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THE SOUTHERN APPALACHIAN SPRUCE-FIR ECOSYSTEM:

ITS BIOLOGY AND THREATS

Edited by Peter S. White

NATIONAL PARK SERVICE - Southeast Region

Research/Resources Management Report SER-71

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Uplands Field Research Laboratory
Great Smoky Mountains National Park
Gatlinburg, Tennessee 37738

November 1984

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The southernmost spruce-fir forests of eastern North America occur in the high peaks region of the southern Appalachians, from southwestern Virginia to eastern Tennessee and western North Carolina. These forests are unique and imperiled. The dominant trees of this ecosystem type are subject to threats. Fraser fir, a narrow southern Appalachian endemic, is directly threatened by an introduced insect (Eagar, DeSelm and Boner, this volume). It has been conjectured that a dramatic decline in red spruce radial increment has been caused by air pollution. Within the next several decades the dramatic alteration of the last old growth stands of this ecosystem type will occur.

The importance of southern Appalachian spruce-fir resides in several properties: though related to northern spruce-fir vegetation, it is biologically unique (White, this volume); it is a geographically restricted type (White, Pittillo, Saunders, this volume); it supports populations of rare plants (White, Pittillo, Dey, Smith, Petersen, this volume) and animals (Linzey, Pelton, Mathews and Echternacht, Rabenold, this volume); it dominates the headwaters of mountain streams and influences downstream water quality and fisheries; and it is aesthetically important to recreational users (Saunders, this volume). The National Park Service manages two areas that include examples of the spruce-fir ecosystem: Great Smoky Mountains National Park (an International Biosphere Reserve and World Heritage Site) and the Blue Ridge Parkway. Great Smoky Mountains National Park contains the largest existing tract of southern Appalachian spruce-fir.

Between 1960 and the mid-1970s, the primary cause for concern about southern Appalachian spruce-fir was the spread of the introduced insect, the balsam woolly aphid (Eagar, DeSelm and Boner, this volume). This pest will probably eliminate mature Fraser fir trees within the next several decades and may eventually cause the extirpation of this southern Appalachian endemic species. Only Fraser fir on Mt. Rogers seems to be resistant (see Rheinhardt, this volume). Loss of Fraser fir will effect the rest of the biota of the spruce-fir forests, including, for example, lichens that inhabit fir bark and branches (Dey, this volume), amphibians effected by stand microclimate (Mathews and Echternacht, this volume), and understory herbs effected by increased insolation. With the production of large amounts of organic debris and the successional replacement of the fir trees, the effects of the balsam woolly aphid will ramify through this ecosystem.

In the past decade another concern has been raised: atmospheric deposition of pollutants. Red spruce has undergone a dramatic reduction in annual radial increment, starting as early as 1957 (S. McLaughlin, unpublished data from the FORAST project). The data documenting this sudden shift in vigor have not been fully published; in addition, more data are now being collected. Hence, it is premature to judge how widespread the growth decline is and how it is related to site factors (like

elevation), tree age, and stand history. It is also unclear at this time whether the growth decline results in increased spruce mortality in the southern Appalachians, but studies in Vermont have substantiated heavy (>60 percent of canopy stems), recent, and unexplained mortality in northern red spruce populations.

Speculation about the causes of the spruce decline center on pollutant deposition. Pollutant deposition is known to be significant in the mountainous terrain of the eastern US. Further, though circumstantial, cause for concern is the devastation of high elevation coniferous forests in Western Europe over the last five years--research has shown a strong connection to pollutant deposition there. Whatever the cause of red spruce decline, substantial pollutant deposition is occurring in the southern mountains (Lovett, Bogle and Turner, this volume). The gases and precipitation borne materials that are pervading this ecosystem are likely to cause effects on several levels of biological organization and underscore the importance of ecosystem level research. Predicting these changes will be hampered by the current lack of knowledge about the functioning of this ecosystem.

Because of the biological importance and immediacy of the threats to this ecosystem, the spruce-fir zone has received increasing research attention. Scientists from the National Park Service, Oak Ridge National Lab, the Tennessee Valley Authority, the Forest Service, North Carolina State University, the University of Tennessee, Virginia Polytechnic Institute, and other regional institutions have begun research projects to assess the spruce-fir ecosystem and pollutant deposition. These studies range from baseline data collection on permanent plots to detailed analysis of ecological processes on intensive study sites and laboratory experiments to assess pollutant sensitivity of component species. This research will make possible a more complete understanding of the state and trajectory of the spruce-fir ecosystem, and the effects of pollutants, over the next 2 to 5 years.

In order to assess the data base at the beginning of this research effort, Uplands Field Research Lab, a National Park Service research station in Great Smoky Mountains National Park, held a symposium entitled, "The southern Appalachian spruce-fir ecosystem: status, threats, and management". The goals of this symposium were to summarize the state of our knowledge about the spruce-fir ecosystem, to describe its threats, to assess the quality of the data bases for long term understanding of the changes that are taking place, to discuss management issues, to identify key research areas, and to promote institutional cooperation in the research effort. We specifically addressed the following questions: How will we be able to detect and evaluate change at the population, community, and ecosystem levels? Will we be able to predict extinction risk for vulnerable species? How will we predict the future state of this ecosystem? This volume presents the results of that meeting.

This volume is organized as follows. After a general introduction to the spruce-fir ecosystem (White), the paleoecological history of this vegetation is described (Delcourt and Delcourt). This is followed by a summary of the interaction of balsam woolly aphid and Fraser fir (Eagar) and a description of stand changes after balsam woolly aphid infestation (DeSelm and Boner). Next the geographic areas of spruce-fir are described in chapters on the Blue Ridge (Pittillo) and southwest Virginia (Rheinhardt). The next two chapters deal with recreational impacts (Saunders) and logging history (Pyle). These chapters are followed by seven chapters describing particular groups of organisms: mosses (Smith), lichens (Dey), fungi (Petersen), herpetofauna (Mathews and Echternacht), avifauna (Rabenold), and mammals (Pelton, Linzey). Notable by its absence in this section of the proceedings is an important group for which little data exist: soil organisms. An outline of soil types of the spruce-fir zone (Springer) is followed by a detailed analysis of lead in vegetation and soils (Bogle and Turner). The final chapter (Lovett) describes the potential for high amounts of pollutant deposition in mountainous terrain. We have also prepared two Appendices: Appendix I gives an annotated checklist of the vascular plants of southern Appalachian spruce-fir and Appendix II presents a bibliography of research on southern Appalachian spruce-fir vegetation.

The National Park Service protects the most significant tract of undisturbed southern Appalachian spruce-fir forest (located in Great Smoky Mountains National Park). Additional NPS spruce-fir stands are found along the Blue Ridge Parkway. NPS is committed to maintaining and protecting natural ecosystems and their processes. Further, the role of Great Smoky Mountains National Park in the International Biosphere Reserve program supports NPS biologists and managers in their work on this threatened ecosystem.

The opinions of the authors of the several chapters in this volume do not necessarily reflect the views of the National Park Service. I would like to take this opportunity to thank the authors for their hard work and long patience as this volume was assembled.

P. White
Uplands Field Research Laboratory
Great Smoky Mountains National Park

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LIST OF CONTRIBUTORS

M. A. Bogle
Environmental Sciences Division
Oak Ridge National Lab
Oak Ridge, TN 37830

R. R. Boner
The Nature Conservancy
Minneapolis, MN

Hazel Delcourt
Depts. of Geology and Botany
University of Tennessee
Knoxville, TN 37738

Paul Delcourt
Dept. of Geology
University of Tennessee
Knoxville, TN 37996-1100

H. R. DeSelm
Dept. of Botany
University of Tennessee
Knoxville, TN 37996-1100

John Dey
Biology Dept.
Illinois Wesleyan University
Bloomington, IL 61701

Christopher Eagar
Uplands Field Research Lab
Great Smoky Mountains Nat'l Prk
Gatlinburg, TN 37738

A. C. Echternacht
Dept. of Zoology
University of Tennessee
Knoxville, TN 37996-1100

Donald W. Linzey
2101 Nellies Cove Rd
Blacksburg, VA 24060

Gary Lovett
Environmental Science Division
Oak Ridge National Lab
Oak Ridge, TN 37830

M. R. Pelton
Forestry, Fisheries, and Wildlife
University of Tennessee
Knoxville, TN 37901-1071

R. Petersen
Dept. of Botany
University of Tennessee
Knoxville, TN 37996-1100

J. Dan Pittillo
Dept. of Biology
Western Carolina University
Cullowhee, NC 28723

Richard D. Rheinhardt
305 N. Boundary St.
Williamsburg, VA 23185

Charlotte Pyle
Uplands Field Research Lab
Great Smoky Mountains National Park
Gatlinburg, TN 37738

K. N. Rabenold
Department of Biological Sciences
Purdue University
West Lafayette, IN 47907

L. A. Renfro
Uplands Field Research Lab
Great Smoky Mountains National Park
Gatlinburg, TN 37738

P. R. Saunders
Forest and Range Management
Washington State University
Pullman, WA 99164-6410

D. K. Smith
Dept. of Botany
University of Tennessee
Knoxville, TN 37996-1100

Max Springer
1600 Autry Way Laboratory
Knoxville, TN 37919

CONTRIBUTORS, CONTINUED:

