousand areas of host type. Beetle activity in the Fighting Creek Gap area, however, was very intense. Brood densities averaged 575 insects per square foot of bark, one of the

highest densities on record for the South. There was an estimated 33 ± 11 spots containing 293 ± 166 discolored trees per thousand acres of host type. Because of the high potential for expansion and accessibility of the Fighting Creek Gap infestations the Forest Service recommended sanitation or salvage cuttings (Ward et al., 1971). Control measures were not conducted however.

Although detailed information is unavailable, it appeared that the outbreak spread from Fighting Creek Gap to the Cherokee Orchard, Roaring Fork, and Bullhead areas in the following years. By 1975 the general outbreak had declined significantly and high brood densities that may have remained would not have survived the extreme winter temperatures of 1976-1977 (C. Pless, Personal Communication).

CHAPTER IV

FIELD METHODS

Prior to field reconnaissance, potential locations for beetle-killed stands were determined from interviews with local residents and National Park Service personnel; from a National Park Service map of the 1958 sanitation operations; and from two aerial surveys, (1) a sketch map flown in December, 1967 (Clerke et al., 1968a) and (2) a roll of 9 × 9 infrared imagery flown in August, 1968 (Clerke et al., 1968c). Both aerial surveys were donated by the U.S. Forest Service Division of Forest Pest Management in Asheville, North Carolina. These were the only available aerial surveys for bark beetles in the Cades Cove section of Great Smoky Mountains National Park. Although this information was helpful, the majority of beetle kills sampled were located by ground reconnaissance.

A total of eighty-one plots was established in forty-nine individual infestations. Criteria for selecting sampling sites were: (1) that stands had formerly been infested by the southern pine beetle (this was verified by the beetles' distinctive gallery patterns and adult emergent holes in bark remnants), and (2) that the beetle kill area be at least one-fifth acre in size and shaped to accommodate a tenth acre circular plot. Plots were placed within beetle kills in such a way as to avoid edge effects and, on large kills, to represent varying topographic features. Overall, sampling sites were selected to give a wide spectrum of topographic exposures and elevations.

Once the plot center had been determined, the center tree was flagged, and an aluminum tag designating the plot number and date was attached. A .04 hectare (.10 acre) circular plot was then established by flagging six or more points along the circumference. The radii were adjusted for slope as described by Bryan (1956). A .004 hectare (.01 acre) concentric plot was also flagged, and four one-meter square plots were lined out along the outside of the .004 hectare plot up, down, and across the slope.

Within the .04 hectare plot, live trees greater than 10 cm were tallied in 5 cm size classes, and live stems between 3 cm and 10 cm were recorded as saplings. Beetle killed trees on many sites were in advanced states of decay and were often wind-thrown and broken making recognition of individual boles very difficult. Where recognition was possible, dead trees were tallied as a group by size classes. Originally, dead trees were to be used for an index for each plot of the severity of stand disturbance, but dead stem measurements were practical only in 60 plots (74% of the sample). Percent cover for shrubs over a meter tall and less than a meter tall were estimated on the .04 hectare plot.

Within the .004 hectare plots, trees over one meter tall and less than 3 cm dbh were recorded as subsaplings. Reproduction (tree stems under one meter tall) was tallied and herbaceous cover was estimated in the four one-meter square plots.

Location and elevation of plots were determined from U.S. Geological Survey 7.5 minute topographic maps. Slope position was also derived from maps and recorded as an index based on the distance to slope base.

divided by the total distance from slope base to ridgetop. Aspect was taken with a Silva Ranger compass. Slope was measured with an Abney Level from the upper circumference and the lower circumference to plot center,and the two readings were averaged. Annual potential solar beam irradiation, hereafter referred to as solar radiation, was roughly estimated using tables developed by Frank and Lee (1966) based on azimuth and percent slope measurements. Since solar radiation was not measured directly and this transformation was an estimate obtained from other measured site variables, the values derived are subject to question, especially on flat ridgetops and sheltered foot slopes. However, where direct measurements were not feasible, this transformation provided satisfactory estimates of incident solar radiation (Smith, 1977; Wade, 1977).

Depth to bedrock was measured to 85 cm with a soil auger. If rock was encountered at less than 85 cm,two additional probes were made, and the measurements were averaged. The O horizon soil depth was measured and A horizon soil samples were collected at three points in the plot. Soil samples were later analyzed by U.T. Agriculture Extension Service Soil Testing Lab in Nashville for soil water pH, phosphorus, and potassium availability.

Increment cores were taken from 3 living trees per plot in an attempt to date the year of infestation by the release reflected in annual ring width. Very few trees, however, showed an obvious response to the infestation, preventing accurate dating of kills. Woods and Shanks (1959) reported the same problem in attempting to use pitch pine for dating release after the chestnut blight.

CHAPTER V

RESULTS AND DISCUSSION

A. REPLACEMENT TYPES

Introduction

The majority of stands sampled had been attacked by pine beetles four to eight years earlier, and in each case disruption of the original canopy had been severe. Canopy closure at the time of sampling averaged less than 30%. The general appearance of individual stands varied depending on site, preinfestation composition, and intensity of the attack. Because of the irregular structure of the residual canopy and sapling strata, dominance and relative importance of species, as well as trends in replacement stand types, were not initially obvious.

Methods

Two computer programs were used to statistically describe vegetation on individual plots and to group similar plots for determining replacement types. Raw data for stems over 3 cm dbh were transferred to punch cards and processed on the University of Tennessee IBM 360/65 computer using a Fortran program, for this study named INFEST, originally developed by Mrs. Virginia Patterson (Golden, 1974). The program calculated relative and absolute density, basal area, and importance value for each species on each plot.

Relative density values of stems over 3 cm dbh for 21 species with frequencies over 5% were then used in cluster analysis to determine

replacement community types. A polythetic agglomerative cluster technique developed by Orloci (1967) was used. This technique was one of two clustering systems recommended for vegetation analysis by McCarthy (1976) in his comparison of vegetation classification methods. Clustering was run on the IBM 360/65 computer using a program written by Post and Shepard (1974).

A simplified dendrogram produced by cluster analysis is shown in Figure 2. The base line in the figure represents the array of all 81 plots analyzed. Vertical branches of the dendrogram connect the center points of individual clusters. The vertical axis indicates the within-group sum of squares expressed as a percentage of the total sum of squares, but it may be more easily conceptualized as the percentage of information lost due to progressive clustering of the total information contained in individual plots.

Although cluster analysis provided an objective and quantitative method for arraying groups of plots, the selection of community types from the array was ultimately subjective. Six replacement types, clustered at the 50% information level, were selected. Criteria for selection of the types were that they be recognizable in the field and that the types make sense in terms of stand history and environmental processes. Accordingly, the six replacement communities identified were: (1) red maple-dogwood, (2) red maple-sourwood, (3) blackgum-mixed pine, (4) Virginia pine-blackgum, (5) mixed pine-scarlet oak, and (6) table mountain pine-pitch pine. As replacement types, these are strictly seral communities and should not be interpreted as stable or climax vegetation

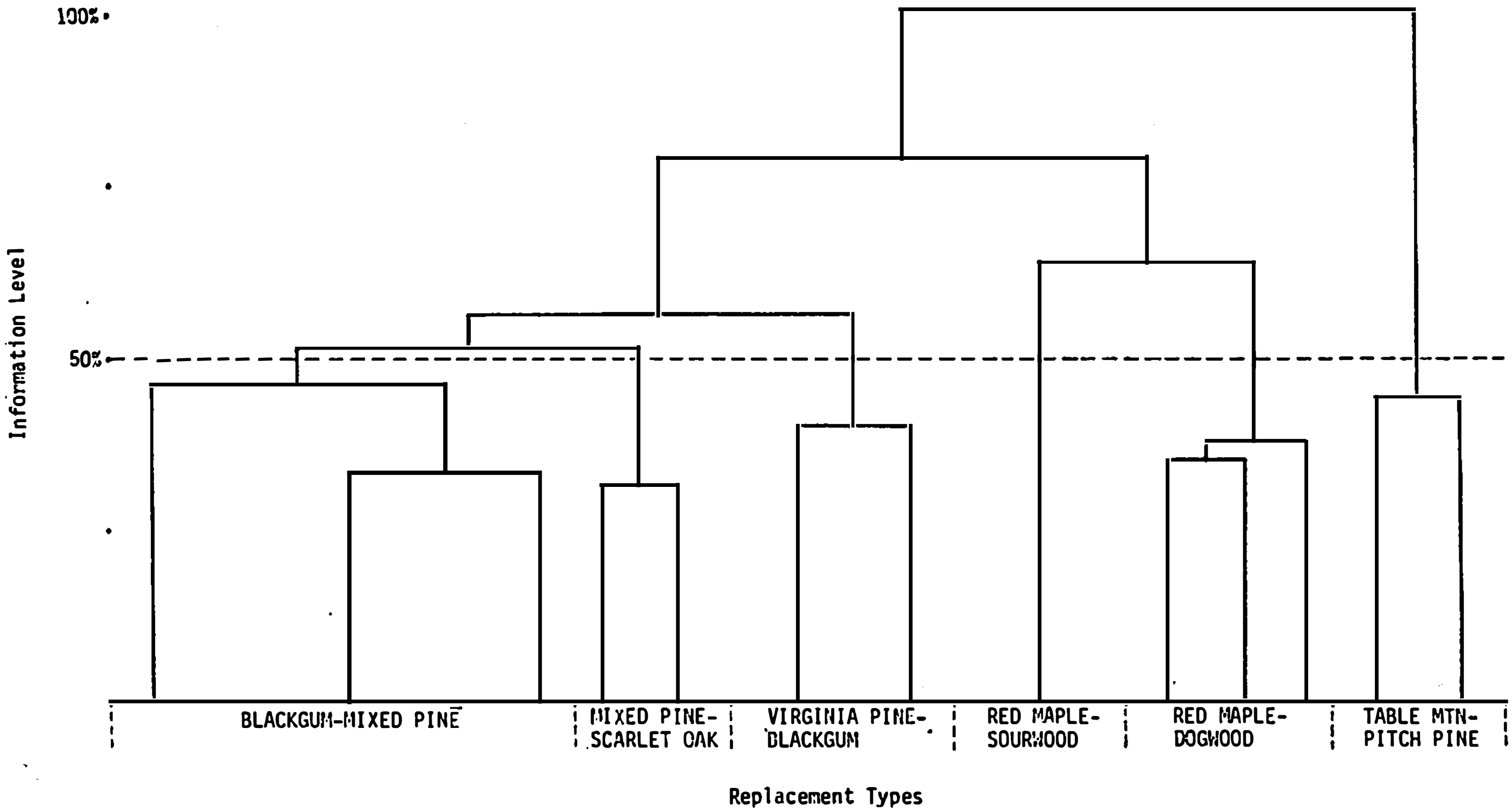

Figure 2. Cluster analysis of overstory relative densities for 81 plots.

types. Structural and compositional change is anticipated in all stands sampled.

After these types had been selected, a disk file containing site and cover variables for plots within each type was created on the DEC System-10 computer. Descriptive statistics for these variables were then calculated using the STATPACK statistical package program (Houchard, 1974).

Descriptions of each replacement type are given below, generally in order of decreasing moisture availability from mesic to xeric sites. Several phrases have specific meanings in the descriptions and require definition. "Original canopy" refers to the overstory coverage prior to the southern pine beetle attack, and it is assumed to have been composed of all stems, living and dead, greater than 10 cm dbh at the time of sampling. Correspondingly, "residual canopy" refers to living remnants of the original canopy, here defined as all living stems greater than 10 cm dbh. The residual canopy combined with the sapling stratum (stems greater than 3 cm and less than 10 cm) form a discontinuous cover designated the "replacement canopy," or simply "overstory," "Understory" refers to stems less than 10 cm dbh and over 1 meter tall, and "reproduction" includes stems less than 1 meter tall.

In initial references to species both the common and scientific names are given; thereafter only common names are used. Nomenclature follows Radford et al. (1968).

Red Maple-Dogwood Replacement Type

Site conditions for this type varied, but sites were generally sub-mesic, low elevation (338-585 meters, 1110-1920 feet), lower to mid slope or protected upper slope locations (Table 1 in Appendix). Aspects ranged from northeast to southwest (20°-250°), slopes were moderately steep (av = 36%), and average solar radiation was the lowest of the six replacement types defined in this study. Soil depth was thin (av = 68.5 cm) and the average depth of the O horizon was only 3.6 cm. The A horizon was the least acid of the replacement types. Available phosphorus in the A layer was typically low,and potassium availability was moderate relative to the other replacement types.

It is probable that most or all of these sites were influenced by human use prior to the establishment of the Great Smoky Mountains National Park. Half of the plots were likely cultivated in the past. The remainder were probably logged, grazed, periodically burned or all three. Chestnut sprouts occurred in 16% of the stands indicating its former presence.

The original canopy basal area averaged 70% yellow pine, dominated by either Virginia pine (*Pinus virginiana* Miller) or a mixture of Virginia pine and shortleaf pine (*P. echinata* Miller) and often included some pitch pine (*P. rigida* Miller) and table mountain pine (*P. pungens* Lambert) (Table 2 in Appendix). The beetle attack killed 97% of the canopy pine basal area leaving 32% of the original total basal area intact. Canopy closure was 44% at the time of sampling. Living yellow pines were completely eliminated from 25% of the stands by the infestation.

The composite stand description showed that dry phase oaks, particularly scarlet oak (Quercus coccinea Muenchh.) and white oak (Q. alba L.) along with white pine (Pinus strobus L.) were the most common associates of yellow pines in the original stands. Individual stands diverged from this composite picture. In three of the most mesic plots, tuliptree (Liriodendron tulipifera L.) was an important canopy hardwood in two, while in the other plot large white pines accounted for 77% of the residual basal area. On two drier sites, the residual canopy was composed of mockernut hickory (Carya tomentosa (Poiret) Nuttal) and scarlet oak. In all cases the original canopy consisted of early to mid seral species in old field stands.

The Society of American Foresters (S.A.F., 1967) lists two forest cover types which are similar to the original stands, the shortleaf pine-Virginia pine type (Type 77) and the Virginia pine type (Type 79). Both types are described as old field stands succeeded by "shortleaf pine and oaks" and "shortleaf pine and various hardwoods" respectively. Whittaker (1956), in describing the vegetation of the Great Smoky Mountains, mentions old field stands in his Virginia pine forest classification citing scarlet oak as second to pine in importance with white pine, blackgum (Nyssa sylvatica Marshall), black oak (Quercus velutina Lam.), and white oak listed as other canopy species. Miller's 1936 vegetation map of the Smokies includes a yellow pine hardwoods type, but his description is general with emphasis on the xeric condition of the sites. He mentions fire as a causal agent but has no reference to agriculture or logging for this type. Thomas (1966) defined two related

types on Chilhowee Mountain, a second growth pine-south slope-cover type and a second growth pine-north slope-cover type, but both are less diverse than the types described here.

The replacement canopy (stems > 3 cm) derived by cluster analysis was characterized by the predominance of red maple (Acer rubrum L.) and dogwood (Cornus florida L.) in the 3 to 10 cm size class (Table 4 in Appendix). Because of the varied and relatively mesic nature of site conditions, this replacement type was the richest in the species. Of 29 overstory species in this community, 22 were found in the replacement canopy. In addition to red maple and dogwood, sourwood (Oxydendoum arboreum (L.) DC.) and blackgum were common in the replacement canopy. Species considered potential dominants in upper canopy positions include mockernut hickory, white oak, hemlock (Tsuga canadensis (L.) Carr), white pine, tuliptree and scarlet oak. In both the understory and reproduction strata, red maple and dogwood accounted for over 50% of the stems. Other common subsaplings were white pine, mockernut hickory, and American holly (Ilex opaca Aiton), while white pine, white oak, and scarlet oak were common seedlings. Virginia pine and table mountain pine seedlings were found in 3 plots. Although their representation was very low, there was an increase in the understory in very tolerant, mesic species such as American holly, American beech (Fagus grandifolia Ehrhart), Eastern hop-hornbeam (Ostrya virginiana (Miller) K. Koch.) and American hornbeam (Carpinus caroliniana Walter.).