R. C. Mathews, Jr.
Geo-Marine, Inc.
Engineering and Environmental Services
1316 Fourteenth St.
Plano, Texas 75074

R. R. Turner
Environmental Sciences Division
Oak Ridge National Lab
Oak Ridge, TN 37830

Peter S. White
Uplands Field Research Lab
Great Smoky Mountains National Park
Gatlinburg, TN 37738

OTHER WORKSHOP PARTICIPANTS

Frank Arthur
Dept. of Entomology
North Carolina State University
Raleigh, NC 27650

Fred Baes
Environmental Sciences Division
Oak Ridge National Lab
Oak Ridge, TN 37830

Larry Barden
Biology Dept.
University of North Carolina
Charlotte, NC 28213

Edward Buckner
Forestry, Fisheries and Wildlife
University of Tennessee
Knoxville, TN 37901-1071

E. E. C. Clebsch
Department of Botany
University of Tennessee
Knoxville, TN 37996-1100

Jean L. Davidson
Dept. of Geology
University of Tennessee
Knoxville, TN 37996-1100

Paula DePriest
Dept. of Botany
University of Tennessee
Knoxville, TN 37996-1100

Leroy Fox
4116 Jomandowa Lane
Knoxville, TN 37919

Doug Holland
Plant and Soil Science
University of Tennessee
Knoxville, TN 37996-1100

Dale Johnson
Environmental Sciences Division
Oak Ridge National Lab
Oak Ridge, TN 37830

Richard Lancia
Forestry Dept.
North Carolina State University
Raleigh, NC 27650

D. A. Lietzke
Plant and Soil Science Dept.
University of Tennessee
Knoxville, TN 37901-1071

John D. McKrone
Dean, School of Arts and Sciences
Western Carolina University
Cullowhee, NC 28723

S. B. McLaughlin
Environmental Sciences Division
Oak Ridge National Lab
Oak Ridge, TN 37830

Don McLeod
Dept. of Biology
Mars Hill College
Mars Hill, NC 28754

Niki Nicholas
Uplands Field Research Lab
Great Smoky Mountains National Park
Gatlinburg, TN 37738

Jerry Olson
Environmental Sciences Division
Oak Ridge National Lab
Oak Ridge, TN 37830

Nancy Reagan
Western Carolina University
Cullowhee, NC 28723

David Sackett
Dept. of Geology
University of Tennessee
Knoxville, TN 37916

David Shafer
Dept. of Geology
University of Tennessee
Knoxville, TN 37916

Alan Smith
Dept. of Biology
Mars Hill College
Mars Hill, NC 28754

THE SOUTHERN APPALACHIAN SPRUCE-FIR ECOSYSTEM, AN INTRODUCTION

Peter S. White¹

Abstract.--Southern Appalachian spruce-fir is a distinctive variant within the complex of North American forests dominated by Picea (spruce) and Abies (fir). Because of the geography and topography of the region, spruce-fir forests in the south are isolated from related northern vegetation and occur as a series of island-like stands at high elevations. These areas are rich in endemics and in rare plants and animals. The integrity of Southern Appalachian spruce-fir is threatened by an exotic insect pest, the balsam woolly aphid, and by atmospheric deposition of pollutants. The balsam woolly aphid will eliminate mature Abies fraseri (Fraser fir) trees from most of its range within the next several decades. Pollutant deposition has been implicated in the recent radial increment suppression in Picea rubens (red spruce) and is probably causing other ecosystem changes as well. Ecosystem oriented research is a key to understanding the role of pollutant deposition in these forests. Previous ecosystem work included characterization of stand biomass, nutrient pools, productivity, and discussion of nutrient cycling trends. Ongoing research in Great Smoky Mountains National Park, which contains the largest existing area of southern Appalachian spruce-fir, is directed at a variety of levels from physiological response in trees to change at the population, community, and ecosystem levels. Logging and fire between 1880 and 1930 removed about 50 percent of the total area of southern Appalachian spruce-fir; the last undisturbed stands of this ecosystem type will probably have been dramatically altered in the next several decades.

Additional keywords: Abies fraseri, ecosystem processes, monitoring, Picea rubens, rarity, southern Appalachian vegetation, threats to ecosystems

INTRODUCTION

The southernmost spruce-fir forests in eastern North America occur on the high peaks of the southern Appalachians in North Carolina and Tennessee (about Latitude 35 degr. N; Ramseur 1960, Pittillo, Rheinhardt, Saunders, this volume). The biological importance of these forests and the factors that threaten the integrity of this ecosystem are the subject of this volume. The goals of this chapter are to define southern Appalachian spruce-fir as a distinctive variant of North American spruce-fir forests, to show the isolation and restricted extent of this

¹/ Research biologist, Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, TN 37738

ecosystem, to present an overview of the threats that are now present, and to review characteristics of this ecosystem that are not specifically treated in other chapters (conservation status and ecosystem processes). I will also outline current research in the spruce-fir forests of Great Smoky Mountains National Park, which contains the largest single tract of southern Appalachian spruce-fir, including important old growth stands.

SOUTHERN APPALACHIAN SPRUCE-FIR: DEFINITION AND CONTRASTS WITH NORTHERN SPRUCE-FIR

Physiognomy and floristics. Forests dominated by spruce (*Picea*) and fir (*Abies*) characterize a broad region of North America, from Alaska to the eastern Provinces of Canada. In the east, spruce-fir forests are also found southward along the Appalachian mountain chain. Southern Appalachian spruce-fir is physiognomically very similar to northern Appalachian spruce-fir. Both southern and northern Appalachian spruce-fir are dominated by needle-leaved, evergreen, conifers, and have conspicuous bryophyte layers (Oosting and Billings 1951). The most distinctive physiognomic differences between northern and southern Appalachian old growth spruce-fir stands are (1) the greater average height and faster growth rates of trees in the south, (2) the greater herb and bryophyte cover in the south, and (3) the occurrence of an evergreen, broad-leaved shrub layer (principally, *Rhododendron catawbiense*) in southern stands on ridges and steep and rocky slopes (Oosting and Billings, 1951, Whittaker 1956, Crandall 1958). Species richness in all strata is similar in southern compared to northern stands (Oosting and Billings 1951).

Because of this physiognomic similarity and because a number of genera and species are found in both southern and northern areas, southern Appalachian spruce-fir is sometimes referred to as "northern" or "boreal" vegetation. This usage, however, obscures the unique characteristics of Appalachian spruce-fir in general and the southern variant of this vegetation in particular. "Boreal" spruce-fir is, properly, the broad, predominantly low elevation, vegetation of high latitudes. The characteristic boreal spruces are *Picea glauca* (white spruce) and *Picea mariana* (black spruce) (La Roi 1967, Larsen 1980). The spruce of the Appalachians is *Picea rubens* (red spruce); it is the predominant spruce species in the northern Appalachians and the sole species in the south. While *Abies balsamea* (balsam fir) is the fir species of both boreal and northern Appalachian spruce-fir, it is replaced by the narrow endemic *Abies fraseri* (Fraser fir) in the southern high peaks region. Thus the two southern Appalachian dominants, *Picea rubens* and *Abies fraseri*, are Appalachian montane, rather than boreal, species.

There are other floristic differences as well--*Betula cordifolia* (heart-leaved paper birch), although rare in the south, is an Appalachian, humid region, species, while *Betula papyrifera* (paper birch) is the boreal forest white birch. While *Betula lutea* is common in the lower elevation part of northern

Appalachian spruce-fir, it is the only birch to achieve importance in southern stands (Oosting and Billings 1951). Additional species are characteristic of boreal forest (e.g., Pinus banksiana, Populus balsamifera), northern Appalachian spruce-fir (e.g., Sorbus decora, Solidago macrophylla), or southern Appalachian spruce-fir (e.g., Vaccinium erythrocarpon, Menziesia pilosa) (White 1976). Endemism is especially marked in the south (Pittillo, Appendix I, this volume; Oosting and Billings 1951, Ramseur 1960, Holt 1970, White 1976).

One hundred and thirty-two vascular plant species are found in GRSM spruce-fir forests (Appendix I). Of these, 46 are reasonably characteristic of this forest type. Of this total, 73 percent are found in both northern and southern Appalachian spruce-fir, and 27 percent are found in southern Appalachian spruce-fir only. Eight species (17 percent of the species characteristic of southern Appalachian spruce-fir) are endemic to the southern Appalachian high peaks: Abies fraseri, Ribes rotundifolium, Vaccinium erythrocarpon, Angelica triquinata, Aster chlorolepis, Cacalia rugelii, Houstonia serpyllifolia, and Solidago glomerata. By contrast, eighteen species absent from southern Appalachian spruce-fir are characteristic of northern Appalachian spruce-fir (Appendix I). Examples are: Sorbus decora, Chiogenes hispidula, Nemopanthus mucronata, Coptis groenlandica, Cornus canadensis, Pyrola spp., Solidago macrophylla, and Trientalis borealis.

Floristic boundaries are not, of course, discrete between the three kinds of spruce-fir, but the unique features of southern spruce-fir argues against the use of the term "boreal" for this vegetation. More appropriate terms in the literature are "subalpine" (borrowed from western mountains where spruce-fir occurs below alpine vegetation--this is also true in the higher New England mountains) and "montane" for the Appalachian spruce-fir type (White 1976). The simplest and most straightforward designation in the south remains "southern Appalachian spruce-fir" and it is the one which is used here. The southern spruce-fir vegetation is related to northern vegetation types, but it is a distinct variant within the complex of North American Picea-Abies dominated ecosystems.

Elevation gradients. The change in forest composition along the elevational gradient is also similar between northern and southern Appalachian spruce-fir. In New England, there is a continuum from Fagus-Acer-Betula forests (northern hardwoods) to Picea-Betula, Picea-Abies, and Abies types (Siccama 1974). Picea ranges to lower elevations than Abies, where it is scattered in the northern hardwood forest or occurs as a local dominant on steep slopes and ridges. Betula lutea ranges to higher elevations than either Acer saccharum or Fagus and is especially prominent in the northern hardwood-spruce-fir interface. The same overall pattern occurs in the south, with Picea ranging to lower elevations, Abies increasing in importance with elevation, and Betula lutea being especially prominent at the hardwood interface (Whittaker 1956). However, there are also differences:

Tsuga is prominent at the lower boundary of spruce-fir on some slopes in the south and the spruce-fir zone sometimes joins communities other than northern hardwoods (e.g., communities dominated by Quercus rubra; Whittaker 1956). Within the northern hardwood community itself are several species absent from the northern Appalachians (Aesculus octandra, Halesia carolina; Schofield 1958).

Average height and biomass of spruce-fir decline on two gradients: from low to high elevations and from moist (coves) to dry (ridges) sites (Whittaker 1956, 1966; Oosting and Billings 1951). The largest red spruce trees are found towards lower elevations and moister sites. There may also be a faster canopy turnover rate on ridges due to increased windthrow of trees. The gradients that control stand characteristics must be considered in the sampling design for testing hypotheses about ecosystem change.

In both northern and southern Appalachian spruce-fir, the ecotone between spruce-fir and hardwood dominance is relatively abrupt. Investigations of this boundary have found that the species distribution fits the continuum model of vegetation change, but that the rate of vegetation change with elevation is greater across the boundary than on either side of it (Siccama 1974, White 1976, Schofield 1958). The continuous nature of the vegetation change, however, means that the exact placement of the elevational ecotone is subjective. For example, Saunders (this volume) defines spruce-fir as relatively pure Abies and Picea dominance on all (convex and concave) sites, while Pyle (this volume) has used a definition which encompasses the spruce ridges, which descend to lower elevations than the vegetation type as a whole, and the spruce-yellow birch type. The result is that Pyle's and Saunders' estimates of the elevation of the spruce-fir-northern hardwood ecotone and of total spruce-fir area differ. Thus, no selection of a representative ecotone elevation is complete without reference to whether that boundary encompasses spruce-birch, spruce-hemlock, or other vegetation types. Further, reference must be made to the amount of landscape dominance accepted as above that ecotone (all sites, ridges but not coves, etc.).

Natural stand dynamics. A recent study of natural disturbance regimes suggested that dynamics of southern Appalachian spruce-fir are dominated by spatially small wind-caused treefalls (White et al., in press). Larger disturbance patches seem more important in northern Appalachian spruce-fir (Reiners and Lang 1979, Foster and Reiners 1983), but this conclusion is tentative since the northern studies did not rigorously define the age of disturbance patches recognized and recent spruce mortality is a complicating factor there (Foster and Reiners 1983). In the relatively pure Abies forests of high elevations in the northern Appalachians, Sprugel (1976) described the narrow bands of fir dieback called "fir waves". These waves are oriented perpendicular to slope gradients and progress upslope at about 2-5 m per yr (Sprugel 1976). Patchwise blowdown

of Fraser fir occurs on the highest summits of the southern Appalachians, but these lack the regularity and orientation of the northern fir waves. They are more like the fir patches described by Reiners and Lang (1979) for the northern Appalachians than they are like the true fir waves.

A difference between montane (both southern and northern) and boreal spruce-fir is the role of fire. Humidity increases eastward within the boreal spruce-fir forest; in more continental areas westward, fire is an important natural disturbance and occurs on rotations of 50-200 years (Heinselman 1981). Natural fire is much less important in the Appalachians, with fire rotations estimated as 500-1000 years in New England (Fahey and Reiners 1981) and even longer than this in the southern Appalachians (Harmon 1981). The predominance of spatially small natural disturbances in the south means that current human-initiated disturbance introduces a new spatial scale into vegetation dynamics. The same could not be said of the northeast where several natural disturbances (e.g., the native spruce budworm) cause large disturbance patches.

Environment. The climate of southern Appalachian spruce-fir differs in several ways from northern Appalachian spruce-fir (Oosting and Billings 1951, Shanks 1954, Stephens 1969, White 1976). Climate varies from low to high elevations in both southern and northern areas; the data that are cited below should be taken as representative of the mid-point of this gradient. The frost free season within the spruce-fir zone is longer in the south (ca. 120-160 days) compared to the north (ca. 100 days or less), minimum winter temperatures are less severe (the mean minimum temperature for the coldest month is about -5 degr. C. in the south, -20 degr. C. in the north), rainfall is higher (ca. 200 cm per yr in the south, 150 cm per yr in the north), less precipitation falls as snow (<150 cm in the south, >400 cm in the north), humidity is higher, and photoperiod is shorter in summer and longer in winter than in the north. The less drastic winter temperatures have, in fact, been offered as an explanation for the observation that the balsam woolly aphid has proved to be an unimportant pest in the north, compared to the south, but biological differences between Fraser fir and balsam fir are also involved (Eager, this volume). The longer growing season has been advanced as an explanation for the fact that spruce and fir reach larger dimensions, higher growth rates, and longer lifespans in the south compared to the north (Oosting and Billings 1951). In fact, the best growth of red spruce is obtained both at its southern range limit and, within southern stands, at its lowest elevation limit.

The disequilibrium hypothesis. Spruce-fir is absent or poorly developed on some southern Appalachian slopes that reach seemingly appropriate elevations. Examples are the abrupt western boundary of spruce-fir in the Great Smoky Mountains (Whittaker 1956) and the absence of *Abies fraseri* from Whitetop in southwestern Virginia (Rheinhardt, this volume). Whittaker (1956) hypothesized that this phenomenon was the result of

historic factors: according to his theory, spruce-fir was restricted to elevations above 5700 ft (1740 m) during the warmest post-glacial times some 5,000 yr before present (Delcourt and Delcourt, this volume). If insufficient area was available above this elevation on a particular mountain, spruce-fir became extinct as a vegetation type and rates of extinction were high for species characteristic of the high elevations. This scenario may underlie patchiness of high elevation species in the southern Appalachians (Ramseur 1960) and the strong relationship between the numbers of rare plants found on mountain areas and the size and maximum elevation of those areas (White et al. 1984, White and Miller, unpublished data). According to this view, the distribution of spruce-fir as a vegetation type and its associated species are not fully in equilibrium with environment and the approach to equilibrium is limited by plant dispersal.

The patchy distribution of plants in the region is illustrated by the presence of local endemics. For example, the flora of GRSM contains three vascular plants narrowly endemic to the park (Cacalia rugelia, Calamagrostis cainii, and Glyceria nubigena--see White and Wofford 1984); these occur within or adjacent to the spruce-fir zone. Cacalia in particular has an enigmatic distribution: it is a frequent throughout high elevation forests of the Great Smoky Mountains but occurs nowhere outside this range. Roan Mountain contains several narrow endemics as well (e.g., Houstonia montana; Paul Somers, unpublished data).

The disequilibrium hypothesis should be used with caution, however. Southern Appalachian spruce-fir regenerated very poorly after logging and slash fires (Saunders, Pyle, this volume) and is absent from some areas due to this past human disturbance.

THE ISOLATION AND ISLAND-LIKE NATURE OF SOUTHERN APPALACHIAN SPRUCE-FIR

The latitude-elevation relationship. Two edaphic kinds of spruce-fir vegetation occur along the Appalachian mountain chain: spruce-fir of mountain slopes (freely drained, upland sites) and spruce-fir of swamps and bogs (poorly drained, lowland sites). The latter type is scarce southward, but becomes frequent on glaciated lands northward. I will discuss only the upland spruce-fir type here.