Shrub and herbaceous cover was light compared to other replacement types (Table 3 in Appendix). Shrub cover was very dense (70-100%) in

25% of the samples, but in the remaining plots it never exceeded 5%. Mountain laurel (Kalmia latifolia L.), huckleberry (Galussacia baccata (Wang.) K. Koch.) and blueberry (Vaccinium spp.), typical pine understory heaths, were present in only 50% of the sample plots. On more mesic sites common shrubs were strawberry bush (Euonymus americanus L.) and maple-leaf viburnum (Viburnum acerfolium L.). Virginia creeper (Parthenocissus quinquefolia (L.) Planchon) was often present, and Smilax vines were found in every plot.

It is difficult to project the next sere for this type. From the composite description it appears to be succeeding to a white pine-white oak forest. Such a forest type has been recently identified in the Smokies by research currently in progress, and general site characteristics for the two types are comparable (H. R. DeYoung, Personal Communication). Miller's 1936 type map contains a white pine hardwood type, and his floristic description includes many of the understory species found in this study. Miller states that the stands are often on old field sites. Braun (1950) refers to white pine or white pine-white oak forests on sub-mesic sites in the Asheville basin. The Society of American Foresters' (1967) white pine cover type (Type 21) also fits this projection with the following description:

> In the Southern Appalachians on moist sites, yellow-poplar, hemlock, northern red oak, and white oak are the main associates. On drier sites, chestnut oak, scarlet oak, shortleaf pine, and pitch pine come in. . . . It occupies mountain slopes, flats, and valleys varying widely in soil character . . . from moist to relatively dry.

The description also reports that the white pine type is a long-lived temporary community, eventually succeeding to various tolerant hardwoods.

Individual stands in this study will likely succeed to differing communities dominated by a mixture of mesic hardwoods, by white pine-white oak, by oak-hickory or by scarlet oak depending on the site and stand history.

Red Maple-Sourwood Replacement Type

Sites for this type were on upper slopes and ridgetops with moderately deep soils (av. = 73 cm) and aspects ranging from southeast to northwest (135°-320°) (Table 1 in Appendix). Average percent slope was the least of the forest types identified in this study, and solar radiation was comparatively low. The stands were mid elevational, ranging from 701 to 832 meters (2300-2730 feet). O horizons were thin to moderately deep (av. = 4.0 cm), and pH of the A horizon, though acidic, was relatively high (av. = 4.7) compared to the other stands sampled.

Chestnut sprouts were found in two plots (20% of the sample). Several of the sites were near old roadways, and logging, grazing, and intentional burning probably affected the stands prior to the establishment of the park.

The original canopy averaged 79% yellow pine, primarily pitch pine with some Virginia and table mountain pine, of which 91% was killed leaving 28% of the original canopy alive (Table 2 in Appendix). In one plot all yellow pines were killed. Dead pines varied in size, and all but one plot contained trees greater than 30 cm dbh. Average canopy closure after the kill was 33%. The most prevalent original canopy hardwoods were scarlet oak, chestnut oak, and red maple. Similar stands

are described by the Society of American Foresters (1967) as their pitch pine type (Type 45), and by Whittaker's (1956), pitch pine-heath type. Thomas' (1966) pitch pine-scarlet oak scrub cover type for Chilhowee Mountain is floristically similar to these original stands but structurally different. The original stands are encompassed by Miller's (1936) yellow pine-hardwood type and are compositionally described by Shanks (1954b) as open oak and pine stands.

After the beetle kill, red maple became dominant in the replacement canopy because of its high frequency in the residual canopy and high densities in the residual sapling stratum (Table 5 in Appendix). Replacement stands averaged 49% red maple and included sourwood (*Oxydendrum arboreum* L.) (10%), chestnut oak (8%), and scarlet oak (7%). Although the relative density of oak was not high, its importance in the replacement canopy cover was magnified by large-crowned residual canopy trees. In 90% of the sample plots living yellow pines remained in the replacement canopy as scattered individuals. Red maple dominated the understory and reproduction strata accounting for over 50% of the stems in both cases. Scarlet oak and white pine, both potential canopy dominants, were well represented in the understory, and both responded to the drastic reduction in overstory cover. Chestnut oak dropped in relative importance in the understory as did sourwood and blackgum. Pitch pine was reproducing in 3 plots, and table mountain pine seedlings were found along with pitch pine in one plot.

Typically, a layer under 1 meter tall of *Vaccinium* with some *Gaylussacia* covered much of the ground (av. = 50.6% cover) (Table 3 in

Appendix). Larger shrubs, especially mountain laurel, oilnut (*Pyrularia pubera* Michaux), and occasionally lyonia (*Lyonia lingustrina* (L.) DC.) were scattered in the plots, averaging 28.5% cover. Herbaceous cover was sparce with *Uvularia pudica* (Walter) Fernald, bracken (*Pteridium quilinum* (L.) Kuhn), teaberry, and trailing arbutus (*Epigea repens* L.) among those present.

In the future a mid seral mixture of scarlet oak, chestnut oak, red maple, and scattered pines will fill the canopy gap created by the infestation. Scarlet oak will increase in overstory cover and will decrease in understory density until maximum canopy closure is achieved. White pine will increase in the canopy and will remain an associate of the oaks. Chestnut oak, slower growing and more tolerant than scarlet oak (Fowells, 1965), will probably increase in understory density and in lieu of fire or other disturbance may ultimately dominate the overstory. Individual pitch and table mountain pines will remain in the canopy for many years but will eventually be replaced by hardwoods. These seral communities probably contain stages similar to the S.A.F.'s (1967) scarlet oak (Type 41) and chestnut oak (Type 44) cover types. Golden (1974) described a chestnut oak type on similar sites in the Great Smokies, noting that scarlet oak and in some cases pitch pine shared the canopy.

Blackgum-Mixed Pine Replacement Type

Cluster analysis grouped one-third of the total sample (27 plots) into this type, making it the most common replacement type encountered (Table 1 in Appendix). The sites were located at mid to high elevations

(av. = 820 meters, 2689 feet) on steep, mid to upper slopes. Aspects ranged from southeast to southwest (120° to 250°), and average solar radiation was high. Total soil depth tended to be thin though the organic layer was relatively deep compared to other replacement types (av. = 5.2 cm). The A horizon pH ranged from 4.2 to 5.0, and the horizon was high in phosphorus and fairly low in potassium.

Chestnut sprouts were recorded in 44% of the plots, although large chestnut stumps or other signs of canopy size chestnuts were not common. Signs of fire were seen in very few plots, and it is not likely that any major fires had occurred since park establishment. Most of the sites were unsuitable for past agriculture and logging operations. Periodic burning may have been a major factor controlling species composition in stands during pre-park settlement days. Yellow pines in one plot had been partially cut as part of the 1958 bark beetle sanitation operation, but the stand had been intensely reinfested ten years later.

Yellow pines of all four species were present in the original canopy, with pine basal area accounting for 82% of the total stand (Table 2 in Appendix). Infestations killed 90% of the canopy pines leaving approximately 27% of the original canopy alive. In 3 plots (11% of the sample) all canopy size pines were killed, but all plots contained yellow pines in at least one stratum. Canopy closure averaged 25.5% at the time of sampling. Residual canopy pines indicated that pitch pine was the predominant species in the original stands, usually sharing the canopy with table mountain and Virginia pine and in one case with shortleaf pine. In three stands table mountain pine was

dominant, and it was co-dominant with pitch in 30% of the plots. Hardwoods accounting for the greatest volume in the original canopy were scarlet oak (relative basal area = 6%) and chestnut oak (relative basal area = 5.5%). Other hardwoods included red maple, sourwood, blackgum, black oak, and white pine. A total of 18 species was present in the original canopy. In general, the original stands belonged to the S.A.F. (1967) pitch pine cover type (Type 45). They closely paralleled Whittaker's (1956) pitch pine heath type, however, shrub cover was less dense than he described. The three table mountain pine stands mentioned above were as described by Whittaker's table mountain pine-heath and Golden's (1974) table-mountain pine-pitch pine type.

Twenty-six of 30 tree species tallied in this type had stems greater than 3 cm dbh (Table 6 in Appendix). At the time of sampling, blackgum was the most abundant tree (relative density = 29%) in the replacement stands. Yellow pines as a group were second in abundance (relative density = 24.5%), and they were well represented in the residual canopy with 33% of the basal area. Pitch pine was the most common in the sample (frequency = 92.5%), but table mountain pine, which was present in only 63% of the sample, had a higher average residual basal area. Virginia pine was present in 52% of the plots; shortleaf pine was in only one stand. Chestnut oak (frequency = 81.5%) and scarlet oak (frequency = 78%) were about equally represented in the replacement canopy, each accounting for approximately 7.5% of the total stems. Black oak, blackjack oak, and white oak were also present. In addition to blackgum, other common small tree species were red maple and sourwood.

Small-tree species were very abundant in the understory with red maple, blackgum, sassafrass, and sourwood accounting for 77% of the stems. Scarlet oak, black locust (Robinia pseudoacacia L.) and black oak were the most prevalent potential canopy hardwoods. Yellow pines in the understory stratum were Virginia pine and, in one plot, pitch pine. Together they were present in 26% of the sample plots.

The reproduction stratum in this replacement type was diverse with 28 species represented. Like the understory layer, reproduction was also dominated by small-tree species. Potential canopy dominants with significant reproduction were scarlet oak (present in 59% of the plots), the yellow pines, especially Virginia and pitch pines (total frequency = 55.5%), white pine (frequency = 26%), and chestnut oak (frequency = 22%). In both the understory and reproduction strata, mockernut and pignut hickories and some mesic species were present but in low percentages.

There was considerable variation in shrub and herbaceous cover (Table 3 in Appendix). In a few stands mountain laurel formed a very dense stratum at 2-3 meters; in others there were virtually no shrubs over 1 meter tall. Average cover for mountain laurel, blueberry, lyonia, oilnut and other shrubs taller than a meter was 37%. Blueberries and huckleberries under a meter tall were more common and averaged 45% cover. Herbaceous plants averaged 13.5% cover. Smilax was copious.

With reclosure of the canopy, this replacement type will be dominated by scarlet oak, chestnut oak, and a mixture of pitch, table mountain, and Virginia pines. In some stands black oak and white pines will be important associates. Due to very xeric site conditions, the

oak-pine community will be long-lived, but without effective fire it will slowly succeed to chestnut oak dominated stands comparable to the S.A.F.'s (1967) chestnut oak cover type (Type 44) and Golden's (1974) chestnut oak type.

Virginia Pine-Blackgum Replacement Type

The sites for the Virginia pine-blackgum replacement type were mid to low elevational (344-853 meters, 1130-2800 feet) on predominantly south to southwest facing (160°-270°) mid and upper slope positions and ridgetops (Table 1 in Appendix). Side slope sites were steep, averaging 40% slope, and solar radiation was high. Soil depth averaged 71 cm which was moderate compared to other replacement types, and the O horizons were thin (av. = 3.9 cm). Soil A horizons were acid (av. = 4.58) and phosphorus and potassium availability relative to the other stands sampled was high.

Chestnut sprouts were present in 15% of the plots. With the exception of 2 or 3 plots out of the 13 in this type, it is unlikely that these sites were cultivated or logged. Grazing may have affected some of the sites, and although there was no visible evidence of periodic burning prior to park establishment, fire was probably an important factor.

Prior to infestation, yellow pines accounted for 86% of the canopy (Table 2 in Appendix). The original canopy contained all four species of yellow pines. Based on residual canopy trees, Virginia pine was the most common dominant either alone or in mixture with other pines. In one plot shortleaf pine was the former dominant. An average

of 85% of the pine basal area was killed leaving 27% of the total original canopy basal area alive. In only 2 plots were all canopy pines killed,and remnant sapling pines were found in all plots. Scarlet oak (relative basal area = 3.5%) and chestnut oak (relative basal area = 3%) were the most important hardwoods in the original stand. Canopy closure at the time of sampling averaged 20.5%. Black oak, blackjack oak, white oak, and southern red oak were present in the original canopy, but were minor components. Blackgum and sourwood were prevalent small-tree species in the original community. Prior to the beetle epidemic, individual plots within this replacement type would probably have been categorized in the S.A.F.'s (1967) shortleaf pine cover type (Type 75), shortleaf pine-Virginia pine cover type (Type 77), Virginia pine cover type (Type 74), or pitch pine cover type (Type 45). The stands would have been included in Miller's (1936) yellow pine-hardwood type and overlapped with Whittaker's (1956) Virginia pine forest type.

As a group, residual yellow pines were the most abundant trees in the replacement stands (Table 7 in Appendix). They averaged 42% of the stems over 3 cm dbh and accounted for 56% of the residual basal area. The most prevalent species was Virginia pine which composed 33% of the residual basal area and accounted for 31% of the replacement canopy density. Virginia pines greater than 3 cm dbh were found in all plots. Blackgum (relative density = 24%) was second in species abundance followed by sourwood (relative density = 9%). Scarlet oak was the third most abundant hardwood in the replacement community. It was found in 85% of the plots and accounted for 7% of the replacement stems and 15.5%

of the residual canopy. Other hardwoods of lesser frequency included red maple, chestnut oak, and black oak.

In the understory, blackgums and red maples were most abundant with Virginia pine third in importance (Table 3 in Appendix). Yellow pines were present in 46% of the sample plots. Scarlet oak and white pine were each present in 38.5% of the understory plots, and chestnut oak was in 31%.

In the reproduction strata, red maple, sassafras, and blackgum were the most prevalent species. Scarlet oak seedlings had a frequency of 46%, black oak seedling frequency was 38%, and Virginia pine and white oak seedlings were each in 23% of the plots. Yellow pine reproduction was found in 38.5% of the plots.

Shrub and herbaceous plants were those typically found in pine stands. Blueberries and huckleberries less than a meter tall averaged 38% cover, and mountain laurel, blueberry and other shrubs taller than a meter covered 26.5% of the area. Herbaceous cover was scattered, averaging 10% coverage, and included teaberry, trailing arbutus, galax (*Galax apylla* L.), panic grass (*Panicum* spp.) and others.

In the near future, yellow pines (primarily Virginia pine) will share dominance with scarlet and chestnut oak. Without disturbance there will be a gradual shift toward chestnut oak. However, on the most xeric sites, pines and scarlet oak may maintain themselves in the canopy indefinitely.

Mixed Pine-Scarlet Oak Replacement Type

The mixed pine-scarlet oak replacement type occupied low to mid elevation (366-823 meters, 1200-2700 feet) sites on ridgetops and upper slopes (Table 1 in Appendix). Aspects were southeast to southwest (130°-210°), and slope angle varied from flat ridgetops to side slopes averaging 41%. Solar radiation was moderate relative to the other forest types in the study. Soils were deep for the total sample (av. = 77.2 cm), and organic horizons thin (av. = 3.8 cm). The A horizons were acid (av. pH = 4.58) and low in available phosphorus and potassium.

Yellow pines in the original canopy accounted for 78% of the total stand basal area (Table 2 in Appendix). All four yellow pine species were represented in the composite description of the original canopy. Although individual dead trees could not be identified,the relative density of the four species apparently varied by site, and judging from residual trees, Virginia and pitch pines were the most common.

The beetles killed an average of 88% of the canopy pines. In three plots (33% of the sample) all yellow pines greater than 10 cm were killed, but in none of the stands were living pines completely eliminated. Scarlet oak was present in every plot and averaged 13% of the original canopy basal area; it was by far the most important hardwood. Chestnut oak was present in two-thirds of the plots and made up 2.5% of the total original basal area. Black oak, blackjack oak (Quercus marilandica Muenchh) and white oak were minor components. Prior to infestation these stands probably contained examples of 4 of the S.A.F.'s (1967) cover types: shortleaf pine (Type 75), shortleaf

pine-Virginia pine (Type 77), Virginia pine (Type 79) and pitch pine (Type 45). Whittaker's (1956) Virginia pine and pitch pine types would include most of the original stands, as would Miller's (1936) general yellow pine-hardwood type.