While spruce-fir occurs as low as 500 m (1500 ft) in elevation, especially on ridges, on the higher New England mountains (ca. 44 degr. N), the average transtion between broad-leaved hardwood forest and relatively pure forests of spruce and fir is at about 750 m (2500 ft) (Figure 1). Southward, the transition elevation increases at a rate of about 100 m per degree Latitude (Cogbill and White, unpublished data; Figure 1). At 35 degr. N, spruce-fir is found as low as 1400 m (4500 ft), but a relatively pure zone of these conifers begins at 1600 to 1700 m (5300 to 5500 ft) (Ramseur 1960, Schofield 1958, Whittaker 1956). As noted above, these figures are dependent on

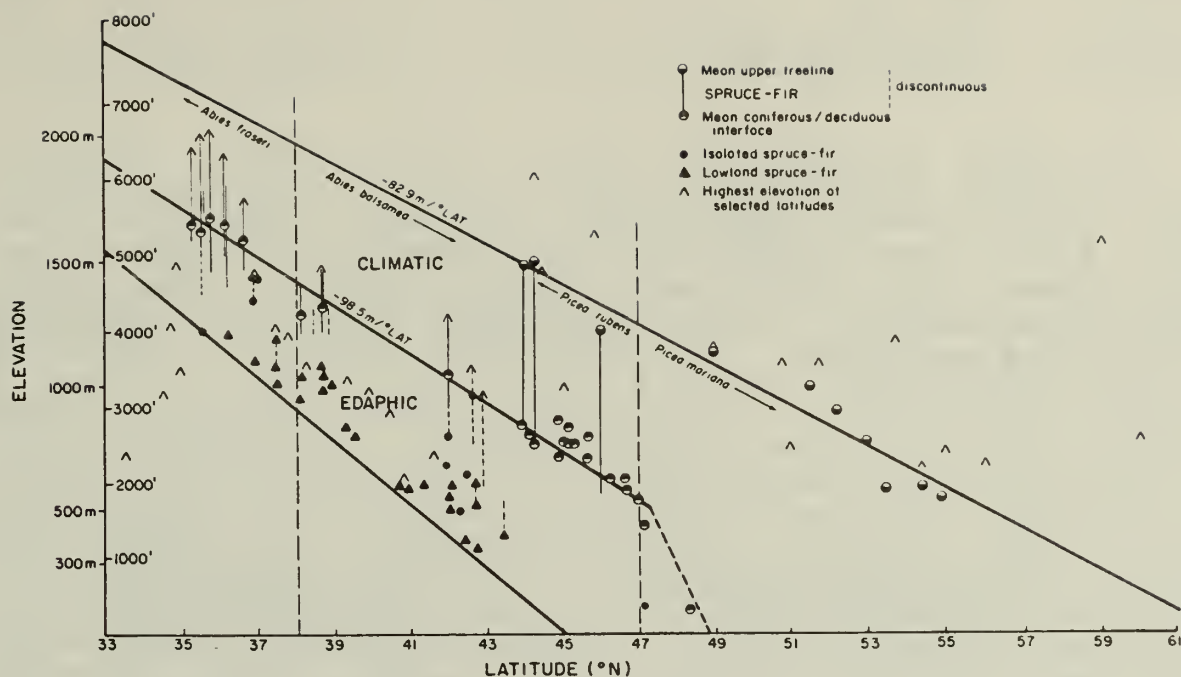


Figure 1. The latitude-elevation relationship for spruce-fir of the Appalachian mountain chain (from Cogbill and White, in review). Climatic stands are those of well-drained mountain slopes. Edaphic stands are those of poorly drained lowlands.

definition--I have used a conservative definition here and include only relatively pure dominance by spruce and fir on a variety of sites within the ecotone elevation.

Figure 1 illustrates four important characteristics of southern Appalachian spruce-fir. First, there is a sizeable gap in the distribution of spruce-fir between about latitude 38 and 42 degr. N, because the mountain chain does not reach high enough elevations within this region. Southern stands are thus quite isolated from northern spruce-fir. Second, the southern mountains are at least 100-200 m too low for a true climatic treeline at this latitude, thus underscoring the conclusion that grassy balds and heath balds (treeless southern plant communities) are not related to true alpine vegetation (a conclusion also supported on floristic grounds--see Stratton and White 1982, and literature cited therein). Further, the total available habitat for southern spruce-fir is not large. As narrowly defined by Saunders (1979, this volume), the original extent of southern Appalachian spruce-fir and spruce was probably only about 282 square kilometers. Figure 1 of Saunderson's chapter in this volume shows the island-like nature of this ecosystem quite dramatically. In all there are only seven mountain areas with spruce-fir forests and an eighth with spruce forest only (Saunders, this volume). Finally, using the relationship portrayed in Figure 1 we can readily see why the areal extent of

pre-logging spruce-fir forests in West Virginia and northern Virginia has been controversial (Pielka 1981; see also literature discussed in Pyle, this volume): the maximum elevations reached in that area are very close to the expected ecotone.

A relict alpine flora. Despite the the lack of mountains high enough for a climatic treeline, six vascular plant species occur in the southern Appalachians which also occur at or above treeline in the New England mountains (Appendix I; White et al. 1984, Ramseur 1960, Bliss 1963): Agrostis borealis, Alnus crispa, Arenaria groenlandica, Lycopodium selago, Potentilla tridentata, and Scirpus cespitosus. To these six species can be added two southern Appalachian endemics which are closely related to northern alpine species: Juncus trifidus var. monanthes and Geum radiatum. Although these taxa represent a small fraction of the 75 vascular plants restricted to the alpine zone of New England (Bliss 1963), they are significant because of speculation that the southern mountains were cold enough for a treeline some 12,000-20,000 yrs ago (Delcourt and Delcourt, this volume). All eight species are rare and occur on rock outcrops and other high elevation treeless habitats. Southern Appalachian endemics also occur in these open habitats (e.g., Carex ruthii, Hypericum graveolens, Hypericum mitchellianum, Krigia montanum, and Prenanthes roanensis); this assemblage may represent the remnant of a southern Appalachian alpine meadow flora that occurred during the Pleistocene when a treeline was found in the southern mountains (White et al., 1984, Delcourt and Delcourt, this volume). The importance of high elevation open habitats in GRSM is further underscored by the presence of two vascular plants which are strictly endemic to the park: Calamagrostis cainii (a strict endemic of Mt. LeConte) and Glyceria nubigena (which also occurs in moist shaded ground in the spruce-fir zone) (White and Wofford, 1984).

The general importance of high elevation open habitats in the distribution of GRSM rare plants (here defined as those species on state or national rare and endangered species lists) is depicted in Figure 2. The richness of the GRSM flora as a whole decreases from low to high elevations; however, when the richness decrease for high elevation open habitat rare species is normalized against this trend (as in Figure 2B), it is seen that the percent of the flora which is rare increases from low to high elevations (see also Pittillo, this volume on the importance of this habitat).

Floristic richness and the island model. The numbers of vascular plants (White et al. 1984) and macrolichens (Dey this volume) are directly predictable from the mountaintop area of the southern Appalachian high peaks. Both of these studies investigated the hypothesis that the species-area relationship had the steep slope characteristic of oceanic islands (MacArthur and Wilson 1967), but in both cases the slope values were continental in character when based on all ten of the southern Appalachian high peak areas. Both studies found that the data

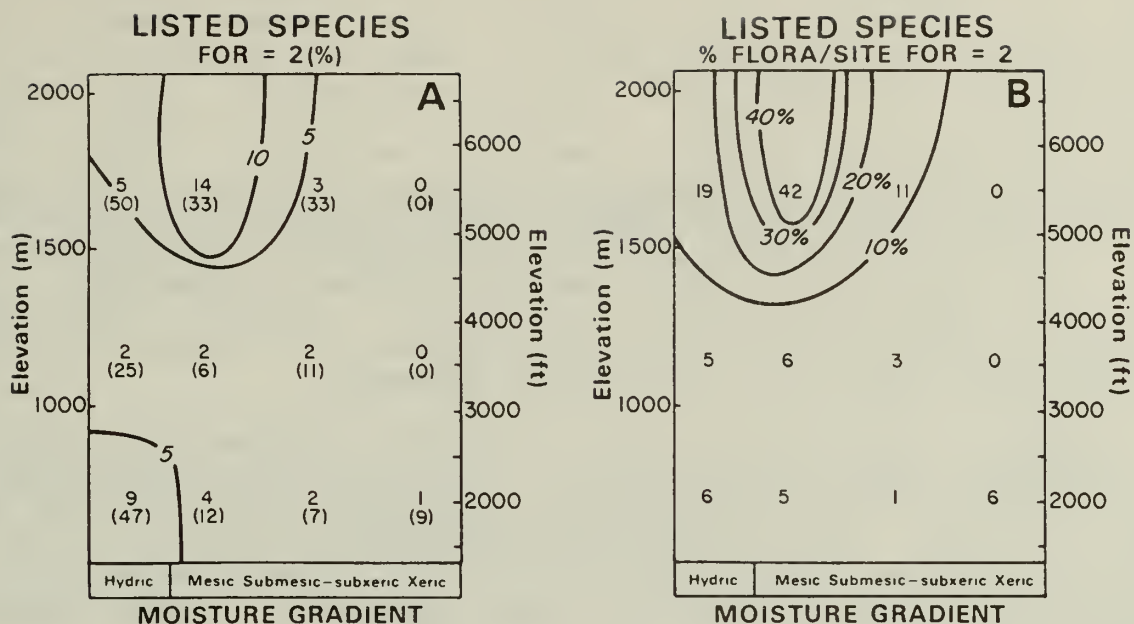


Figure 2. Listed species of GRSM in open habitats (FOR=2) displayed in a 2-dimensional environmental field (from White 1984). A. Richness (values in parentheses are the percents of all listed species restricted to open habitats). B. Richness expressed as a percent of total expected richness at a particular environmental location.

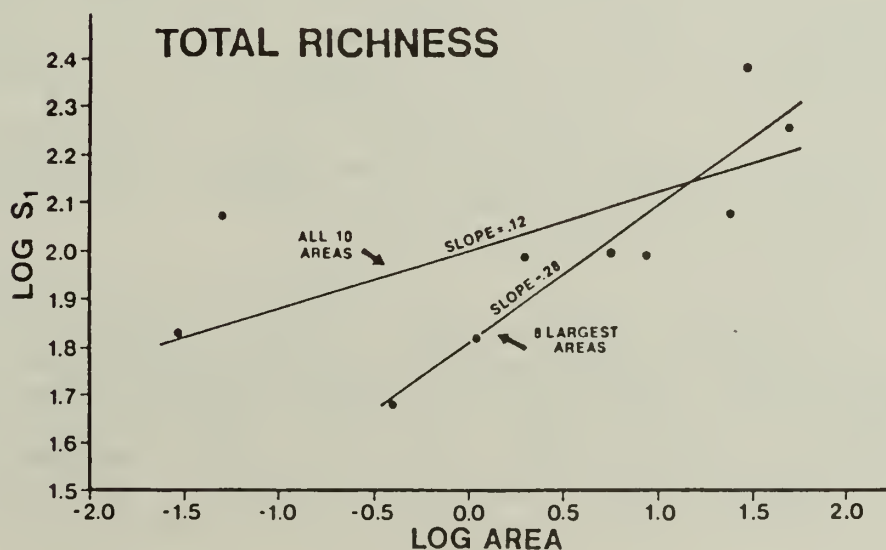


Figure 3. Species-area relation for vascular plants of the southern Appalachian high peaks (log-log formation; from White et al. 1984).

set had a stronger species-area relation if the 2 or 3 smallest areas were excluded. (i.e., these areas had higher richness than would be predicted based on their size alone) (Figure 3). Interestingly, rare vascular plants (slope=.30; White and Miller, unpublished data) had the steep species-area relationship characteristic of islands. For most vascular plants, then, these mountaintops cannot be said to be truly insular--true ecological isolation is absent and the ecological contrast across the contour used in these studies (1680 m, 5500 ft) is probably low. For rarer species, however, the mountain tops may possess true island characteristics. Immigration and extinction rates were not measured by either White et al. (1984) or Dey (this volume); such measurements of the dynamics of species richness are needed to test the island theory directly.

Rabenold (this volume) speculates that reduced bird richness in southern, compared to northern, spruce-fir may be related to the island-like characteristics of this habitat type in the south. It is, thus, likely that different biological groups as well as different individual species within these groups perceive spruce-fir differently--these may represent true insular situations to some groups, but not to others.

CONSERVATION STATUS OF SOUTHERN APPALACHIAN SPRUCE-FIR

The southern Appalachian high peaks (those that surpass 1680 m (5500 ft)) include ten mountain areas (Table 1; see also Saunders, this volume). Of these, seven have well-developed spruce-fir forests and an eighth has well-developed spruce forest without fir (Saunders, Pittillo, this volume; Ramseur 1960). All ten areas have been at least partially disturbed by logging, post-logging fires, or grazing (on grassy balds that adjoin spruce-fir). Logging and fire between 1880 and 1930 proved devastating to southern Appalachian spruce-fir (see Pyle, this volume, and literature cited therein) and removed about 50 percent of the total extent of southern Appalachian spruce-fir ecosystem (Saunders, Pyle, this volume). Great Smoky Mountains National Park includes the largest remnant old growth tracts of this ecosystem (Pyle, Saunders, this volume) (Table 1). All of the areas occur within the watersheds of the Tennessee Valley Authority; the National Park Service (Great Smoky Mountains National Park, Blue Ridge Parkway), and the US Forest Service are important land managing agencies (Table 1).

The ten mountain areas are not biologically uniform (Pittillo, Rheinhardt, this volume). Some of these differences can be attributed to differences in geology, disturbance history, or environment. Other differences are less easily understood and may be the result of more remote historic events (e.g., those of the Pleistocene, Delcourt and Delcourt, this volume). Local differences, whether of environment or history, will complicate the assessment of the ecosystem change across the region.

Table 1. Land ownership and presence of old growth spruce-fir stands on southern Appalachian high peaks. The areas are listed in decreasing order of size.

Area	Disturbance/Notes	Land ownership ¹
Great Smoky Mts.	Logging, fire, grazing Old growth stands Largest area of spruce-fir	NPS-GRSM
Balsam Mts.	Logging, fire, grazing	USFS, NPS-BRP, Private
Black Mts.	Logging, fire, grazing Old growth stands	USFS, NPS-BRP, NC State Park
Roan Mt.	Logging, fire, grazing	USFS, Private, Nature Conservancy
Plott Balsams	Logging, fire, grazing	NPS-BRP, Private
Craggy Mts.	Logging, fire, grazing Well-developed spruce-fir	USFS, NPS-BRP absent
Grandfather Mt.	Logging, fire, grazing	Private, National Natural Landmark
Mt. Rogers	Logging Old growth stands	USFS, VA State Park
Mt. Pisgah	Logging, fire, grazing Well-developed spruce-fir	USFS, NPS-BRP absent
Whitetop	Logging Spruce forests present without fir	USFS, VA State Park

¹ Agency abbreviations: NPS=National Park Service, GRSM= Great Smoky Mountains National Park, BRP=Blue Ridge Parkway, USFS=US Forest Service

THE THREATS

Despite legal protection within GRSM and several other conservation areas (Table 1), the integrity of this ecosystem is threatened by two indirect human influences: the balsam woolly aphid (=adelgid, Eagar, DeSelm and Boner, this volume), an introduced insect pest that has been spreading in the region since about 1960, and atmospheric deposition of pollutants (Bogle and Turner, Lovett, this volume). Within the next two decades, remnant undisturbed southern Appalachian spruce-fir forests will have changed greatly in character. The changes involve several levels of biological organization, including physiological response, the loss of genotypes, local and regional extirpations of species, species extinction, and changes in populations, community structure, dynamics, and ecosystem function. The changes are occurring more quickly than those of post-Pleistocene climatic fluctuation (Delcourt and Delcourt, this volume). To the immediate threats of the balsam woolly aphid and atmospheric deposition, we must add climatic warming due to increased carbon dioxide content of the atmosphere as a likely additional stress (Becking and Olson, 1978; Delcourt and Delcourt, this volume).

Whereas the balsam woolly aphid problem stimulated initial spruce-fir research in the mid-seventies (Eagar, this volume, and literature cited therein), recent attention has shifted to the role of pollutant deposition in these high elevation ecosystems. Red spruce may be directly threatened by air pollutants: since 1960 there has been a dramatic decline in the annual radial increment of red spruce in the southern Appalachians (S. McLaughlin, unpublished data; R. Bruck, unpublished data). Whether or not spruce decline can be associated with atmospheric deposition of pollutants and whether or not the decline is associated with increased spruce mortality is the subject of ongoing research involving the National Park Service, Oak Ridge National Lab, the Tennessee Valley Authority, North Carolina State University, and other regional institutions. Earlier work showed that mortality was low compared to New England (Johnson and Siccama 1983), but this is clearly a dynamic situation. Several researchers have expressed the hypothesis that vulnerability of Fraser fir to the balsam woolly aphid is effected by air pollutant stress (Eagar, this volume; R. Bruck, personal communication).

High elevation conifer ecosystems may be particularly vulnerable to pollutant deposition (Lovett, this volume). High elevation systems probably receive more deposition, as a function of higher precipitation and cloud immersion, than lower elevations. The high surface area of the needle-leaved conifers results in greater collection of cloud moisture. High elevation soils may be prone to acidification and nutrient leaching. Concern for high elevation ecosystems in the southern Appalachians is supported by reports of forest degradation in the northeastern United States (Siccama et al, 1982) and western Europe, where conifers in mountainous landscapes have also been involved (Plochmann 1984).

Although data on red spruce decline has not yet been published, Baes and McLaughlin (1984) have described increment suppression in Pinus echinata from Great Smoky Mountains National Park. Two periods of growth suppression were found, one between 1863 and 1912 (during a period of smelting activity at Copperhill, Tennessee, 88 km upwind from the park) and the past 20-25 years. Metal concentrations in the rings were used to suggest that growth suppression was caused by pollutant deposition.

Pollutants in the southern Appalachians include ozone, nitrogen oxides, nitrate, sulfate, trace elements, and acidity (Lovett, Bogle and Turner, this volume; Hermann and Baron 1980). These enter the system as gases, dryfall, wetfall, and cloud droplet impaction (Lovett, this volume). The interaction of the pollutants with vegetation and soils are not completely known at this time. Possible pathways include: (1) direct effects on leaves (e.g., ozone symptoms on sensitive species, leaching of nutrients from leaves, nitrogen fertilization through nitrate absorption in the canopy); (2) effects on soil fertility (e.g., through deposition of hydrogen ions leading to leaching of nutrient cations, through mobility of anions in soil solution leading to vulnerability of nutrient cations to leaching--Johnson and Cole 1980, Johnson and Todd 1983); (3) accumulation and enhanced availability of toxic elements in soils (e.g., lead, other trace elements, some made more available by anthropogenic sources of acidity, leading to toxic effects in below or above ground plant parts--Bogle and Turner, this volume); and (4) effects on root systems (e.g., aluminum or other trace element toxicity, leading to reduced uptake of water or nutrients, whether or not these are available in the soil). All of these pathways may pertain in the southern Appalachians. Further, different pathways may be relatively more important for certain ecosystems or for certain species. Finally, these stresses interact with natural stresses like drought, as well as with the effects of the balsam woolly aphid.