Scarlet oak was the dominant species in replacement stands both in terms of residual canopy basal area (RBA = 42%) and total stems over 3 cm dbh (RD = 20%) (Table 8 in Appendix). Yellow pines as a group averaged 23.5% of the total stems and 32% of the residual canopy basal area with Virginia and pitch pines predominant. Blackgum and red maple were the second and third most abundant species in the replacement canopy. Seven oaks were represented, the five mentioned above plus sapling size southern red oak (*Quercus falcata* Michaux) and post oak (*Q. stellata* Wang.). The understory stratum was dominated by blackgum with red maple second in abundance. Scarlet oak accounted for one-third of the relative density and was present in 44% of the plots. Only one plot, 11% of the sample, contained yellow pine in the understory strata. Red maple and sassafras (*Sassafras albidum* (Nuttall) Nees.) were the most prevalent seedlings, each having a frequency of 78%. Scarlet oak reproduction had a frequency of 44% and a density of 11.5%. Black and blackjack oak, mockernut, and pignut (*Carya glabra* (Miller) Sweet) hickory seedlings were present but in low frequencies and densities. Yellow pine reproduction was present in one-third of the plots.

Shrub and herbaceous cover was very similar to the red maple-sourwood replacement type previously described; however, the shrub layer was less dense.

Scarlet oak and mixed pines will maintain dominant positions in these stands even in late seral stages. Pine density will diminish gradually and without further disturbance will eventually be represented only by widely scattered individual trees. Understory samples showed no major competitor with scarlet oak for future canopy dominance, though more tolerant oaks such as chestnut oak and white oak may eventually become established. From present information, however, it appears that the stands will be similar to the S.A.F. (1967) scarlet oak cover type (Type 41) which is described as approaching climax on dry soils.

Table Mountain Pine-Pitch Pine Replacement Type

Cluster analysis separated plots in this type from all others sampled (Figure 2, p. 28) suggesting high dissimilarity with other replacement types. The sites were the most xeric of those sampled and were the highest in elevation, averaging 1030 meters (3380 feet) (Table 1 in Appendix). Slopes as steep as 61% in combination with typically southwestern aspects (av. = 202°) and exposed upper slope positions resulted in high solar radiation. Soil depths were shallow (av. = 67.2 cm), and rock outcrops were not uncommon. The organic horizon was a deep mor mat (av. = 8.2 cm) derived from a dense ericaceous shrub layer, and A horizon pH was the most acid of the six replacement types (av. = 4.38). Available potassium and phosphorus in the A horizon was very low in relation to other sites.

In all 10 plots identified in this type, the original cover was either a mixture of table mountain and pitch pine or exclusively table

mountain pine (Table 2 in Appendix). Dominance of pine in the original cover was high, with the two species averaging 98% of the pre-infestation basal area. A very dense stratum of mountain laurel (70%-100% cover) was characteristic in all but one plot, and a ground cover of galax and teaberry was common.

Floristically, the stands were much like Shank's (1954b) open oak and pine stands, and structurally the original stands corresponded very closely to Golden's (1974) table-mountain pine and table-mountain pine-pitch pine types. Whittaker's (1956) table mountain pine heath community encompasses this replacement type also. Both Whittaker and Golden describe the canopy trees in their types as small in bole diameter and with poorly developed crowns. Similarly, the largest of the beetle-killed trees found in this study was 40 cm dbh and the largest residual pine was only 25 cm dbh. Stratal distribution of pines in the original canopy tended to be very heavily concentrated in the 3 to 10 cm size class with varying densities in higher size classes but with very little representation in the subsapling and reproductive layers, probably due to the dense heath layer.

Infestations in these stands were very damaging, eliminating 80% of pine basal area greater than 10 cm and destroying many lesser pines also. Canopy closures following kills average only 11.5%, and in 30% of the plots closure was estimated at 5% or less (Table 3 in Appendix). Replacement stands were predominately dense, small diameter table mountain and pitch pines with scattered hardwood saplings. Although pines accounted for over 70% of the living stems greater than 3 cm dbh,

their relative density dropped to 17.79% in subsapling stratum and to 1.25% in the seedling layer (Table 9 in Appendix). Golden relates low pine reproduction in his study to inefficient sampling size noting that pine seedlings tend to be established in patches. Both Golden and Whittaker state that pine reproduction should be adequate for stand maintenance due to the open nature of the mature canopy, and Cain (1937) thought that such stands are self-maintaining only on extremely xeric sites. Cain and Whittaker suggest that ultimately fire is the determiner of pine maintenance, although Golden found no evidence of recent fire in his sampling areas, and fire evidence was noted in only one plot in the present study.

The dearth of pine regeneration after beetle infestation is noteworthy since the maintenance of pine on these sites in the absence of fire would require relatively abundant pine seedling establishment following the severe canopy disruption caused by beetle-kills. This does not appear to be the case. Rather, pine seedling relative densities in the infested stands were a fraction of those that Golden found in undisturbed stands, possibly reflecting differences in methods, but probably relating to the failure of pine regeneration in competition with hardwood regeneration and shrub cover expansion. Optimum seedbed conditions for pitch and table mountain pines include mineral soils and open sunlight (Fowells, 1965), conditions almost totally lacking on deep organic mats under dense Kalmia and herbaceous cover at these sites.

Reproduction densities for all tree species were suppressed in this community. The average total seeding density for this type was

approximately two-thirds or less that of any of the other five forest types derived from this study. Moreover, one plot with a 100% cover of mountain laurel and Vaccinium and a 90% herb layer cover included no tree seedlings at all.

Hardwoods in the table mountain pine-pitch pine type are primarily small-trees, especially red maple, blackgum, and sourwood. Sapling blackgums were found in all plots, and sapling red maples were in 90% of the sample. In lower strata, blackgum diminished in density in favor of the more shade tolerant red maples which accounted for over 58% of the reproduction. Sourwood was not reproducing. Three oaks were present in the understory: chestnut oak (40% of the plots), scarlet oak (30% of the plots), and northern red oak (10% of the plots). In the reproduction sample, scarlet oak was found in 30% of the plots, northern red oak in 10%, and chestnut oak seedlings were absent indicating their very scattered reproduction.

In the future, the predominance of table mountain and pitch pine in infested stands will decline unless some major disturbance, particularly fire, opens up the ericaceous shrub cover and improves seedbed conditions for pine. Pole-size blackgums and red maples will increase in cover constituting a mid seral community with residual pines. Ultimately, these stands will succeed to widely scattered scarlet and chestnut oaks sharing the open canopy with patches of residual pines, or pine could conceivably be completely replaced by hardwoods. The controlling plant will probably be mountain laurel. As envisioned, the future cover type will be compositionally similar to

Golden's (1974) oak-pine type. In the long run, Whittaker's prediction that fire frequency is on a shorter cycle than pine removal may very well prove true, in which case dense pine stands would surely be reestablished and a new vegetative cycle would begin.

B. CORRELATION AND REGRESSION ANALYSIS

Methods

Relationships between site and vegetation variables were examined by correlation and multiple regression analyses. These analyses have been used extensively in ecological studies over the past three decades. Both techniques aided in the interpretation of data by statistically quantifying relationships.

Significant correlation between two variables demonstrated their strong tendency to covary with one another. While not necessarily implying causality, correlations were useful in identifying inconspicuous relationships and in lending statistical support to hypothesized interactions.

Multiple regression proved to be a stronger interpretive tool. It was used to describe the functional relationship between absolute density, the dependent variable, and a set of selected site and vegetation variables, the independent variables, assumed to influence density. The regression equations and their associated statistics provided a means for evaluating contributions of each independent variable to variance in density, and the equations also serve to a limited extent as prediction models.

Ten vegetation variables were selected for their importance in the structure of replacement stands, and regression equations were calculated for each variable for the overstory, understory, and reproduction strata. The vegetation parameters used as dependent variables were total pine, table mountain pine, pitch pine, total oak, scarlet oak, chestnut oak, red maple, blackgum, and dogwood density (stems per hectare).

In the overstory models, independent variables were elevation (feet), slope position, percent slope, solar radiation (1000 Langleys/year), depth to bedrock (cm), depth of the O horizon (cm), pH of the A horizon, potassium and phosphorus availability in the A horizon (Kg/ha), and estimated acreage of the beetle kill. In the understory models the same independent variables plus total density, percent shrub cover taller than a meter, and shrub cover under a meter tall were used. In the reproduction models independent variables were the same as in the understory models except that depth to bedrock was dropped as a causative factor and total understory density and herbaceous cover were added.

The entire sample (81 plots) was used in regression analysis without subdivision to give the widest variance in the variables tested. In spite of this, coefficients of determination (R-square) were rather small for most models due to the ubiquity of most species involved within the narrow limits of southern pine beetle infestations. A limitation of the models was that the only available independent variable relating directly to the intensity of beetle infestations was acreage killed. As explained earlier, an index based on pine basal area killed by beetles

was originally planned, but data collection for the index proved impractical for many plots.

Overstory densities for the selected vegetation variables were compiled from the INFEST program previously mentioned and understory and reproduction densities for the same species and groups were calculated from field sheets. This information plus cover and site variables for each plot were combined in a disk file created on the DEC System-10 computer.

In its final form the file contained 81 observations, corresponding to the 81 field plots, with 58 vegetation and site variables in each observation. Zero values were assigned to vegetation variables not present in specific observations, and the only missing values in the file were for aspect transformation on level plots.

Initially correlation and stepwise multiple regression analyses were run on the DEC System-10 computer using STATPACK (Houchard, 1974). However, this program could not process missing values, and it offered few options for maximizing regression equation reliability and produced comparatively limited statistical information. For those reasons, the analyses were rerun using the Statistical Analysis System (SAS) (Barr et al., 1976) with more satisfactory results. The SAS programs were written on the DEC System-10 and submitted for computation on the University of Tennessee IBM-360/65 computer.

Stepwise multiple regression was run using the SAS maximum R-square improvement option (Barr et al., 1976; Wade 1977). This technique generates equations using all possible combinations of

independent variables, compares R-square values, and prints out the best one variable model, the best two variable model, and so on. Criteria for selecting models were, first that the reliability of the equation determined by an F test be significant at P = 0.05 and, secondly, that the reliability of each partial regression coefficient be significant at P = 0.10.

In most cases correlations and regression equations supported field observations and confirmed environmental trends suggested by the replacement types derived from cluster analysis. Topographic and edaphic relationships in particular affirmed that water-stressed trees on xeric or otherwise deficient sites were more susceptible to southern pine beetle attack (Beal, 1927; Craighead, 1925; Lorio, 1968; Lorio and Hodges, 1977). Thus, the stands sampled appeared to have been selected by the pine beetles because of low vigor. For this reason many correlations were the opposite of patterns associated with gradient analysis or transect sampling.

For regression models of vegetation parameters independent variables are listed in order of importance according to their Type II sum of squares. Independent variables which also showed significant correlation (P = 0.05) with the dependent variable are marked in the text with an asterisk (*). Such variables were assumed to be strongly related to the dependent variable due to their inclusion in both correlation and regression.

Site-Site Correlations

Elevation correlated with three other topographic features (Table 10 in Appendix). As elevation increased, the beetle kills sampled tended to be more southwest facing, steeper, and had greater solar radiation. This pattern was probably due to increased precipitation at higher elevations relegating pure pine stands of low vigor to increasingly steep and exposed sites.

Because solar radiation was derived from slope direction and percent slope, there were strong correlations between it and aspect and percent slope.

Higher slope positions were less steep than lower slope positions. The highest slope positions were relatively flat ridgetops, and although solar radiation estimates for such sites were lower than side slopes, wind exposure and other desiccating factors often created very xeric conditions. On lower slope positions beetle kills occurred more frequently on steeper slopes, the more xeric of these generally mesic sites.

Soil depth was greater on upper slope positions. This is in accord with the trend toward steeper slopes in the lower elevation beetle kills. Steeper slopes resulted in increased erosion, colluvial movement, and reduced soil accumulation and development.

O horizon thickness was greater at higher elevations, a trend which was also apparent in the replacement type descriptions (Table 1 in Appendix). The preponderance of deeper humus layers at higher elevations was due in large part to increased ericaceous shrub cover,

especially mountain laurel, and reduced decomposition rates. While deep, peaty organic mats were common at the highest elevations sampled, the lowest elevation plots were usually old field areas with limited O horizon development and high erosion potential. Thin O horizons probably caused reduced infiltration, greater soil water evaporation, and reduced nutrient availability to plants (Losche, 1967), all affecting tree vigor and susceptibility to beetle attack.

A horizon pH decreased with elevation, more southwestwardly aspects, increased isolation, and deeper O horizons. Cain (1931) related increased acidity with elevation in the Smokies primarily because of the leaching effects of increased precipitation and peat formation under dense evergreen ericaceous shrubs. Strong correlations between pH and herbaceous cover (especially ericads) and cover for tall-shrubs (predominantly mountain laurel) and correlation between pH and depth of the O horizon parallel Cain's findings.

Phosphorus in the A horizon showed no significant relationships with other site variables tested. Potassium increased with upper slope positions, more gentle slopes, and reduced solar radiation. Unlike phosphorus, potassium is readily leached from soils (Bray, 1974), so that beetle-kills on steeper slopes tended to lose potassium because of increased runoff. The correlation between potassium and solar radiation was probably due to the paired relationship between slope steepness and solar radiation.

Size of beetle kills correlated positively with slope steepness. In the sample, larger, often multi-acreage, kills tended to be on steep, dry slopes.

Herbaceous and Shrub Cover-Site Correlations

Increased herbaceous cover correlated strongly with increased elevation, depth of the O horizon, and acidity of the A horizon, and there was a significant correlation between herbaceous cover and southwest facing aspects. These trends were evident in the replacement type descriptions (Table 10 in Appendix). Most of the herbs on the deepest O horizons were ericaceous (*Gaultheria*, *Epigea*, *Chimaphila*) or closely allied (*Galax*), and cover was considerably higher in the table mountain pine-pitch pine type than any of the other replacement types identified.

Shrub cover less than a meter high (predominantly *Gaylussacia* and *Vaccinium*) significantly increased with decreased slope steepness and increased phosphorus availability in the A horizon. However, neither trend is evident from the replacement type descriptions. Increased low shrub cover on ridgetop positions was noticed in the field.

Shrub cover over a meter high (predominantly mountain laurel but also including *Gaylussacia*, *Lyonia*, and others) correlated strongly with herbaceous cover, and, as with herbaceous cover, increased with elevation, aspect, depth of the O horizon, and A horizon acidity. In addition, it increased with slope, solar radiation, and A horizon phosphorus. It was noted in the field that mountain laurel cover increased with site elevation and xeric site conditions. The significant correlation between tall shrub cover and phosphorus was difficult to explain and may have been by chance. The table mountain pine-pitch pine type had the densest tall shrub cover but was low in phosphorus.

Herbaceous and tall-shrub cover were more dense under overstory table mountain and pitch pines, a relationship clearly visible in the table mountain pine-pitch pine replacement type. In contrast, both herbaceous and tall-shrub cover decreased and low-shrub cover increased with increasing scarlet oak overstory density. Both classes of shrub cover diminished as dogwood increased in the replacement canopy on more mesic sites.

Overstory Relationships

Total overstory. Regression analysis related increasing total overstory density to less acidic soils*, reduced solar radiation, and steeper slopes (Table 19 in Appendix; Table 11 in Appendix). The most dense stands found in the field were stands of sapling size pines, and it appeared that high density values from these plots dominated the total overstory statistical analysis. Pine density correlated very highly with total density (Table 12 in Appendix), and the site factors selected by the regression model for total density were applicable to pine sites. All pine stands were on very acidic soils. Stands dominated by table mountain pine and pitch pine were on very steep slopes, and Virginia pine stands were on flat ridgetops on which solar radiation estimates were low due to their low slope angle. Further, shrub and herbaceous cover increased as total density increased, a characteristic of table mountain pine-pitch pine stands (Table 9 in Appendix).

Pine overstory. Regression analysis showed that residual pines were more abundant on sites with high soil acidity*, steep slope*, and high slope positions (Table 20 in Appendix). Paradoxically, stands on such sites were also the most attractive to southern pine beetles. Prior to infestation, pine stands on these sites had open canopies allowing the maintenance of suppressed pines in the subcanopy. Whittaker (1956) described climax pine stands in the Smokies as having a biomodal size class distribution, and Golden (1974) found examples of this community structure in his table mountain pine-pitch pine type. In these stands, bark beetles tended to attack the largest trees while usually not attacking adjacent saplings (Hoffman and Anderson, 1945). As a result, although infestations on dry, upper slopes were very intense and often killed all pines in the original canopy, surviving pine saplings were more abundant than on less xeric sites where hardwood saplings had become well established prior to the kill.

Correlation analysis indicated that other site factors relating to increased pine overstory density were increased elevation and thicker organic horizons (Table 11 in Appendix). Pine overstory density also correlated very strongly with pitch and table mountain pines. These relationships indicate that high sapling density in the table mountain pine-pitch pine type were responsible.

The inability of sapling pines to compete with hardwoods on mesic sites was illustrated by the inverse relationship between pine overstory density and both red maple and dogwood overstory density (Table 12 in Appendix).

Table mountain pine and pitch pine in the overstory were very closely associated (Table 12 in Appendix), and regression models for both species included increased A horizon acidity* and elevation* (Table 21 in Appendix). The table mountain pine model also included increased slope angle*, implying an affinity for more xeric conditions.

Other relationships evident from correlations were that thicker O horizons were under dense stands of both of these pines, no doubt due to increased mountain laurel cover (Table 11 in Appendix). Table mountain pine appeared to be more successful on sites with low potassium.

Although the R-square value was very low, Virginia pine in the overstory was best predicted at decreasing elevations with increasing soil acidity (Table 23 in Appendix). Virginia pine was limited to elevations below 902 meters (2960 feet) and was typically found on moderate to strongly acid soils.

Oak overstory. Variation in oak overstory density did not appear to be directly related to any of the site variables measured, probably because oaks were widely distributed on all sample sites.

Scarlet oak in the overstory was best explained by more gentle slopes* and increasing soil depth* (Table 25 in Appendix; Table 11 in Appendix) indicative of its occupation of relatively flat ridgetop sites (Whittaker, 1956; Stupka, 1964; Racine, 1971).

Chestnut oak overstory density was predicted by increased elevation*, thinner organic soil horizons, and increased potassium availability (Table 26 in Appendix; Table 11 in Appendix). These

conditions were best met in the blackgum-mixed pine replacement type. This type will probably eventually succeed to stands dominated by chestnut oak.

Red maple overstory. The dominance of red maple on protected sites was reflected in the regression model which related red maple overstory density to lower slope positions, reduced solar radiation*, increased elevation, and reduced slope (Table 27 in Appendix; Table 11 in Appendix).

There was an inverse relationship between red maple and blackgum abundance in the overstory (Table 12 in Appendix). In beetle kills both trees appeared to be in intermediate seral positions, and they had very similar site requirements. Red maple, however, had a competitive advantage on more mesic sites while blackgum was better adapted to high solar radiation and xeric conditions.

Blackgum overstory. Phosphorus availability in the A horizon* and increased solar radiation* best explained blackgum overstory density (Table 28 in Appendix; Table 11 in Appendix). This trend was also seen in the replacement type description for the blackgum-mixed pine type (Table 6 in Appendix) which had the highest mean soil phosphorus content and the second highest mean solar radiation. Apparently blackgum could endure low moisture availability but was sensitive to low soil fertility.

Blackgum and oak density was positively correlated in the overstory indicating that they compete for similar sites (Table 12 in Appendix). Oaks were usually larger trees and were scattered in the plots allowing sapling size blackgums to occupy intervening openings.

As statistical analysis suggests, the general behavior of blackgum in beetle killed stands indicated relatively low tolerance. Dense patches of small sized trees were found on exposed sites where the original canopy had probably been fairly open allowing a relatively high amount of sunlight to reach the understory. Fowells (1965) reports that blackgum usually is found in the intermediate crown class in mixture with other species, and that it responds poorly to release. Further, there are no known reports of mature even-aged blackgum stands on xeric sites in the Southern Appalachians. Accordingly, in spite of blackgums' dominance in many replacement stands, it is expected that few blackgums will grow to fill the gaps in the original canopy. Most will probably remain small and will eventually be overtopped by other hardwood species.

Dogwood overstory. Regression analysis indicated that dogwood in the replacement canopy increased with lower elevations*, decreased solar radiation*, deeper organic horizons, less acid soils* and steeper slopes (Table 29 in Appendix). In addition dogwood correlated with more protected aspects (Table 11 in Appendix). These variables confirmed the field observation that dogwood was restricted to relatively protected old field sites. The restriction is probably due to its susceptibility to drought (Fowell, 1965), a regular microclimatic occurrence on extremely exposed sites (Racine, 1966).

The inverse relationship between dogwood and blackgum overstory densities was similar to the relationship between red maple and blackgum. Although site requirements for dogwood and blackgum were similar,

dogwood apparently had the competitive advantage on mesic sites relegating blackgum to xeric sites where dogwood was restricted by lack of moisture.

Dogwood is normally an understory species,and it will rapidly decline in replacement overstory cover as other tolerant hardwoods overtop it.

Understory Relationships

Total understory. As would be expected, in the understory stratum hardwood subsaplings were more prevalent than pines. The regression model indicated that total understory density increased with lower elevations*, smaller kills, increased potassium availability, thinner organic horizons*, more dense overstories, and reduced soil acidity* (Table 19 in Appendix; Table 13 in Appendix). These variables suggested that understory density was higher at low elevations on somewhat protected old field sites. Such understories were dominated by red maple, dogwood, and white pine.

Correlations between total understory density and its species constituents (Table 15 in Appendix) showed that red maple, Virginia pine, chestnut oak, and dogwood were the common components of dense understories. All of these except Virginia pine are fairly tolerant and were often found in understories of mixed species. Virginia pine subsaplings, however, grew in dense, almost pure understory stands on dry ridges. Scarlet oak and blackgum were widely distributed and showed a less pronounced tendency to grow in dense understories.

Pine understory. The regression model for density of understory pines identified lower elevations, upper slope positions, shallower soils, and denser overstory (Table 20 in Appendix). These conditions best describe Virginia pine understory on ridgetop sites, and the regression model for Virginia pine was similar (Table 23 in Appendix). Of the pines, Virginia pine was the most dense in the understory (Table 15 in Appendix) because of its characteristic of forming very dense thickets under open stands and because of the suppression of pitch and table mountain pine subsaplings by mountain laurel.

Table mountain pine and pitch pine were very closely associated in the understory (Table 15 in Appendix). Regression models for both species included increased total overstory density (Table 21 in Appendix; Table 22 in Appendix). The table mountain pine equation also included increased slope steepness* indicating that it was more restricted to exposed sites than was pitch pine. Understory density for both species increased as their density in the overstory increased (Table 14 in Appendix).

Virginia pine and oaks in the understory increased in density together indicating that they were often found on the same sites. Virginia pines in the understory were usually suppressed trees and most will probably not persist to maturity.

Oak understory. Oak in the understory was best predicted by thinner soils*, lower elevation*, higher slope positions, and increased low shrub cover (Table 24 in Appendix; Table 13 in Appendix). From field observations these were ridge sites at low elevations. Post, southern

red, and white oaks dropped out of the sample as elevations increased, possibly accounting for the negative correlation with elevation.

The chestnut oak understory density model included smaller beetle kills*, increased low-shrub cover*, increased soil potassium availability, and lower elevations, while correlations also related it with reduced slope (Table 26 in Appendix; Table 13 in Appendix). These all point to low elevation ridge sites as optimum locations. Chestnut oak was the prevalent understory species beneath Virginia pine overstories (Table 14 in Appendix); it will likely replace Virginia pine on such sites.

Scarlet oak in the understory increased as its overstory density increased (Table 14 in Appendix) probably due to prolific sprouting (Fowells, 1965).

Red maple understory. Red maple was very common in the understory, and because of its wide distribution it was poorly explained by regression and correlation. Reduced A horizon acidity was the only significant variable identified in either analysis (Table 27 in Appendix; Table 13 in Appendix), indicating a slight tendency to increase at low elevation where red maple was a common overstory dominant.

Blackgum understory. The blackgum understory density model included thinner O horizons, increased potassium availability, increased solar radiation, and increased A horizon acidity (Table 28 in Appendix), indicating that relatively fertile xeric sites are optimum, as was true

with blackgum in the overstory. Correlation analysis indicates a positive relationship between blackgum in the overstory and understory (Table 14 in Appendix).

Understory blackgums increased with more open stands dominated by low-tolerance oaks, particularly scarlet oak, but decreased under more closed understories containing red maple and dogwood (Table 14 in Appendix).

Dogwood understory. Dogwood understory density was best explained by reduced solar radiation*, less acidic soil*, steeper slopes, reduced low-shrub cover*, and smaller kills (Table 29 in Appendix; Table 13 in Appendix). Correlation alone indicated an increase with lower elevations, more protected aspects, thinner O horizons, and dogwood in the overstory (Table 14 in Appendix). All of these site variables except O horizon thickness were the same in the dogwood overstory analyses. Apparently there was increased sprouting on sites with thinner O horizons.

Reproduction Relationships

Total reproduction. Regression tied increased reproduction to reduced low-shrub cover*, less acidic soils*, lower slope positions, smaller kills, reduced slope steepness, and increased understory density* (Table 19 in Appendix, Table 16 in Appendix; Table 17 in Appendix). Correlation analysis added lower elevations, more protected aspects, reduced solar radiation, thinner O horizons, and reduced herb

and tall-shrub cover also correlated with total reproduction. The conditions were typical of submesic old field sites where red maple and dogwood reproduction was very dense (Table 4 in Appendix). Comparing total overstory, understory, and reproduction densities, there was a definite tendency toward more mesic species and site conditions with lower strata.

Total reproduction decreased under table mountain and pitch pine overstories (Table 14 in Appendix). This was due to the corresponding increase in mountain laurel which severely restricted all seedling establishment.

Pine reproduction. As expected, predictions from regression equations for pine reproduction and its species components were very poor with R-squares of .10 or less. Generally pine reproduction was meager throughout the sample. Virginia pine reproduction was the most prolific (Table 18 in Appendix), and as a result, the variables for total pine reproduction were identical with those for Virginia pine. Both regression equations contained only tall-shrub cover*, and correlation added only aspect (Table 20 in Appendix; Table 23 in Appendix; Table 16 in Appendix). The positive correlation with aspect was because Virginia pine seedlings were more dense on southeast facing rather than southwest facing slopes. Such sites were often old fields.

Table mountain pine reproduction was highest on higher elevation sites with thin O horizons (Table 21 in Appendix). The positive relationship between seedling density and thin organic layers suggested

that peaty humus layers in the table mountain pine-pitch pine type restricted table mountain pine seedling establishment.

Table mountain pine reproduction increased as it increased as a component of the understory, and pitch pine reproduction increased with both understory pitch and table mountain pines (Table 17 in Appendix). Pitch pine reproduction also positively correlated with red maple understory density. The relationship appeared weak and may have reflected a chance correlation, since it would seem that intolerant pitch pine seedlings would be shaded out by a dense red maple understory.

Pitch pine and red maple reproduction tended to increase together (Table 18 in Appendix). From tally sheets it was found that high density for both coincided only on a very few upper slope sites. The positive correlation between Virginia pine and dogwood was not apparent from field data and was perhaps just a chance correlation.

Oak reproduction. Regression showed increased oak reproduction associated with thinner O horizons*, less acid A horizons*, lower slope positions, and reduced shrub cover*, and additional correlates were decreased elevation and reduced herbaceous and tall-shrub cover (Table 24 in Appendix; Table 16 in Appendix). These conditions were typical of old field sites in contrast to exposed ridgetops on which oak was a more common component of the understory. This site-density distribution for oak is in keeping with the findings of Carvell and Tryon (1961) in West Virginia.

Oak reproduction was inversely related to table mountain and pitch pine in the overstory and was positively related to dogwood overstory density further suggesting an affinity for more mesic sites (Table 14 in Appendix).

Increased scarlet oak reproduction was predicted by thinner organic horizons*, higher elevations, increased solar radiation, less acid soils*, reduced low-shrub cover and reduced slope steepness (Table 25 in Appendix). Such conditions were found on upper slope and ridgetop positions where scarlet oak was most abundant in the overstory and sprouting was prolific. The intolerance of scarlet oak was evident in its dependence on increased solar radiation and reduced low-shrub cover.

Chestnut oak reproduction increased with blackgum overstory density (Table 14 in Appendix), implying that chestnut oak may be an important successor on sites presently dominated by blackgum.

Red maple reproduction. Regression analysis related increased red maple reproduction to decreased potassium in the A horizon*, reduced herb cover, reduced solar radiation, reduced low-shrub cover, increased elevation, and increased understory density (Table 27 in Appendix; Table 16 in Appendix). Red maple reproduction tended to be high beneath red maple or blackgum subsaplings (Table 17 in Appendix) on protected upper slope positions. Reproduction did not appear to be sensitive to low soil nutrition (Fowells, 1965), but it was limited by extremely xeric site conditions.

<u>Blackgum reproduction</u>. Variance in blackgum reproduction was best explained by increased elevation, thinner organic layers*, and reduced tall-shrub cover*, and correlation weakly related blackgum reproduction to less exposed aspects, less acidic soils, and increased potassium availability (Table 28 in Appendix; Table 16 in Appendix). Optimum sites tended to be mid elevation, southeast facing upper slopes suggesting slightly less xeric conditions than those where blackgum overstory was predominant. Blackgum reproduction correlated with overstory density indicating its tendency to sprout (Fowells, 1967).

<u>Dogwood reproduction</u>. Increased dogwood reproduction was best predicted by decreased solar radiation*, reduced low-shrub cover*, and less acid A horizons*; other correlates were decreased elevation, more protected aspects, and thinner O horizons (Table 29 in Appendix; Table 16 in Appendix). As with dogwood in the other strata (Table 14 in Appendix; Table 17 in Appendix), reproduction was most abundant on low elevation submesic sites.

CHAPTER VI

SUMMARY AND CONCLUSIONS

A. SUMMARY

Results of this study support the findings of Hoffman and Anderson (1945) that southern pine beetle infestations convert pine stands to mixed pine-hardwood stands with poor pine reproduction. Prior to infestation, sampled stands averaged 83% pine, and beetles killed an average of 88% of the canopy pine basal area or 72% of the original canopy. Surviving pines averaged 30% of the replacement overstory (stems greater than 3 cm), while pine accounted for only 8% of the understory stems and 5% of the reproduction. In absence of further disturbance, yellow pines will probably continue to diminish in importance as more tolerant hardwoods fill canopy gaps.

Six replacement types were derived from cluster analysis, and these were grouped into three broader type-groups. The first type-group consisted of stands dominated by red maple and included the red maple-dogwood and the red maple-sourwood types. The controlling factor for red maple dominance appeared to be relatively low incident solar radiation which was expressed as a combination of protected aspects and low slope angle. Before infestation, pines probably occupied these sites because of disturbance by humans and poor soil conditions. Sites occupied by this type-group were the most mesic of those sampled, and replacement of overstory pines by hardwoods was the most complete.

The two replacement types within the red maple type-group were separated by elevation and topgraphic position, the red maple-dogwood type occupying low elevations and mid to low slope positions,and the drier red maple-sourwood type occupying mid elevation, broad ridgetops and protected upper slopes. The red maple-dogwood type appeared to be rapidly converting to mixed hardwoods and white pine. The future canopy of the red maple-sourwood type will be a mixture of chestnut oak, scarlet oak, and residual pines, probably succeeding to stands dominated by chestnut oak.

The second general type-group consisted of stands in which surviving pines shared dominance in the replacement canopy with either blackgum or scarlet oak. Stands in this category made up 60% of the total sample, and included the blackgum-mixed pine, Virginia pine-blackgum, and mixed pine-scarlet oak replacement types. Elevations ranged from 345 to 1250 meters (1130-4100 feet) but were typically mid elevational, and sites were steep side slopes or narrow ridgetops receiving high insolation. Soil fertility, specifically phosphorus availability in the A horizon, appeared to be an important factor in separating these three replacement types. Relatively fertile but steep mid to upper slope positions were occupied by blackgum-mixed pine stands. On upper slopes and ridgetops in which phosphorus was somewhat more limited the Virginia pine-blackgum type was prevalent, and similar topographic sites where phosphorus and potassium availability was very low were occupied by scarlet oak-mixed pine stands.