The complicated nature of forest decline and difficulty of establishing cause and effect are illustrated by the situation in West German forests. Five specific hypotheses have been advanced (adapted from Cowling 1983, C. Cronan, personal communication): (1) the gaseous pollutant hypothesis (ozone and sulfur dioxide direct effects on above ground parts); (2) the magnesium deficiency hypothesis (deposition of acidity leaches calcium and magnesium from leaves and soils, enriches nitrogen supply via nitrate, leading to nutrient cation deficiency); (3) the aluminum toxicity hypothesis (increased acidity leads to increased concentrations of soluble aluminum, which leads to toxicity to fine roots); (4) the foliar fertilization hypothesis (nitrate and ammonium uptake in canopies leads to limitation of other nutrients and a lack of frost hardiness leadings to winter mortality of shoots and needles); and (5) the general stress hypothesis (air pollution leads to reduced photosynthesis and low root vigor by a variety of mechanisms, including accumulation of

trace elements and interactions with natural stresses). A variety of species and forest types are affected in West Germany; all of the hypotheses may pertain in given situations and all of the factors interact with natural stresses as well.

The acidification of soils and transmission of acidity to drainage waters has been a primary concern in southern Appalachian spruce-fir (Hermann and Baron 1980). Spruce-fir soils are naturally acidic and low in buffering capacity. Recently, D. W. Johnson (Johnson and Cole 1980, Johnson and Todd 1983) shifted attention from the direct effects of hydrogen ion deposition to the effects of anion (nitrate and sulfate) deposition. Since cation mobility and vulnerability to leaching are a function of anion mobility, Johnson hypothesized that the ability of a soil to immobilize anions was the key factor in acidification. Johnson and Todd (1983) concluded that spodosols under spruce-fir in the northeast had a poor sulfate absorption capacity (because of high organic matter content); this would presumably also apply to southern spruce-fir stands. If these ecosystems are near saturation for nitrate and sulfate, continued deposition will lead to leaching of nutrient cations and, hence, accelerating acidification (Johnson and Todd 1983). This hypothesis forms the basis of ongoing research by D. W. Johnson (see below).

The role of organic acids in this system is poorly understood (Johnson and Cole 1980). These acids may have an overriding influence on soil solution acidity; acidity in Raven Fork, Great Smoky Mountains National Park, was shown to be controlled by organic acids in a way that suggested independence from precipitation pH (Tennessee Valley Authority, 1983).

There are many factors that can cause sudden losses of vigor and increases in tree mortality. The possibility remains that tree decline in southern Appalachian spruce-fir is the result of natural factors (an undetected pathogen, drought stress).

Even if air pollutants were not involved, the loss of mature Fraser fir trees (one of two major dominants of this forest zone) will bring widespread change to this ecosystem (DeSelm and Boner, this volume). This loss will probably be complete in all areas except Mt. Rogers within the next several decades (Rheinhardt, Eagar, this volume). This change will effect associated species, including lichens of Fraser fir (Dey, this volume), birds (Rabenold, this volume), and salamanders (Mathews and Echternaut, this volume). Our assessment of the threats to bryophytes, invertebrates, and mammals is hampered by lack of past population or community data. Changes will occur in stand microclimate (with increased insolation after fir death) and in ecosystem structure (with production of large amounts of dead organic matter--Nicholas and White, in press). Lack of baseline data on the fungi seriously hampers efforts to predict effects on that group (Petersen, this volume). The changes may also influence soil solution chemistry and, thus, potentially effect stream

communities as well. Indirect effects to understory plants will occur as a result of increased shrub cover and release of understory saplings (DeSelm and Boner, this volume). The response of organisms and soils to air pollutants will also be affected by the concurrent loss of Fraser fir.

The possibility of aphid resistant Abies genotypes on Mt. Rogers is of particular interest (Rheinhardt, Eagar, this volume). There is also a possibility for longterm Fraser fir persistence elsewhere in the southern Appalachians. Since aphid infestations on seedlings and saplings are possibly maintained by spread from mature trees (Eagar, this volume) and since mortality of younger trees is less pronounced, the possibility remains that a shifting steady state of infested and uninfested patches will occur, with the aphid becoming locally extinct as mature trees are lost, thus giving an opportunity for stand regeneration. It is not now known whether a long term equilibrium of such patches will occur; further, it will be of crucial importance to find out if the cycle between patches is long enough for successful seed crop production of Fraser fir. This does suggest an important research direction in terms of projecting the future state of this system: local persistence of aphids after death of mature trees, spread rates from isolated infestations, and growth rates of fir saplings would all have to be quantified and modelled. The conservation importance of such an effort is clear: that research will define the extinction probability of Fraser fir as a species over the next two to five decades.

The structure and dynamics of undisturbed spruce-fir forest changes with elevation, slope aspect, and slope position (Whittaker 1956, Crandall 1958). Growth rates and maximum tree sizes tend to decrease with elevation and from moist (coves) to dry (ridge) sites. Within one site type and elevation, treefall gaps cause more local variations in density and basal area (White et al., in press); the frequency of windthrow probably increases from sheltered to exposed locations. Disturbance history is also a controlling influence on stand structure and growth. As a result, the phrasing of hypotheses and the organization of sampling stratification will be crucial factors in the assessment of the impact of threats to the spruce-fir ecosystem. Investigators must control for the other influences on stand structure and growth in order to examine the independent effects of the loss of fir and deposition of pollutants.

ECOSYSTEM STUDIES: BIOMASS, PRODUCTIVITY, AND NUTRIENT CYCLING

The spread of air pollutants to the southern Appalachians underscores the importance of ecosystem level research. Example of key research areas include the influence of pollutant chemistry on nutrient cycling and the importance of decomposers in the fate of large amounts of organic debris. Therefore, I will briefly review past work on ecosystem structure and function in southern Appalachian spruce-fir.

Standing crop biomass and net annual production was been assessed in the Great Smoky Mountains by R. H. Whittaker in a series of papers (Whittaker 1961, 1962, 1963, 1965, 1966; Whittaker and Garfine 1962). Whittaker's initial papers assessed sampling technique for annual production. Shrub species and heath balds were the focus of much of this work. The most important summary is presented by Whittaker (1966), in which five of the samples were spruce-fir or fir stands. Spruce-fir forests were shown to have lower biomass than low elevations forests, but higher biomass than old growth hardwood forests at comparable elevations. Spruce-fir had relatively high biomass accumulation ratios (total biomass/net annual above ground production), low ratios of annual net production to leaf weight or leaf area, and high leaf areas. Although Whittaker's data are important for comparative purposes, he did not publish allometric equations for the estimation of biomass from measurement of stand basal area.

Shanks and Olson (1961) investigated the decomposition of leaves in a series of stands. They demonstrated the comparatively slow decomposition of organic matter in spruce-fir stands. Shanks and Clebsch (1962) used allometric equations to estimate the standing crop biomass and elemental composition in red spruce. Other data collected in the 1960s (Shanks et al. 1961) described the standing crop biomass, and elemental concentrations and pools of a variety of woody and herbaceous plants. Standing crop biomass, elemental concentration, and total element content was also described for annual litter fall.

Wolfe (1967) analyzed spruce-fir soils and reported the influence of vegetation, tree throws, and bedrock on soil morphology and nutrient content. Profile charts were presented showing elemental composition with soil depth.

Weaver (1972; Weaver and DeSelm, 1973) studied a series of stands in the Balsam Mountains, some of which occur within the Blue Ridge Parkway corridor. These stands included young (40-50 yr old) spruce-fir, young yellow birch, and mature (>100 yr old) yellow birch. Although Weaver studied a narrow range of stand types and elevations, his data include the best allometric equations for the estimation of biomass in southern spruce-fir. Annual production, net assimilation rates, deposition chemistry and rates, nutrient pools, and cycling rates were discussed.

These studies found that biomass was heavily concentrated in the tree stratum and varied from 100 metric tons/ha (in young spruce-fir stands, Weaver 1972) to 340 metric tons/ha (in old growth spruce-fir stands, Whittaker 1966). Summit type pure Fraser fir stands had 200 metric tons/ha (Whittaker 1966). Net annual production varied from about 600 to 1500 grams/square meter/yr (Shanks et al. 1961, Weaver 1972). Important nutrient pools were living biomass and organic matter in the soil. Transfer of nutrients out of these pools was found to be a slow process (Shanks and Olson 1961, Shanks et al. 1961). The ratio of biomass to annual productivity is high; thus, the rate of

nutrient availability is limited under normal conditions (Shanks and Olson 1961). Heavy tree mortality may result in pulses of nutrient availability. Because of slow growth rates, the vegetation may not be able to immobilize these nutrients in biomass, resulting in vulnerability to degradation in site fertility.