Blackgum-mixed pine stands are expected to succeed to scarlet oak, chestnut oak, and residual pines for a considerable time, possibly eventually succeeding to open chestnut oak. Virginia pine will probably continue to make up a large portion of the Virginia pine-blackgum overstory. However, scarlet oak and chestnut oak will ultimately dominate these sites with scattered pines present in the canopy. The mixed pine-scarlet oak type is expected to succeed to stands dominated by scarlet oak with blackjack oak, black oak, chestnut oak, and scattered pines as associates.

The third type-group consisted of the single remaining replacement type, table mountain pine-pitch pine. This type occupied exposed steep upper slope beetle kills at elevations averaging over 1000 meters (3280 feet). Soils were thin, O horizons were deep and peaty, and A horizons were highly acidic and extremely low in both phosphorus and potassium. Residual pines, largely sapling size, accounted for 70% of the overstory density. Dense mountain laurel and ericaceous herb cover restricted the establishment of an understory stratum. Without disturbance, table mountain and pitch pines will dominate in very open patchy stands associated with red maple, blackgum, and scattered scarlet oaks. Little pine reproduction was found, and additional pine regeneration under prevailing conditions is highly unlikely. From stratal patterns it appeared that pine will not maintain dominance and that red maple, blackgum, scarlet oak and chestnut oak will slowly increase in importance. Overstory canopies on such sites will remain very open indefinitely.

The distribution of replacement types in relationship to elevation and moisture is summarized in Figure 3.

The permanent conversion of pine stands to mixed pine-hardwoods by southern pine beetles would seem to be detrimental to the beetle as well as to pines. Barden (1974) inferred that modern outbreaks of pine beetles in the Great Smoky Mountains were opportunistic and were the result of increased pine acreage due to man-caused fire since European settlement of the area. He predicted that the importance of the beetles will diminish as most pine forests in the park are allowed to naturally succeed to hardwoods. To an extent will will certainly be the case. However, the fact that the southern pine beetle has evolved in a very complex and highly selective system for mass attacking pines on moisture deficient sites (Gara, 1967; Rudinsky, 1973) suggests that such behavior should be favorable to the continuance of both beetle populations and pure pine stands as the beetle's host type.

Fire is perhaps the key to this interpretation. The accumulation of dry, resinous pine debris after an infestation is dramatic, and heavy fuel loadings greatly increase the potential for hot fires. In investigating the impacts of an extensive lightning-caused fire in the Cades Cove subdistrict, National Park Service researchers found that height of leaf-scorch increased threefold in beetle kills over the surrounding uninfested area implying a much greater fire intensity (Mark Harmon, Personal Communication). As Barden (1974) demonstrated, hotter fires tend to favor pine seedling establishment while cooler surface fires favor hardwood sprouts.

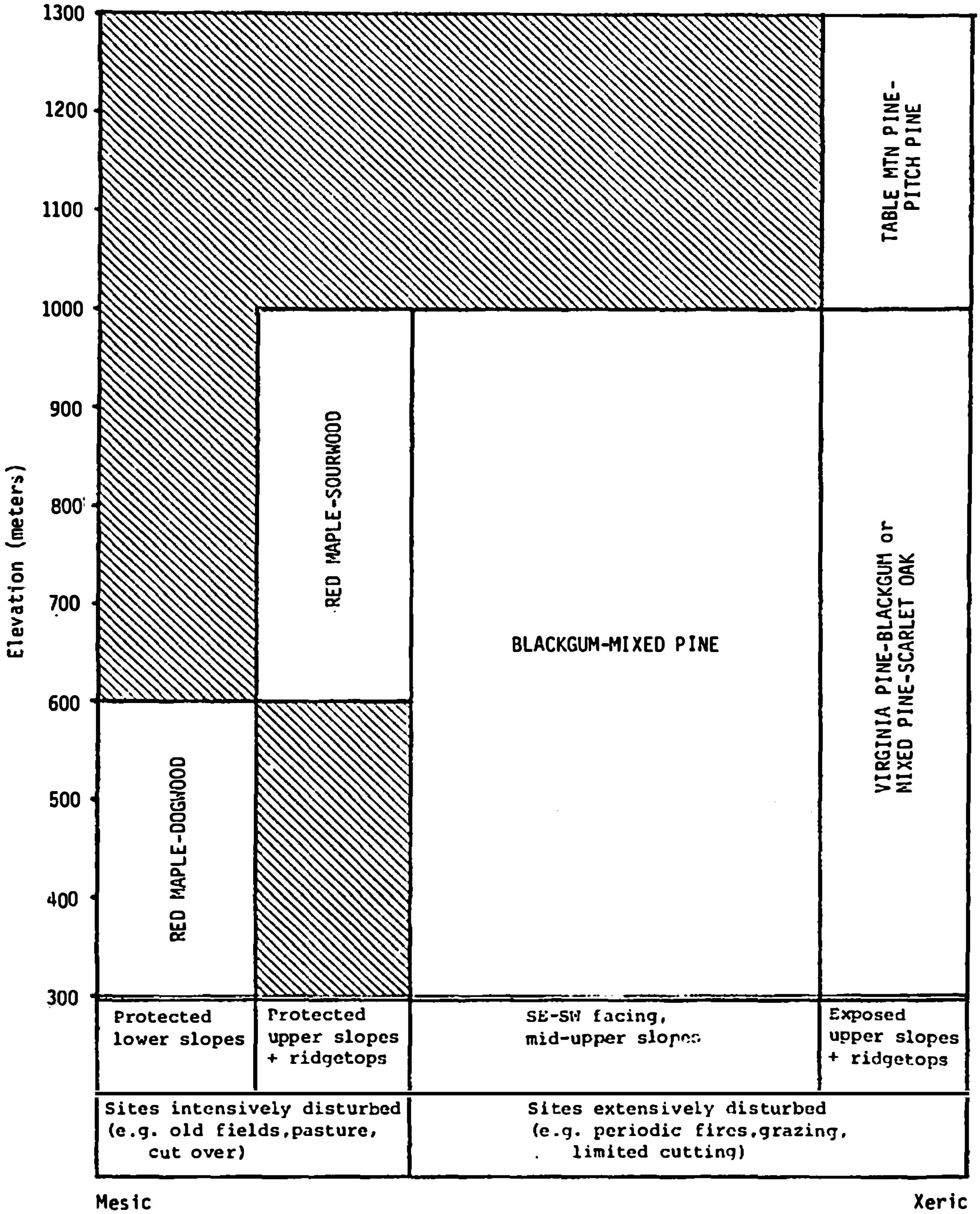

Figure 3. Replacement type patterns in relation to elevation and moisture.

It is possible, then, that southern pine beetle infestations may encourage reestablishment of pure pine or pine dominated stands by increasing the inflamability of stands. Beetle kills may serve as primers for kindling surface fires into crown fires which reduce competing hardwoods and prepare excellent pine seedbed conditions.

B. CONCLUSIONS

The following conclusions appear warranted from the results of this study.

1. In the Great Smoky Mountains the southern pine beetle greatly reduced the importance of pine in infested stands, in most cases converting pine dominated stands to open mixed pine-hardwood stands having abundant hardwood regeneration but little pine.
2. Six replacement types derived from cluster analysis were:
   (a) the red maple-dogwood type,
   (b) the red maple-sourwood type,
   (c) the blackgum-mixed pine type,
   (d) the Virginia pine-blackgum type,
   (e) the mixed pine-scarlet oak type,
   (f) the table mountain pine-pitch pine type.
3. Lack of upper canopy, the prevalence of sapling size and smaller stems, and the dominance of residual pines and mid seral and intolerant hardwoods indicated that sampled stands were in early stages of recovery.

4. Environmental factors influencing replacement stand composition appeared to be elevation, incident solar radiation, topographic position, and soil nutrient availability. Generally, sites were topographically xeric or on infertile soils or both.
5. In the absence of further disturbance, pines will continue to decline in importance in all stands. Replacement will be as follows:
   (a) on sub-mesic old field sites pines will be replaced by mixed hardwoods and white pines,
   (b) on sub-xeric and relatively fertile xeric sites chestnut oak will eventually dominate with scarlet oak as an associate,
   (c) on infertile xeric sites scarlet oak will dominate with scattered pines in the canopy.

LITERATURE CITED

LITERATURE CITED

Albright, John. 1974. Historic overview, Great Smoky Mountains National Park. National Park Service, Denver Service Center, Denver (typewritten report).

Bakèr, Whiteford L. 1972. Eastern forest insects. USDA Forest Service, Washington, D.C. 642 pp.

Balch, R. E. 1928. The influence of the southern pine beetle on forest composition in western North Carolina. Unpublished Master's thesis, Syracuse University. 33 pp.

Barden, L. S. 1974. Lightning fires in the Southern Appalachian forests. Unpublished Ph.D. dissertation, The University of Tennessee, Knoxville. 65 pp.

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1976. A user's guide to SAS 76. SAS Institute Inc., Raleigh, N.C. 329 pp.

Barry, P. J., J. D. Ward, and W. E. McDowell. 1971. Evaluation of southern pine beetle infestations on the Cheoah Ranger District, Nantahala National Forest, North Carolina, and the Great Smoky Mountains National Park, North Carolina and Tennessee. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 72.

Barry, P. J., and E. T. Wilson. 1971. Evaluation of southern pine beetle infestations on the Cheoah Ranger District, Nantahala National Forest and the Great Smoky Mountains National Park, North Carolina, USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 71-1-14.

Bass, Q. R., C. Falkner, and M. C. R. McCollough. 1975. First interim report: archeological survey of Great Smoky Mountains National Park. University of Tennessee, Knoxville. (Typewritten report with map.)

Beal, J. A. 1927. Weather as a factor in southern pine beetle control. J. Forestry 25:741-742.

Beal, J. A. 1933. Temperature extremes as a factor in the ecology of the southern pine beetle. J. Forestry 31:329-336.

Bennett, W. H. 1968. Timber management and southern pine beetle research. For. Farmer 27(9):12-13.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Press, New York. 596 pp.

Bray, N. C. 1974. The nature and properties of soils. Macmillan Pub. Co., New York. 639 pp.

Bryan, M. B. 1956. A simplified method of correcting for slope on circular plots. J. Forestry 54:442-445.

Cain, S. A. 1931. Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee. I. Soil reaction and plant distribution. Bot. Gaz. 91:22-41.

Cain, S. A. 1937. A preliminary guide to the Greenbrier-Brushy Mountain nature trail, the Great Smoky Mountains National Park. University of Tennessee, Knoxville. Mimeographed, 29 pp.

Campbell, C. C. 1960. A birth of a national park in the Great Smoky Mountains. University of Tennessee Press, Knoxville. 155 pp.

Carvell, K. L., and E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. Forest Sci. 7:98-105.

Ciesla, W. M., H. L. Lambert, and R. T. Franklin. 1965. Forest insect and disease detection survey of the Great Smoky Mountains National Park and the Cherokee Indian Reservation, North Carolina and Tennessee. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 65-1-21.

Clerke, W. H., R. F. Bassett, and H. L. Lambert. 1968a. Detection and evaluation of southern pine beetle infestations on the Great Smoky Mountains National Park. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 68-1-18.

Clerke, W. H., R. F. Bassett, and J. L. Knighten. 1968b. Evaluation of southern pine beetle infestations on the Great Smoky Mountains National Park. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 68-1-21.

Clerke, W. H., A. E. Landgraf, and W. E. McDowell. 1968c. Evaluation of southern pine beetle infestations in the Great Smoky Mountains National Park, Tennessee. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 69-1-12.

Clerke, W. H., and R. F. Bassett. 1969. An evaluation of southern pine beetle infestations, Great Smoky Mountains National Park in Tennessee and North Carolina. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 69-1-51.

Coe, J. L. 1974. Archeological overview, Great Smokies region, North Carolina portion. University of North Carolina, Chapel Hill. (Typewritten)

Craighead, F. C. 1925. Bark-beetle epidemics and rainfall deficiency. J. of Econ. Entomol. 18(4):577-586.

Craighead, F. C., and R. A. St. George. 1928. Some effects of fire and insect attack on shortleaf pine. Forest Worker 4(2):11-12.

Dixon, John C., and E. A. Osgood. 1961. Southern pine beetle: a review of present knowledge. USDA Forest Service, SE Forest Exp. Sta., Asheville, N.C. 34 pp.

Elder, J. E. 1959. Soil survey of Blount County, Tennessee. USDA Soil Conservation Service. 119 pp.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill, New York. 714 pp.

Flavel, T. H., P. J. Barry, J. D. Ward, and W. M. Clerke. 1970. An evaluation of the effects of sub-zero temperatures on an epidemic southern pine beetle population, Nantahala and Cherokee National Forests and the Great Smoky Mountains National Park, Tennessee and North Carolina. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 70-1-46.

Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA, U.S. For. Serv., Agr. Handbook 271. 762 pp.

Frank, Ernest C., and Richard Lee. 1966. Potential solar beam irradiation on slopes: Tables for 30° and 50° Latitude. U.S. For. Serv., Research Paper RM 18. (Rocky Mtn. Forest and Range Experiment Station).

Gara, R. I. 1967. Studies on the attack behavior of the southern pine beetle. I. The spreading and collapse of outbreaks. Contributions of the Boyce Thompson Institute 23(10):349-354.

Hay, R. C., C. Eagar, and D. Johnson. 1976. Status of the balsam wooly aphid in the Great Smoky Mountains National Park—1976. Management Report No. 20. Uplands Field Research Lab., Gatlinburg, Tennessee. 18 pp.

Hesler, L. R. 1962. List of fungi of the Great Smoky Mountains National Park. Botany Dept., University of Tennessee. (Typewritten, 83 pp.)

Hodges, J. D., and L. S. Pickard. 1971. Lightning in the ecology of the southern pine beetle, Dendroctonus frontalis (Coleoptera: Scolytidae). Canadian Entomologist 103:44-51.

Hoffman, C. H., and R. F. Anderson. 1945. Effects of southern pine beetle on timber losses and natural restocking. J. Forestry 43:436-439.

Hoffman, H. L. 1966. Notes on vascular plant families in the Great Smoky Mountains. Castanea 31:301-307.

Hopkins, A. D. 1899. Report on investigations to determine the cause of unhealthy conditions of the spruce and pine from 1880-1893, pp. 271-425. In the pine investigation. W. Va. Agric. Exp. Stn. Bull. 45, Pt. 2.

Houchard, Richard. 1974. STATPACK statistical package. Western Michigan University, Kalamazoo. (Computer program).

Hubbard, E. H. 1956. Soil survey of Sevier County, Tennessee. USDA Soil Conservation Service. 203 pp.

Johnson, C. E. 1959. Memorandum dated Jan. 28, 1959, from Acting Superintendent Johnson to Regional Director of NPS Region 1. Great Smoky Mountains National Park, Gatlinburg, Tennessee. (Typewritten).

Kephart, H. 1922. Our southern highlanders. University of Tennessee Press, Knoxville. 469 pp.

King, E. 1972. Rainfall and epidemics of the southern pine beetle. Environ. Entomol. 1:279-285.

King, P. B., and A. Stupka. 1950. The Great Smoky Mountains—their geology and natural history. Sci. Month. 61:31-43.

King, P. B., Robert B. Newman, and J. B. Hadley. 1968. Geology of the Great Smoky Mountains National Park, Tennessee and North Carolina. Geol. Surv. Prof. Pap. 587. 23 pp.

Kowal, R. J. 1958. Letter to Edward A. Hummel, Superintendent, GSMNP dated April 24, 1958. USFS, USDA Div. of For. Pest Control, Asheville, N.C. (Typewritten).

Kozlowski, T. T., and C. E. Ahgren. 1974. Fire and ecosystems. Academic Press, New York. 542 pp.

Light, James B. 1956. Memorandum from GSMNP Assist. Chief Ranger Light to the Chief Ranger dated May 12, 1956. Great Smoky Mountains National Park, Gatlinburg, Tennessee. (Typewritten).

Lindsay, Mary. 1976. History of the Grassy Balds in Great Smoky Mountains National Park, Management Report No. 4. Uplands Field Lab., GSMNP, Gatlinburg, Tennessee. 217 pp.

Lorrio, Peter I. 1968. Soil and stand conditions relating to southern pine beetle activity in Hardin County, Texas. J. Econ. Entomol. 6(2):565-566.

Lorrio, Peter I., and John D. Hodges. 1977. Tree water status affects induced southern pine beetle attack and brood production. South. For. Exp. Stn., New Orleans, Louisiana. 7 pp. (USDA For. Serv. Res. Pap. SO-135.)

Losche, Craig Kendall. 1967. Soil genesis and forest growth on steeply sloping landscapes of the Southern Appalachians. Unpublished Ph.D. dissertation, North Carolina State, Raleigh, N.C.

MacAndrews, A. H. 1926. The biology of the southern pine beetle. Unpublished thesis, Syracuse University. 103 pp.

McCarthy, D. M. 1976. Numerical techniques for classifying forest communities in the Tennessee Valley. Unpublished Ph.D. dissertation, University of Tennessee, Knoxville. 164 pp.

McCracken, W. H. 1978. Comparison of forest cover prior to and following disturbance in two areas of the Great Smoky Mountains National Park. Unpublished Master's thesis, University of Tennessee, Knoxville. 87 pp.

McGinnis, J. T. 1958. Forest litter and humus types of East Tennessee. Unpublished Master's thesis, University of Tennessee, Knoxville. 82 pp.

Miller, F. H. 1938. The vegetation types in the Great Smoky Mountains National Park. Great Smoky Mountains National Park, Gatlinburg, Tennessee. (Typewritten report with map.)

National Park Service. 1955a. Great Smoky Mountains National Park, summary of southern pine beetle 1954-1955. Unpublished typed report, Gatlinburg, Tennessee, dated September 24, 1955.

National Park Service. 1955b. Southern pine beetle control report from July 1 to November 5, 1955. Great Smoky Mountains National Park, Gatlinburg, Tennessee. Typewritten, unpublished report, undated.

National Park Service. 1976. Environmental assessment of alternatives for the General Management Plan, Great Smoky Mountains National Park. NPS, Denver Service Center, Denver. 311 pp.

Orloci, L. 1967. An agglomerative method for the classification of plant communities. J. Ecol. 55:193-206.

Osgood, E. A. 1958. A study of site and stand characteristics of southern pine beetle infestation. U.S. Forest Serv. Southeast. Forest Expt. Sta. (Office Rpt., 5 pp.)

Overly, Fred J. 1959. Memorandum from GSMNP Superintendent Overly to Regional Director, NPS Region 1 dated February 12, 1959. Great Smoky Mountains National Park, Gatlinburg, Tennessee. (Typewritten).

Post, W. M., and J. D. Shepard. 1974. Hierarchical agglomeration. University of Tennessee, Knoxville. (Mimeographed, 8 pp.)

Racine, C. H. 1966. Pine communities and their site characteristics on the Blue Ridge escarpment. J. Elisha Mitchell Sci. Soc. 82:172-181.

Racine, C. H. 1971. Reproduction of three species of oak in relation to vegetational and environmental gradients in the Southern Blue Ridge. Bull. Torrey Botany Club 98:297-310.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill. 1183 pp.

Renwick, J. A. A., and J. P. Vite. 1970. Systems of chemical communication in Dendroctonus. Contributions of the Boyce Thompson Institute 24(13):283-291.

Shanks, R. E. 1954a. Climates of the Great Smoky Mountains. Ecol. 35:354-361.

Shanks, R. E. 1954b. Reference lists of native plants of the Great Smoky Mountains. Botany Dept., University of Tennessee, Knoxville. (Mimeographed, 17 pp.)

Shields, A. Randolph. 1977. The Cades Cove story. Great Smoky Mountains Natural History Association, Gatlinburg, Tennessee. 116 pp.

Smith, L. R. 1977. The swamp and mesic forests of the Cumberland Plateau in Tennessee. Unpublished Master's thesis, University of Tennessee, Knoxville. 121 pp.

Society of American Foresters. 1964. Forest cover types of North America. Soc. Amer. For., Washington. 67 pp.

Springer, M. E., H. DeSelm, and J. A. Elder. 1975. Soils-ecology tour in the Ridge and Valley and Great Smoky Mountains of East Tennessee and Western North Carolina. University of Tennessee, Knoxville. (Mimeographed, 14 pp.)

Stupka, A. 1964. Trees, shrubs, and woody vines of the Great Smoky Mountains National Park. University of Tennessee Press, Knoxville. 186 pp.

Tennessee Valley Authority. 1968. Precipitation in the Tennessee River Basin, Annual, 1968. TVA, Knoxville, Tennessee.

Thatcher, R. C. 1960. Bark beetles affecting southern pines: A review of current knowledge. USDA, USFS, South. For. Exp. Sta., Occas. Pap. 180. 25 pp.

Thomas, R. D. 1966. The vegetation and flora of Chilhowee Mountain. Unpublished Ph.D. dissertation, University of Tennessee, Knoxville. 355 pp.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Georg. Rev. 38:55-94.

United States Department of Agriculture. 1974. Environmental Impact Statement. Strategy for control of the southern pine beetle in the southeastern U.S.

United States Department of Commerce. 1969. Climatological data: Tennessee annual summary. U.S. Government Printing Office, Washington. 74(13).

United States Department of Commerce, National Oceanic and Atmospheric Administration. 1973. Climatological summary: Gatlinburg, Tennessee. NOAA, Nashville, Tennessee.

Wade, Gary L. 1977. Dry phase vegetation of the uplands of the Cumberland Plateau of Tennessee. Unpublished Master's thesis, University of Tennessee, Knoxville. 116 pp.

Ward, J. D., K. H. Knaver, and P. J. Barry. 1969. An evaluation of southern pine beetle infestations, Great Smoky Mountains National Park in Tennessee and North Carolina. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 70-1-30.

Ward, J. D., and W. E. McDowell. 1970. An evaluation of southern pine beetle infestations, Great Smoky Mountains National Park in Tennessee and North Carolina. USDA, USFS, Div. of For. Pest Control, Asheville, N.C. Report No. 70-1-47.

Ward, J. D., E. T. Wilson, and W. E. McDowell. 1971. An evaluation of southern pine beetle infestations on the Great Smoky Mountains National Park. USDA, USFS, Div. of For. Pest Management, Asheville, N.C. Report No. 72-1-14.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. 26:1-80.

Wiggens, James P. 1969. Memorandum: status of southern pine beetle. Great Smoky Mountains National Park, Gatlinburg, Tennessee. (Typewritten, unpublished memorandum dated October 27, 1969.)

Woods, F. W., and R. E. Shanks. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecol. 40:349-361.

APPENDIX

TABLE 1

MEAN SITE VARIABLES FOR REPLACEMENT TYPES

Replacement Type	Elev. (m)[a]	Aspect	% Slope[b]	Solar Radiation[c]	Slope Position[d]	Soil Depth (cm)	O Depth (cm)	pH of A	P in A (kg/ha)[e]	K in A (kg/ha)[e]
Red Maple-Dogwood	422	180°	36.0%	276.0	.55	68.5	3.6	4.80	2.2	111.8
Red Maple-Sourwood	757	221°	36.7%	277.7	.80	73.1	4.0	4.70	2.6	113.0
Blackgum-Mixed Pine	820	185°	40.6%	296.3	.72	69.8	5.2	4.66	3.1	108.5
Virginia Pine-Blackgum	596	201°	40.3%	291.3	.78	70.7	3.9	4.58	2.7	113.7
Mixed Pine-Scarlet Oak	549	167°	38.5%	290.2	.80	77.2	3.8	4.58	2.2	108.1
Table Mtn. Pine-Pitch Pine	1030	202°	45.1%	301.9	.76	67.2	8.2	4.38	2.2	93.0

[a]For conversion to feet, multiply by 3.28 feet/m/

[b]Slopes averaged for side slope positions only, and the mean does not include flat ridgetops.

[c]Determined by slope and aspect transformation (Frank and Lee, 1966).

[d]Ratio of distance from draw vs. total distance from draw to ridge (i.e., draw position = 0, ridge position = 1.0).

[e]For conversion to pounds per acre, multiply by 0.90.

TABLE 2

ESTIMATED RELATIVE CANOPY PINE VOLUMES FOR REPLACEMENT TYPES BEFORE AND AFTER INFESTATIONS

Replacement Type	Pine Relative Basal Area in Original Stand (%)	% of Pine Basal Area Killed	% of Total Basal Area Killed
Red Maple-Dogwood	70	97	68
Red Maple-Sourwood	79	91	72
Blackgum-Mixed Pine	82	90	73
Virginia Pine-Blackgum	86	85	73
Mixed Pine-Scarlet Oak	78	88	68
Table Mtn. Pine-Pitch Pine	98	80	79

TABLE 3

MEAN COVER ESTIMATES FOR REPLACEMENT TYPES

Replacement Type	% Canopy Closure	% Cover-Shrubs > 1 m Tall	% Cover-shrubs < 1 m Tall	% Cover-Herbs
Red Maple-Dogwood	43.8	23.6	12.2	2.2
Red Maple-Sourwood	32.9	28.5	50.6	4.6
Blackgum-Mixed Pine	25.5	37.2	45.1	13.5
Virginia Pine-Blackgum	20.5	26.5	37.7	10.2
Mixed Pine-Scarlet Oak	31.4	16.8	38.0	4.1
Table Mtn. Pine-Pitch Pine	11.5	77.5	30.3	38.6

TABLE 4

COMPOSITION OF THE RED MAPLE-DOGWOOD REPLACEMENT TYPE ACCORDING TO RELATIVE DENSITY OF OVERSTORY (N = 12)

Taxon	Overstory							Understory[d]		Reproduction[e]	
	Total Stems[a]		Residual Canopy[b]			Saplings[c]					
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Acer rubrum	19.6	91.7	13.7	10.4	83.3	21.9	100.0	13.8	83.3	23.0	91.7
Cornus florida	19.4	75.0	9.2	6.2	50.0	23.5	91.7	37.6	66.7	32.7	75.0
Oxydendrum arboreum	8.7	83.3	11.3	7.7	75.0	7.6	91.7	1.7	16.7	0.5	16.7
Nyssa sylvatica	8.6	75.0	4.2	2.5	41.7	10.3	83.3	2.6	16.7	1.6	25.0
Carya tomentosa	7.4	58.3	8.3	7.5	41.7	6.8	66.7	4.8	41.7	1.0	25.0
Quercus alba	7.0	50.0	11.6	13.8	50.0	5.1	50.0	0.4	8.3	5.8	58.3
Tsuga canadensis	5.8	58.3	2.1	2.0	33.3	7.4	66.7	3.5	33.3	1.8	25.0
Pinus strobus	4.5	58.3	5.3	11.1	41.7	4.4	50.0	12.6	66.7	13.9	66.7
Liriodendron tulipifera	3.5	50.0	7.4	7.0	33.3	2.0	58.3	1.3	25.0	2.1	41.7
Quercus coccinea	3.1	58.3	8.4	14.8	58.3	1.0	25.0	8.6	8.3	3.1	50.0
Ilex opaca	3.0	41.7	1.0	0.6	8.3	3.8	41.7	3.5	41.7	2.6	33.3
Carya glabra	2.0	41.7	1.8	0.9	33.3	2.1	41.7	3.0	33.3	--	--
Quercus prinus	1.6	8.3	3.9	2.2	8.3	0.7	8.3	0.4	8.3	--	--
Quercus veluntina	1.0	41.7	2.8	3.0	41.7	0.3	16.7	0.9	16.7	1.0	16.7
Sassafras albidum	1.0	50.0	1.0	0.7	16.7	1.0	41.7	1.3	33.3	1.3	8.3
Pinus virginiana	0.6	25.0	1.8	1.4	25.0	0.1	8.3	2.2	8.3	1.6	16.7
Pinus echinata	0.5	16.7	1.8	2.9	0.5	--	--	--	--	--	--

TABLE 4 (continued)

Taxon	Overstory							Understory[d]		Reproduction[e]	
	Total Stems[a]		Residual Canopy[b]			Saplings[c]					
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Quercus falcata	0.5	25.0	1.8	1.5	25.0	--	--	--	--	--	--
Pinus rigida	0.4	25.0	1.0	2.2	16.7	0.1	8.3	0.4	8.3	--	--
Diospyros virginiana	0.3	16.7	0.7	0.6	8.3	0.1	8.3	0.4	8.3	--	--
Castanea dentata	0.2	16.7	--	--	--	0.3	16.7	0.4	8.3	0.3	8.3
Acer pensylvanicum	0.2	25.0	--	--	--	0.3	25.0	3.0	16.7	--	--
Betula lenta	0.2	8.3	--	--	--	0.3	8.3	1.3	8.3	--	--
Carpinus caroliniana	0.2	8.3	--	--	--	0.3	8.3	--	--	0.8	8.3
Ostrya virginiana	0.2	8.3	--	--	--	0.3	8.3	1.3	8.3	0.5	8.3
Prunus serotina	0.1	8.3	--	--	--	0.1	8.3	--	--	0.3	8.3
Liquidambar styraciflua	0.1	8.3	0.4	0.9	8.3	--	--	--	--	--	--
Acer saccharum	0.1	8.3	--	--	--	--	--	0.1	8.3	--	--
Magnolia fraseri	--	--	--	--	--	--	--	0.9	16.7	0.8	8.3
Fraxinus pennsylvanica	--	--	--	--	--	--	--	0.9	16.7	--	--
Amelanchier laevis	--	--	--	--	--	--	--	0.4	8.3	--	--
Fagus grandifolia	--	--	--	--	--	--	--	0.4	8.3	--	--
Ilex ambigua var montana	--	--	--	--	--	--	--	--	--	5.0	25.0
Pinus pungens	--	--	--	--	--	--	--	--	--	0.3	8.3

TABLE 4 (continued)

[a]Stems greater than 3 cm dbh.

[b]Stems greater than 10 cm dbh.

[c]Stems greater than 3 cm and less than 10 cm dbh.

[d]Stems less than 3 cm dbh and taller than 1 meter.

[e]Stems less than 1 meter tall.

TABLE 5

COMPOSITION OF THE RED MAPLE-SOURWOOD REPLACEMENT TYPE ACCORDING TO RELATIVE DENSITY OF OVERSTORY (N = 10)

Taxon	Overstory										
	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Acer rubrum	48.7	100.0	25.1	15.5	100.0	56.8	100.0	59.5	90.0	51.8	90.0
Oxydendrum arboreum	10.4	100.0	9.3	4.8	100.0	10.0	90.0	0.8	10.0	--	--
Quercus prinus	7.9	90.0	15.8	17.3	90.0	5.1	70.0	0.8	10.0	2.2	20.0
Nyssa sylvatica	7.4	100.0	2.2	7.1	40.0	9.3	90.0	15.7	70.0	2.9	20.0
Quercus coccinea	7.0	100.0	18.6	22.2	80.0	3.0	80.0	3.3	20.0	7.9	40.0
Pinus rigida	6.2	80.0	12.0	17.2	70.0	4.2	60.0	--	--	3.6	30.0
Pinus pungens	2.8	30.0	6.0	5.3	30.0	1.7	30.0	0.8	10.0	1.4	10.0
Pinus strobus	2.4	50.0	3.3	4.2	50.0	2.0	50.0	2.5	30.0	15.8	30.0
Pinus virginiana	2.4	40.0	3.3	2.9	20.0	2.0	40.0	--	--	--	--
Carya glabra	2.1	20.0	1.6	1.1	10.0	2.3	20.0	0.8	10.0	--	--
Quercus veluntina	0.8	10.0	2.2	2.2	10.0	0.4	10.0	--	--	0.7	10.0
Acer pennsylvanicum	0.6	20.0	--	--	--	0.8	20.0	1.6	20.0	1.4	10.0
Halesia caroliniana	0.4	10.0	--	--	--	0.6	10.0	1.6	10.0	--	--
Amelanchier laevis	0.3	20.0	--	--	--	0.4	20.0	--	--	1.4	20.0
Robinia pseudoacacia	0.3	20.0	--	--	--	0.4	20.0	0.8	10.0	0.7	10.0
Castanea dentata	0.1	10.0	0.5	0.5	10.0	--	--	0.8	10.0	0.7	10.0
Tsuga canadensis	0.1	10.0	--	--	--	2.0	10.0	1.6	20.0	0.7	10.0

TABLE 5 (continued)

Taxon	Overstory										
	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Ilex ambigua var montana	--	--	--	--	--	--	--	4.1	20.0	4.3	10.0
Liriodendron tulipifera	--	--	--	--	--	--	--	2.5	10.0	0.7	20.0
Sassafras albidum	--	--	--	--	--	--	--	1.6	10.0	3.6	10.0
Magnolia fraseri	--	--	--	--	--	--	--	0.8	10.0	--	--

[a]Stems greater than 3 cm dbh.