ONGOING RESEARCH IN GRSM

The ongoing research concerning GRSM spruce-fir and pollutant deposition was recently summarized by Eagar et al. (1984). The projects include research on the physiological (e.g., pollutant effects), population (mortality, regeneration), community (structure, dynamics), and ecosystem (organic matter decomposition, pollutant movements), levels; in addition, there is research characterizing soils, environment, and pollutant loading (Table 2).

This research effort is a recent and developing one. Thus, some research areas are not yet included in the scope of the ongoing studies. For example, the following projects are important additional studies: (1) analysis of historic droughts (which may interact with pollutant stress), (2) more detailed work on plant pathology, (3) population or community level work on additional taxonomic groups (snails, soil macroinvertebrates, salamanders, mosses), (4) tree root studies (e.g., field surveys of vigor and experimental studies of pollutant effects), (5) expansion of modelling (including a Fraser fir patch dynamics model, to address the extinction risk for this species), and (6) expansion of ecosystem process studies (including linkages between terrestrial and aquatic systems). Most of the ecosystem level work concerns specific hypotheses and intensive study sites; a project to characterize ecosystem function on a broader scale is needed. Finally, identification of the causes of ecosystem change will likely require field experiments, in addition to the laboratory experiments now planned.

We have presented a bibliography of southern Appalachian spruce-fir research in Appendix II to this document. Uplands Field Research Lab is also publishes a bibliographic series on the human and natural history of the southern Appalachians. Although these contain references on all regional ecosystems, they are indexed to specific ecosystem types, including spruce-fir. Reports that have been prepared to date include the following subjects: vegetation (DeYoung et al., 1982), phanerogam systematics (Wofford and White 1981), pteridophyte systematics and ecology (Evans et al. 1981), lichen systematics and ecology (DePriest 1984), geology and geomorphology (Yurkovich 1984), soils (Springer et al., in press), and lichen systematics and ecology (DePriest, in press).

Table 2. Ongoing research projects in Great Smoky Mountains National Park on spruce-fir and pollutant deposition.

Research category/project	Institution	Year
Physiological level		
Tree ring and trace element analysis	ORNL	1983-85
Tree vigor/condition	NPS	1984-85
Tree vigor/condition	NCSU	1984
Rare plant sensitivity to pollutants	NCSU	1983-85
Red spruce sensitivity to pollutants	NCSU	1984-85
Population level		
Rare plant population monitoring plots	NPS	1981-83
Small mammal survey	UT	1984-86
Community level		
Permanent vegetation plots (incl. tree mortality, regeneration, community composition and structure, all strata)	NPS	1984-85
Disturbance history and mapping	NPS	1983-85
Vegetation mapping/remote sensing	NPS	1982-85
Vegetation mapping/aerial photography	NPS	1982
History/chronosequence of fir and spruce mortality using aerial photography	USFS	1984-85
Forest fuel loadings as affected by balsam woolly aphid	NPS	1983
Gap dynamics/modelling	UT	1983
Ecosystem level		
Organic matter decomposition	NPS	1984-85
Pollutant deposition and interactions with canopy and soils	ORNL	1984-88
TVA Raven Fork study	TVA	1981-84
Soil characterizations		
Soils map	SCS	1984-85
Soil samples on vegetation plots	NPS	1984-85
Soil samples on vegetation plots	NCSU	1984
Pollutant loading/monitoring		
Elemental analysis of herbs, tree foliage, litter, and soils	ORNL	1984
Fog interception/throughfall processes	ORNL	1984-88
Sulfur accumulation in lichens	NPS	1983-84
Meteorological/atmospheric deposition	NPS,TVA,TN	1981-90

¹Institutional abbreviations: NPS=National Park Service, ORNL=Oak Ridge National Lab, UT=University of Tennessee, NCSU=North Carolina State, TVA=Tennessee Valley Authority, TN=state of Tennessee, SCS=Soil Conservation Service, USFS=US Forest Service.

CONCLUSIONS

Southern Appalachian spruce-fir is a unique, island-like and geographically restricted ecosystem type. The last undisturbed stands of this ecosystem are now threatened. These stands are a remnant of the pre-logging distribution of this type. Even pre-logging spruce-fir had been in a state of flux, however (see Delcourt and Delcourt, this volume). Natural changes in climate and distribution probably allowed local evolution of gene pools on the isolated, island-like, spruce-fir areas. More recent, human-caused, changes are occurring more quickly than those of the post-Pleistocene: Abies fraseri, a forest dominant, populations will have become drastically altered within the relatively short period between 1960 and 2000. During this period of change, there is an opportunity for the study of an ecosystem under stress and to evaluate changes in natural ecosystem processes and the risk of species loss. The nature of the threats changes underscores the importance of ecological and whole system research. The pervading influence of pollutants mandates research on an ecosystem process level. Because the structure, composition, and function of this ecosystem vary with site factors (elevation, slope aspect, slope shape), geography, and disturbance history, studies on ecosystem change will require careful phrasing of hypotheses. The research is likely to be long term. Whether the stability of this ecosystem can be promoted and whether its component species can be better protected is a matter of research and policy debate. On the one hand, the southern Appalachian spruce-fir ecosystem represents a bell-weather of change in man's environment and can be studied on that level alone. On the other hand, protection of stands or individual species may in some cases be both desirable and feasible and may require active management.

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LATE-QUATERNARY HISTORY OF THE SPRUCE-FIR ECOSYSTEM
IN THE SOUTHERN APPALACHIAN MOUNTAIN REGION

Hazel R. Delcourt^{1/} and Paul A. Delcourt^{2/}

Abstract.--We have prepared contoured maps of dominance for spruce (Picea) and fir (Abies) for selected times between 18,000 YR BP (Years Before Present) and 0 YR BP. These maps are based on calibrated fossil pollen data derived from thirteen radio-carbon-dated late-Quaternary sites located south of the glacial margin in eastern North America. During the full- and late-glacial interval, from 18,000 YR BP to 12,500 YR BP, spruce-fir forests were distributed across a broad latitudinal belt, extending eastward from Missouri across Tennessee and into the Carolinas. With major climatic amelioration after 12,500 YR BP, populations of both spruce and fir were progressively restricted in distribution to the Southern Appalachian Region, first to the area from the Cumberland and Allegheny Plateaus across to the Piedmont, and then to higher elevations in the Blue Ridge Province, such as in the Great Smoky Mountains. During the period of peak warmth and aridity in the mid-Holocene, from about 8,000 YR BP to 4,000 YR BP, spruce and fir populations were isolated at high elevations in the southern Appalachians and were separated from their main population centers in the northern Appalachians, New England, and Canada. During the past 4,000 years, climatic cooling has resulted in reexpansion of boreal species populations southward and to lower elevations in the Appalachian Mountains. The areal extent of boreal forests in the southeastern United States has changed greatly in the past 18,000 years, from a full-glacial maximum of 1,800,000 km² to a mid-Holocene minimum of about 100 km². The future trend would be toward expansion in area, unless the populations of the dominant arboreal species are eliminated by uncontrolled pathogens or by anthropogenic factors such as CO₂-induced climatic change.

Additional keywords: Abies fraseri, paleoecology of boreal forests, Picea rubens, pollen-vegetation calibrations, tree migrations.

1/

Research Assistant Professor, Department of Botany and Graduate Program in Ecology, University of Tennessee, Knoxville, Tenn.

2/

Assistant Professor, Department of Geological Sciences and Graduate Program in Ecology, University of Tennessee, Knoxville, Tenn.

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INTRODUCTION

Forests dominated by red spruce (Picea rubens Sarg.) and Fraser fir (Abies fraseri (Pursh.) Poir.) occupy approximately 120 km² in the southern Appalachian Mountains of southwestern Virginia, western North Carolina, and East Tennessee (Ramseur 1960; White this volume). Spruce and fir forests of the southern Appalachian region are generally confined to ten mountain peaks above an elevation of 1675 m, with the largest contiguous area of spruce-fir forest located in the Great Smoky Mountains National Park of Tennessee-North Carolina (Ramseur 1960; White this volume). These "islands" of spruce-fir forest are the object of intensive study because of the recent introduction and outbreak of an insect pathogen, the balsam wooly aphid that today threaten to eliminate their host tree species from the southern Appalachian region.

In the Great Smoky Mountains, the spruce-fir ecosystem traditionally has been viewed as the high-elevation endpoint in vegetation along an environmental gradient from warm-temperate to boreal communities (Whittaker 1956). Although the structure, composition, and climatic requirements of spruce-fir forests of the Great Smoky Mountains have been compared with those of red spruce-balsam fir (Abies balsamea (L.) Mill.) forests at low elevations farther north in Maine and New Brunswick (Shanks 1954), relatively little research has been attempted to determine the historical relationships of these forest communities through paleoecological studies of late-Quaternary changes in their distribution, areal coverage, and composition. Yet, such studies are vital as a perspective for understanding the development of the present-day communities as well as determining the potential for their resilience following anthropogenic disturbance.