[b]Stems greater than 10 cm dbh.

[c]Stems greater than 3 cm and less than 10 cm dbh.

[d]Stems less than 3 cm dbh and taller than 1 meter.

[e]Stems less than 1 meter tall.

TABLE 6

COMPOSITION OF THE BLACKGUM-MIXED PINE REPLACEMENT TYPE ACCORDING TO RELATIVE DENSITY OF OVERSTORY (N = 27)

	Overstory										
Taxon	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Nyssa sylvatica	29.3	100.0	7.5	4.8	63.0	36.0	100.0	28.2	77.8	9.0	51.8
Acer rubrum	14.6	100.0	10.0	7.1	8.15	15.8	96.3	39.9	85.2	42.8	88.9
Pinus rigida	11.7	92.6	14.5	12.4	77.8	10.9	88.9	--	--	1.8	18.5
Pinus pungens	8.5	63.0	18.1	14.9	51.8	5.6	59.2	0.3	3.7	0.8	7.4
Quercus prinus	7.8	81.5	14.5	21.0	74.1	5.8	66.7	--	--	1.8	22.2
Quercus coccinea	7.6	77.8	14.7	22.9	77.8	5.4	63.0	3.4	25.9	9.5	59.3
Oxydendrum arboreum	6.6	74.1	8.5	4.8	59.2	6.0	66.7	3.4	33.3	4.6	7.4
Pinus virginiana	4.1	51.8	4.9	4.7	37.0	3.9	44.4	2.5	22.2	3.4	18.5
Quercus veluntina	2.7	51.8	2.1	3.1	18.5	2.8	51.8	2.0	18.5	0.8	11.1
Pinus strobus	1.3	22.2	1.9	2.7	14.8	1.2	22.2	1.7	14.8	3.1	25.9
Sassafras albidum	1.0	18.5	0.2	0.1	3.7	1.3	18.5	5.6	29.6	4.6	37.0
Castanea dentata	0.9	29.6	0.2	0.1	3.7	1.1	29.6	3.6	25.9	0.3	3.7
Tsuga canadensis	0.6	22.2	0.2	0.1	3.7	0.7	18.5	1.1	11.1	0.5	7.4
Hamamelis virginiana	0.5	3.7	--	--	--	0.7	3.7	0.8	3.7	2.8	3.7
Carya tomentosa	0.4	11.1	0.4	0.3	3.7	0.4	11.1	0.3	3.7	0.5	7.4
Quercus marilandica	0.4	3.7	0.6	0.3	3.7	0.3	3.7	0.6	7.4	1.0	3.7
Carya glabra	0.4	11.1	--	--	--	0.4	11.1	0.3	3.7	0.3	3.7

TABLE 6 (continued)

Taxon	Overstory										
	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Magnolia fraseri	0.3	14.8	--	--	--	0.4	14.8	--	--	0.3	3.7
Robinia pseudoacacia	0.3	14.8	--	--	--	0.4	14.8	3.1	22.2	2.6	11.1
Acer pennsylvanicum	0.2	7.4	--	--	--	0.3	7.4	0.8	7.4	0.8	11.1
Pinus echinata	0.2	3.7	0.6	1.6	3.7	--	--	--	--	0.5	3.7
Amelanchier laevis	0.2	7.4	--	--	--	0.2	7.4	0.8	3.7	2.6	3.7
Lirodendron tulipifera	0.2	7.4	--	--	--	0.2	7.4	0.6	7.4	0.3	3.7
Cornus florida	0.1	3.7	--	--	--	0.1	3.7	--	--	1.6	7.4
Quercus alba	0.1	3.7	--	--	--	0.1	3.7	0.3	3.7	--	--
Ilex opaca	0.1	3.7	--	--	--	0.1	3.7	--	--	--	--
Ilex ambiqua var *montana*	--	--	--	--	--	--	--	0.8	3.7	2.3	3.7
Rhus glabra	--	--	--	--	--	--	--	--	--	1.0	3.7
Fagus grandifolia	--	--	--	--	--	--	--	--	--	0.3	3.7
Quercus rubrum	--	--	--	--	--	--	--	--	--	0.3	3.7

[a]Stems greater than 3 cm dbh.

[b]Stems greater than 10 cm dbh.

[c]Stems greater than 3 cm and less than 10 cm dbh.

[d]Stems less than 3 cm dbh and taller than 1 meter.

[e]Stems less than 1 meter tall.

TABLE 7

COMPOSITION OF THE VIRGINIA PINE-BLACKGUM REPLACEMENT TYPE ACCORDING TO RELATIVE DENSITY OF OVERSTORY (N = 13)

Taxon	Overstory										
	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Pinus virginiana	30.8	100.0	42.8	32.8	84.6	27.1	100.0	15.1	46.2	3.1	23.1
Nyssa sylvatica	24.3	100.0	8.1	5.8	61.5	29.4	100.0	23.8	92.3	11.7	46.2
Oxydendrum arboreum	9.2	92.3	5.2	3.7	53.8	10.4	84.6	1.2	23.1	0.1	7.7
Quercus coccinea	7.3	84.6	9.7	15.5	76.9	6.5	84.6	3.7	38.5	7.4	46.2
Pinus rigida	6.7	76.9	10.1	16.8	53.8	5.6	53.8	0.3	7.7	1.2	15.4
Acer rubrum	4.8	84.6	2.0	1.8	30.8	5.6	76.9	20.7	84.6	31.4	76.9
Quercus prinus	4.1	69.2	10.5	1.2	53.8	2.1	53.8	1.5	30.8	--	--
Pinus echinata	2.8	23.1	4.8	4.8	15.4	2.1	15.4	1.8	15.4	0.6	7.7
Pinus strobus	2.2	61.5	0.8	0.8	7.8	2.6	53.8	2.5	38.5	8.1	23.1
Pinus pungens	1.7	30.8	2.4	1.8	23.1	1.5	30.8	0.3	7.7	0.6	7.7
Sassafras albidum	1.7	38.5	--	--	--	2.3	38.5	9.9	53.8	20.3	46.2
Quercus veluntina	0.9	38.5	1.2	2.2	15.4	0.8	30.8	3.6	15.4	3.7	38.5
Cornus florida	0.8	23.1	0.4	0.2	7.7	0.9	23.1	0.3	7.7	--	--
Quercus marilandica	0.7	7.7	0.4	0.2	7.7	0.8	7.7	0.9	7.7	--	--
Quercus alba	0.6	15.4	0.8	0.5	7.7	0.5	15.4	0.6	15.4	2.5	23.1
Quercus falcata	0.5	7.7	0.8	0.5	7.7	0.4	7.7	0.3	7.7	--	--
Amelanchier laevis	0.3	15.4	--	--	--	0.4	15.4	--	--	0.6	7.7

TABLE 7 (continued)

Taxon	Overstory: Total Stems[a]		Overstory: Residual Canopy[b]			Overstory: Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Tsuga canadensis	0.2	15.4	--	--	--	0.2	15.4	0.3	7.7	--	--
Rhus glabra	0.2	7.7	--	--	--	0.2	7.7	2.8	7.7	0.6	7.7
Carya glabra	0.2	7.7	--	--	--	0.2	7.7	1.2	7.7	--	--
Castanea dentata	0.1	7.7	--	--	--	0.1	7.7	0.9	15.4	--	--
Ilex ambigua var *montana*	--	--	--	--	--	--	--	8.6	23.1	--	--
Magnolia fraseri	--	--	--	--	--	--	--	1.2	15.4	--	--
Acer pennsylvanicum	--	--	--	--	--	--	--	0.3	7.7	0.6	7.7
Carya tomentosa	--	--	--	--	--	--	--	0.3	7.7	--	--
Ilex opaca	--	--	--	--	--	--	--	0.3	7.7	--	--
Prunus serotina	--	--	--	--	--	--	--	0.3	7.7	--	--

[a]Stems greater than 3 cm dbh.

[b]Stems greater than 10 cm dbh.

[c]Stems greater than 3 cm and less than 10 cm dbh.

[d]Stems less than 3 cm dbh and taller than 1 meter.

[e]Stems less than 1 meter tall.

TABLE 8

COMPOSITION OF THE MIXED PINE-SCARLET OAK REPLACEMENT TYPE ACCORDING TO RELATIVE DENSITY OF OVERSTORY (N = 9)

	Overstory										
Taxon	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Quercus coccinea	20.2	100.0	42.2	42.3	100.0	12.8	100.0	9.4	44.4	11.5	44.4
Nyssa sylvatica	15.8	100.0	1.5	1.3	22.2	20.7	100.0	45.6	100.0	8.6	44.4
Acer rubrum	10.2	88.9	6.1	5.0	44.4	11.6	88.9	16.7	66.7	34.6	77.8
Quercus marilandica	9.9	66.7	2.5	1.6	44.4	12.4	66.7	0.7	11.1	1.0	11.1
Pinus virginiana	9.3	100.0	11.7	12.2	55.6	8.4	88.9	0.7	11.1	5.8	22.2
Pinus rigida	8.0	88.9	6.6	6.3	44.4	8.4	88.9	0.7	11.1	3.8	33.3
Oxydendrum arboreum	6.8	100.0	6.1	4.3	55.5	7.1	100.0	1.4	22.2	--	--
Pinus echinata	4.0	33.3	3.0	2.0	22.2	4.3	33.3	--	--	1.0	11.1
Quercus veluntina	3.6	77.8	2.5	2.4	33.3	4.0	77.8	--	--	3.8	22.2
Quercus prinus	3.0	66.7	5.1	8.2	66.7	2.2	55.6	--	--	--	--
Pinus pungens	2.3	33.3	8.1	11.5	33.3	0.3	22.2	--	--	--	--
Pinus strobus	2.1	33.3	3.0	2.3	22.2	1.7	22.2	2.2	33.3	2.9	11.1
Quercus alba	1.4	44.4	0.5	0.3	11.1	1.7	44.4	--	--	--	--
Quercus falcata	1.0	22.2	--	--	--	1.4	22.2	2.2	22.2	--	--
Cornus florida	0.8	33.3	--	--	--	1.0	33.3	3.6	33.3	--	--
Sassafras albidum	0.6	33.3	--	--	--	0.9	33.3	4.4	44.4	13.5	77.8
Carya tomentosa	0.3	22.2	0.5	0.3	11.1	0.2	11.1	3.6	22.2	1.9	11.1

TABLE 8 (continued)

	Overstory										
Taxon	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Quercus stellata	0.3	11.1	--	--	--	0.3	11.1	--	--	--	--
Robinia pseudoacacia	0.1	11.1	0.5	0.3	11.1	--	--	1.4	22.2	--	--
Juglans nigra	0.1	11.1	--	--	--	0.2	11.1	--	--	--	--
Castanea dentata	0.1	11.1	--	--	--	0.2	11.1	--	--	1.0	11.1
Carya glabra	0.1	11.1	--	--	--	0.2	11.1	--	--	1.0	11.1
Tsuga canadensis	--	--	--	--	--	--	--	4.4	11.1	--	--
Diospyros virginiana	--	--	--	--	--	--	--	2.2	33.3	3.8	22.2
Rhus glabra	--	--	--	--	--	--	--	0.7	11.1	--	--
Ilex ambigua var montana	--	--	--	--	--	--	--	--	--	2.9	11.1
Acer pennsylvanicum	--	--	--	--	--	--	--	--	--	1.0	11.1
Ilex opaca	--	--	--	--	--	--	--	--	--	1.0	11.1
Prunus serotina	--	--	--	--	--	--	--	--	--	1.0	11.1

[a]Stems greater than 3 cm dbh.

[b]Stems greater than 10 cm dbh.

[c]Stems greater than 3 cm and less than 10 cm dbh.

[d]Stems less than 3 cm dbh and taller than 1 meter.

[e]Stems less than 1 meter tall.

TABLE 9

COMPOSITION OF THE TABLE MOUNTAIN PINE-PITCH PINE REPLACEMENT TYPE ACCORDING TO RELATIVE DENSITY OF OVERSTORY (N = 10)

	Overstory										
Taxon	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Pinus pungens	43.2	100.0	72.5	76.2	90.0	35.1	100.0	4.6	30.0	1.2	10.0
Pinus rigida	27.1	80.0	14.6	13.6	70.0	30.5	80.0	14.6	40.0	3.8	30.0
Nyssa sylvatica	9.4	100.0	1.7	1.4	30.0	11.5	100.0	8.5	60.0	8.8	20.0
Acer rubrum	7.0	90.0	2.5	2.0	20.0	8.3	90.0	36.9	90.0	58.8	90.0
Oxydendrum arboreum	3.4	70.0	3.3	2.4	50.0	3.4	70.0	0.8	10.0	--	--
Sassafras albidum	3.1	60.0	0.4	0.3	10.0	3.8	60.0	11.5	30.0	3.8	30.0
Quercus coccinea	1.8	30.0	1.7	1.4	20.0	1.8	30.0	--	--	6.2	40.0
Castanea dentata	1.3	40.0	--	--	--	1.6	40.0	3.8	40.0	--	--
Quercus prinus	1.2	40.0	2.1	1.8	30.0	0.9	30.0	1.5	10.0	--	--
Hamamelis virginiana	1.0	30.0	--	--	--	1.4	30.0	3.8	10.0	2.5	10.0
Amelanchier laevis	0.6	20.0	0.4	0.3	10.0	0.7	30.0	6.2	10.0	--	--
Tsuga canadensis	0.4	20.0	0.8	0.6	20.0	0.3	20.0	0.8	10.0	2.5	10.0
Quercus rubra	0.2	10.0	--	--	--	0.2	10.0	--	--	--	--
Pinus strobus	0.1	10.0	--	--	--	0.1	10.0	--	--	--	--
Betula lenta	0.1	10.0	--	--	--	0.1	10.0	--	--	--	--
Robinia pseudoacacia	0.1	10.0	--	--	--	0.1	10.0	--	--	--	--
Ilex ambigua var montana	--	--	--	--	--	--	--	4.6	40.0	--	--

TABLE 9 (continued)

Taxon	Overstory										
	Total Stems[a]		Residual Canopy[b]			Saplings[c]		Understory[d]		Reproduction[e]	
	RD	F	RD	RBA	F	RD	F	RD	F	RD	F
Diospyros virginiana	--	--	--	--	--	--	--	1.5	10.0	--	--
Acer pennsylvanicum	--	--	--	--	--	--	--	0.8	10.0	5.0	40.0
Fagus grandifolia	--	--	--	--	--	--	--	--	--	2.5	20.0
Magnolia fraseri	--	--	--	--	--	--	--	--	--	2.5	10.0
Quercus rubra	--	--	--	--	--	--	--	--	--	1.2	10.0
Cornus florida	--	--	--	--	--	--	--	--	--	1.2	10.0
Ilex opaca	--	--	--	--	--	--	--	--	--	1.2	10.0

[a]Stems greater than 3 cm dbh.

[b]Stems greater than 10 cm dbh.

[c]Stems greater than 3 cm and less than 10 cm dbh.

[d]Stems less than 3 cm dbh and taller than 1 meter.

[e]Stems less than 1 meter tall.

TABLE 10

SIMPLE LINEAR CORRELATIONS BETWEEN SITE AND COVER VARIABLES*

	Elev.	Aspect	Slope Pos.	% Slope	Solar Radiation	Soil Depth	O Depth	pH of A	P in A	K in A	Kill Size	Herb Cover	Low Shrub	Tall Shrub
Elev.	1.00	-.23[b]		.22[b]	.25[b]		.68[a]	-.47[a]				.59[a]		.58[a]
Aspect		1.00			-.47[a]		-.38[a]	.42[a]				-.25[b]		-.42[a]
Slope Pos.			1.00	-.45[a]	-.34[a]	.29[a]				.36[a]				
% Slope				1.00	.41[a]					-.25[b]	.27[b]		-.26[b]	.25[b]
Solar Radiation					1.00			-.25[b]		-.42[a]				.25[b]
Soil Depth						1.00								
O Depth							1.00	-.50[a]				.57[a]		.66[a]
pH of A								1.00				-.44[a]		-.49[a]
P in A									1.00				.31[a]	.23[b]
K in A										1.00				
Kill Size											1.00			
Herb Cover												1.00		.47[a]
Low-Shrub													1.00	
Tall-Shrub														1.00

*For all variables other than aspect, N = 81; for aspect and its correlates, N = 70.

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 11

SIMPLE LINEAR CORRELATIONS BETWEEN OVERSTORY ABSOLUTE DENSITIES AND SITE AND COVER VARIABLES*

	Site and Cover Variables													
Overstory	Elev.	Aspect	Slope Pos.	% Slope	Solar Radiation	Soil Depth	O Depth	pH of A	P in A	K in A	Kill Size	Herb Cover	Low Shrub	Tall Shrub
Total								-.32[a]				.34[a]		.32[a]
Pine	.38[a]			.29[a]			.34[a]	-.48[a]				.45[a]		
Table M.P.	.52[a]			.29[a]			.47[a]	-.44[a]		-.22[b]		.49[a]		.45[a]
Pitch P.	.44[a]						.36[a]	-.41[a]				.50[a]		.32[a]
Virginia P.														
Oak												-.31[a]	.24[b]	
Scarlet O.				-.27[b]		.23[b]						-.26[b]	.30[a]	-.25[b]
Chestnut O.	.23[b]													
Red Maple					-.24[b]									
Blackgum					.23[b]				.25[b]					
Dogwood	-.52[a]	.33[a]			-.47[a]			.42[a]					-.39[a]	-.27[a]

*For all variables other than aspect, N = 91; for aspect and its correlates, N = 70.

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 12

SIMPLE LINEAR CORRELATIONS BETWEEN OVERSTORY ABSOLUTE DENSITIES (N = 81)

	Total	Pine	T.M.P.	P.P.	V.P.	Oak	S.O.	C.O.	R.M.	Bg.	Dw.
Total	1.00	.75[a]	.62[a]	.67[a]						.24[b]	
Pine		1.00	.83[a]	.83[a]	.28[b]	-.26[b]		-.22[b]	-.26[b]		-.26[b]
Table M.P.			1.00	.72[a]		-.34[a]		-.22[b]			
Pitch P.				1.00							-.22[b]
Virginia P.					1.00				-.23[b]		
Oak						1.00	.70[a]	.43[a]		.22[b]	
Scarlet O.							1.00				
Chestnut O.								1.00			
Red Maple									1.00	-.29[a]	
Blackgum										1.00	-.26[b]
Dogwood											1.00

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 13

SIMPLE LINEAR CORRELATIONS BETWEEN UNDERSTORY ABSOLUTE DENSITIES AND SITE AND COVER VARIABLES*

	Site and Cover Variables													
Understory	Elev.	Aspect	Slope Pos.	% Slope	Solar Radiation	Soil Depth	O Depth	pH of A	P in A	K in A	Kill Size	Herb Cover	Low Shrub	Tall Shrub
Total	-.37[a]						-.26[b]	-.29[a]						
Pine														
Table M.P.				.23[b]								.24[b]		
Pitch P.												.26[b]		
Virginia P.	-.28[b]													
Oak	-.29[a]					-.28[b]								
Scarlet O.														
Chestnut O.				-.30[a]							-.26[b]		.28[b]	
Red Maple								.28[b]						
Blackgum														
Dogwood	-.33[a]	.57[a]			-.56[a]		-.22[b]	.42[a]					-.28[b]	

*For all variables other than aspect, N = 81; for aspect and its correlates, N = 70.

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 14

SIMPLE LINEAR CORRELATIONS BETWEEN OVERSTORY AND UNDERSTORY-REPRODUCTION ABSOLUTE DENSITIES (N = 81)

Understory	Total	Pine	T.M.P.	P.P.	V.P.	Oak	S.O.	C.O.	R.M.	Bg.	Dw.
Total											
Pine		.27[b]									
Table M.P.	.32[a]	.42[a]	.51[a]	.34[a]							
Pitch P.	.53[a]	.58[a]	.63[a]	.51[a]							
Virginia P.											
Oak											
Scarlet O.						.23[b]	.31[a]				
Chestnut O.					.25[b]						
Red Maple											
Blackgum						.44[a]	.35[a]		-.28[b]	.36[a]	-.25[b]
Dogwood											.68[a]
Reproduction											
Total		-.32[a]	-.25[b]	-.25[b]							.42[a]
Pine											
Table M.P.											
Pitch P.											
Virginia P.											
Oak		-.27[b]	-.25								.24[b]
Scarlet O.											
Chestnut O.								.23[b]		.24[b]	
Red Maple											
Blackgum											
Dogwood											.48[a]

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 15

SIMPLE LINEAR CORRELATIONS BETWEEN UNDERSTORY ABSOLUTE DENSITIES

Understory	Total	Pine	T.M.P.	P.P.	V.P.	Oak	S.O.	C.O.	R.M.	Bg.	Dw.
Total	1.00	.57[a]			.52[a]	.49[a]	.25[b]	.48[a]	.64[a]	.25[b]	.31[a]
Pine		1.00	.38[a]	.47[a]	.88[a]	.51[a]	.41[a]	.37[a]			
Table M.P.			1.00	.79[a]							
Pitch P.				1.00							
Virginia P.					1.00	.58[a]	.48[a]	.39[a]			
Oak						1.00	.85[a]	.45[a]			
Scarlet O.							1.00				
Chestnut O.								1.00			
Red Maple									1.00		
Blackgum										1.00	
Dogwood											1.00

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 16

SIMPLE LINEAR CORRELATIONS BETWEEN REPRODUCTION ABSOLUTE DENSITIES AND SITE AND COVER VARIABLES

	Site and Cover Variables													
Understory	Elev.	Aspect	Slope Pos.	% Slope	Solar Radiation	Soil Depth	O Depth	pH of A	P in A	K in A	Kill Size	Herb Cover	Low Shrub	Tall Shrub
Total	-.36[a]	.30[b]			-.22[b]		-.36[a]	.41[a]				-.23[b]	-.39[a]	-.34[a]
Pine		.24[b]												-.27[b]
Table M.P.														
Pitch P.														
Virginia P.		.30[b]												-.31[a]
Oak	-.33[a]						-.45[a]	.38[a]				-.26[b]	-.28[b]	-.23[b]
Scarlet O.							-.42[a]	.30[a]						
Chestnut O.														
Red Maple										-.29[a]				
Blackgum		.29[b]					-.27[b]	.23[b]	.22[b]					-.28[b]
Dogwood	-.31[a]	.40[a]			-.35[a]		-.22[b]	.34[a]					-.28[b]	

*For all variables other than aspect, N = 81; for aspect and its correlates, N = 70.

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 17

SIMPLE LINEAR CORRELATIONS BETWEEN UNDERSTORY AND REPRODUCTION ABSOLUTE DENSITIES (N = 81)

	Reproduction										
Understory	Total	Pine	T.M.P.	P.P.	V.P.	Oak	S.O.	C.O.	R.M.	Bg.	Dw.
Total	.30[a]										.26[b]
Pine											
Table M.P.			.24[b]	.31[a]							
Pitch P.				.27[b]							
Virginia P.											
Oak											
Scarlet O.											
Chestnut O.											
Red Maple				.27[b]					.26[b]		
Blackgum									-.27[b]	.25[b]	
Dogwood	.46[a]										.75[a]

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 18

SIMPLE LINEAR CORRELATIONS BETWEEN REPRODUCTION ABSOLUTE DENSITIES (N = 81)

	Total	Pine	T.M.P.	P.P.	V.P.	Oak	S.O.	C.O.	R.M.	Bg.	Dw.
Total	1.00	.31[a]		.22[b]	.27[b]	.47[a]			.61[a]		.66[a]
Pine		1.00	.23[b]	.57[a]	.83[a]						
Table M.P.			1.00								
Pitch P.				1.00					.38[a]		
Virginia P.					1.00						.27[b]
Oak						1.00	.77[a]	.25[b]			
Scarlet O.							1.00				
Chestnut O.								1.00			
Red Maple									1.00		
Blackgum										1.00	
Dogwood											1.00

[a]Significant at P = 0.01.

[b]Significant at P = 0.05.

TABLE 19

REGRESSION EQUATIONS FOR TOTAL STEM ABSOLUTE DENSITY

Overstory stems/ha = 9381.87 -1183.98(pH of A) -7.79(Solar Rad.) +10.60 (% Slope)

$R^2 = 0.17$

Understory stems/ha = -8054.37 -1.30(Elev) -484.5(Kill size) +23.02 (K in A) -35.72(O depth) +.85(Tot. overstory) +3102.41 (pH of A)

$R^2 = 0.27$

Reproduction stems/ha = -139553.04 -481.18(Low-shrub cover) -52942.35 (pH of A) -36627.72(Slope pos.) -5329.44(Kill size) -534.42 (% Slope) +2.00(Tot. understory)

$R^2 = 0.44$

TABLE 20

REGRESSION EQUATIONS FOR PINE ABSOLUTE DENSITY

Overstory stems/ha = 6839.91 -1567.43(pH of A) +15.94(% Slope) +600.35 (Slope position)

$R^2 = 0.17$

Understory stems/ha = 307.99 +1091.88(Slope pos.) +.34(Tot. overstory) -.30(Elev.) -11.02(Soil depth)

$R^2 = 0.14$

Reproduction stems/ha = 2900.9 -27.23(Tall-shrub cover)

$R^2 = 0.07$

TABLE 21

REGRESSION EQUATIONS FOR TABLE MOUNTAIN PINE ABSOLUTE DENSITY

Overstory stems/ha = 1879.58 +.22(Elev.) -511.34(pH of A) +5.34(% Slope)
R^2 = .35
Understory stem/ha = -137.04 +.05(Tot. overstory) +1.54(% Slope)
R^2 = .13
Reproduction stem/ha = -266.92 +.45(Elev.) -125.25(O depth)
R^2 = .10

TABLE 22

REGRESSION EQUATIONS FOR PITCH PINE ABSOLUTE DENSITY

Overstory stems/ha = 1899.68 +.15(Elev.) -439.34(pH of A)

$R^2 = 0.25$

Understory stems/ha = -500.85 +.28(Tot. overstory)

$R^2 = 0.28$

Reproduction stems/ha = (No acceptable equations)

TABLE 23

REGRESSION EQUATIONS FOR VIRGINIA PINE ABSOLUTE DENSITY

Overstory stems/ha = 2203.39 -.14(Elev.) -374.70(pH of A)

$R^2 = 0.09$

Understory stems/ha = 448.09 -.32(Elev.) +663.89(Slope position)

$R^2 = 0.12$

Reproduction stems/ha = 1731.44 -22.95(Tall-shrub cover)

$R^2 = 0.09$

TABLE 24

REGRESSION EQUATIONS FOR OAK ABSOLUTE DENSITY

Overstory stems/ha = (No acceptable equations)

Understory stems/ha = 891.84 -9.60(Soil depth) -.21(Elev.) +539.43(Slope position) +3.46(Low-shrub cover)

$R^2 = 0.30$

Reproduction stems/ha = 114950.26 -707.03(O depth) +5993.49(pH of A) -4448.77(Slope position) -34.67(Low-shrub cover)

$R^2 = 0.31$

TABLE 25

REGRESSION EQUATIONS FOR SCARLET OAK ABSOLUTE DENSITY

Overstory stems/ha = 115.59 -2.42(% Slope)+1.70(Soil depth)	
	$R^2 = 0.10$
Understory stems/ha = (No acceptable equations)	
Reproduction stems/ha = -24720.91 -768.91(O depth) +1.74(Elev.) +37.82 (Solar Rad.) +4098.48(pH of A) -25.91(Low-shrub cover)-50.89(% Slope)	
	$R^2 = 0.30$

TABLE 26

REGRESSION EQUATIONS FOR CHESTNUT OAK ABSOLUTE DENSITY

Overstory stems/ha = -96.03 +.07(Elev.) -14.07(O depth) +.83(K in A)

$R^2 = 0.13$

Understory stems/ha = 23.17 -17.74(Kill size) +.64(Low-shrub cover) +.60(K in A) -.02(Elev.)

$R^2 = 0.18$

Reproduction stems/ha = (No acceptable equations)

TABLE 27

REGRESSION EQUATIONS FOR RED MAPLE ABSOLUTE DENSITY

Overstory stems/ha = 2031.98 -5632.7(Slope pos.) -4.80(Solar Rad.) +.11(Elev.) -4.66(% Slope)

$R^2 = 0.22$

Understory stems/ha = -9418.89 +2291.82(pH of A)

$R^2 = 0.08$

Reproduction stems/ha = 74447.68 -210.46(K in A) -249.97(Herb cover) -164.42(Solar Rad.) -114.99(Low-shrub cover) +5.92(Elev.) +.94(Tot. understory)

$R^2 = 0.23$

TABLE 28

REGRESSION EQUATIONS FOR BLACKGUM ABSOLUTE DENSITY

Overstory stems/ha = -576.69 +79.81(P in A) +2.54(Solar Rad.)

$R^2 = 0.11$

Understory stems/ha = 2255.28 -151.41(O depth) +11.29(K in A) +13.05 (Solar Rad.) -1232.76(pH of A)

$R^2 = 0.18$

Reproduction stems/ha = 1092.24 +2.24(Elev.) -610.88(O depth) -31.44 (Tall-shrub cover)

$R^2 = 0.17$

TABLE 29

REGRESSION EQUATIONS FOR DOGWOOD ABSOLUTE DENSITY

Overstory stems/ha =	148.04 -0.13(Elev) -3.02(Solar Rad.) + 23.13(0 depth) +197.96(pH of A) + 2.18(% slope)
$R^2 = 0.50$	
Understory stems/ha =	928.60 -31.32(Solar Rad.) +1764.21(pH of A) + 23.80(% slope) -7.75(low-shrub cover) - 140.76(kill size)
$R^2 = 0.53$	
Reproduction stems/ha =	-26512.25 -217.90(Solar Rad.) - 153.99(low-shrub cover) + 21533.84(pH of A)
$R^2 = 0.26$	

VITA

Nathaniel White Kuykendall III was born in Memphis, Tennessee, on July 16, 1949. He attended elementary school in that city and graduated from East High School in June, 1967. The following September he entered Maryville College, Maryville, Tennessee, and in June of 1971 received a Bachelor of Arts degree in English.

In 1971 and 1972 he worked with the Youth Conservation Corps and taught elementary school children at Tremont Environmental Education Center near Townsend, Tennessee, and in 1973 and 1974 he was an environmental education instructor at Pine Mountain Settlement School in Harlan County, Kentucky. During 1973, 1974, and 1975 he worked as a seasonal ranger-naturalist in the Great Smoky Mountains National Park.

In 1972 the author began taking prerequisite coursework for entering the Graduate Program in Ecology at the University of Tennessee and was accepted as a degree candidate in January, 1975. From March, 1976, to August, 1977, he was employed on a scholastic appointment by the Denver Service Center of the National Park Service in Colorado. He returned to a permanent position with the Denver Service Center in November, 1978, and received his Master of Science in Ecology in December of that year.