In this paper, we review the Quaternary history of spruce-fir forests as currently known for the region south of the glacial margin in eastern North America. Using calibrations of percent dominance (growing stock volume) versus percent arboreal pollen based upon extensive compilations of forest-inventory and surface pollen-sample data, we present a series of maps that depict changes in dominance of spruce and fir over the past 18,000 years in the southeastern United States. These maps indicate changing patterns in population centers as well as range margins. They make possible, for the first time, analysis of the degree to which the changes in distribution of these two taxa have coincided and the extent to which their migrations have been individualistic. Maps based upon fossil pollen sites spaced widely across the region offer a broad-scale perspective of vegetational change (Davis 1981; Delcourt and Delcourt 1981). Future refinements in paleoecological research will allow examination of climatic and geomorphic processes as elements of changing disturbance regimes affecting plant community composition in the southern Appalachians on time scales of hundreds to thousands of years.

REGIONAL VEGETATION HISTORY

Abies has been an element of the flora of the southeastern United States since the Eocene Epoch of the Tertiary Period, with Picea first recorded in the paleobotanical record in the Miocene Epoch (Graham 1973). Although both genera have persisted in the Southeast since the Tertiary, only in the past 1 to 2 million years of the Quaternary Period have they become regionally dominant in the vegetation. Their areal dominance has fluctuated during approximately 20 glacial/interglacial climatic cycles (Ruddiman and McIntyre 1976). During about 90% of the past 1 million years, climatic conditions were colder than today (Emiliani 1972) and were favorable for widespread occurrence of boreal forests in mid-latitudes of the Southeast (north of 34° N latitude).

The vegetation patterns of the last (Wisconsinan) glacial maximum can be considered representative of the majority of the Pleistocene Epoch. Between 23,000 YR BP and 18,000 YR BP, boreal forests dominated by spruce, jack pine (Pinus banksiana Lamb.), fir, and tamarack (Larix laricina (Du Roi) K. Koch) covered an area of 1,800,000 km² across a broad latitudinal belt between the Ohio and Upper Mississippi river valleys and northern Louisiana, Mississippi, Alabama, Georgia, and South Carolina (Delcourt and Delcourt 1979, 1981; Watts 1980a). Warm-temperate forests occurred south of about 34° N latitude during full-glacial times. Deglaciation of the area in eastern North America covered by the Laurentide Ice Sheet began by 17,000 YR BP (Dreimanis 1977). This climatic amelioration resulted in vegetational response at 34° to 36° N latitude. In Tennessee and the Carolinas, dominance of jack pine began to diminish by 16,500 YR BP. Northern pines were replaced by hardwoods, with an increase in both spruce and fir. These vegetational changes reflected increased moisture and also decreased seasonal extremes in temperature, with increasing predominance of the Maritime Tropical Air mass originating in the Gulf of Mexico (Delcourt and Delcourt 1983). Boreal forests were largely replaced by temperate forests at 36° N latitude by 12,500 YR BP, with jack pine, fir, and spruce migrating rapidly northward on their leading front (Davis 1981). Populations of these boreal taxa declined rapidly at their southern limits of distribution (Bernabo and Webb 1977). During the past 10,000 years of the Holocene Epoch, boreal forests have been restricted to latitudes north of 45° N and to elevations in the central and southern Appalachians generally above 1500 m.

METHODS AND RESULTS

We used the Quaternary pollen records available from thirteen radiocarbon-dated sites in the region south of the glacial margin in eastern North America (fig. 1) to examine broad-scale changes in distribution and dominance of spruce and fir over the past 18,000 years (Barclay 1957; Craig 1969; Watts 1970, 1979, 1980b; King 1973; Delcourt 1979, 1980; Watts and Stuiver 1980; Delcourt et al. 1980, 1983; Kolb and Fredlund 1981; Whitehead 1981). At each of the thirteen fossil-pollen sites, we converted values for percent arboreal pollen (AP) to percent of forest vegetation for selected times from 18,000 YR BP to the present. We used calibrations derived from an array of 1742 county and forest inventory-unit summaries

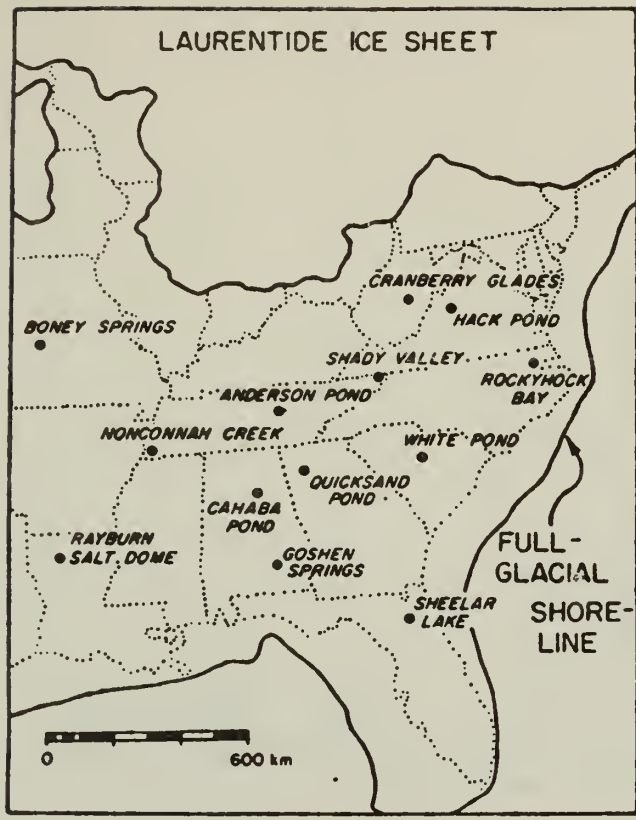


Figure 1.--Location map of late-Quaternary fossil-pollen sites.

and 1684 modern pollen samples distributed between 25° and 60° N latitude and 50° to 105° W longitude (Delcourt *et al.* in press). We used geometric-mean linear regression to establish the modern relationship of percent pollen to percent growing-stock volume for both Picea (table 1, fig. 2) and Abies (table 1, fig. 3).

Table 1.--Results of geometric-mean linear regression of percent arboreal pollen versus percent growing-stock volume for Picea and Abies in eastern North America. Asterisks (**) indicate highly significant values at the 0.01 level.

Taxon	<u>Picea</u>	<u>Abies</u>
Slope (r)	1.10**	0.44**
Y-intercept (p)	-5.28**	-2.35**
Pearson product-moment correlation coefficient	0.80**	0.30**
Number of data pairs	601	491

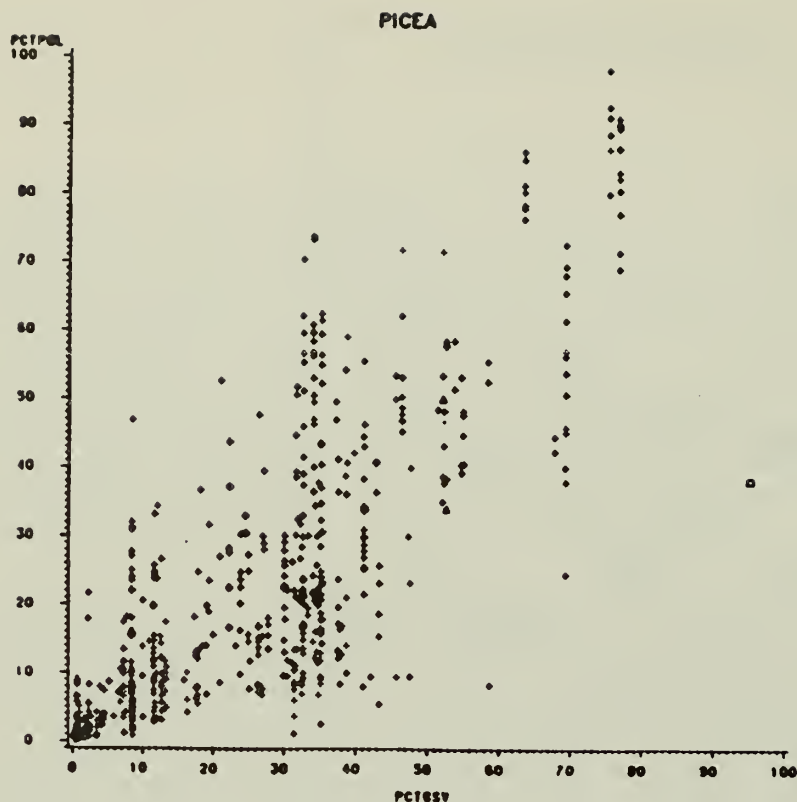


Figure 2.--Scatter plot of percent arboreal pollen (PCTPOL) versus percent growing-stock volume (PCTGSV) for Picea in eastern North America.

The slope and intercept parameters derived from these regressions and those of 18 additional tree taxa were used to recalculate percent dominance of Picea and Abies within the forests at each fossil locality, by the following equations (Prentice 1982):

$$v_a = \frac{p_a - p_o}{r} \quad \text{where } p_a \geq p_o \quad (1)$$

where v_a is a preliminary paleovegetation value,

p_a is the pollen percentage based on the sum of the arboreal pollen,

p_o is the y-intercept of the regression, and

r is the slope of the regression.

$$\text{If } p_a = 0, \text{ then } v_a = 0 \quad (2)$$

The resulting v_a values were corrected, based upon the sum of v_a values for all 20 calibrated taxa at a site for a specific time, in order to represent a paleovegetation value (v_c) for each taxon based upon 100% recalculated vegetation:

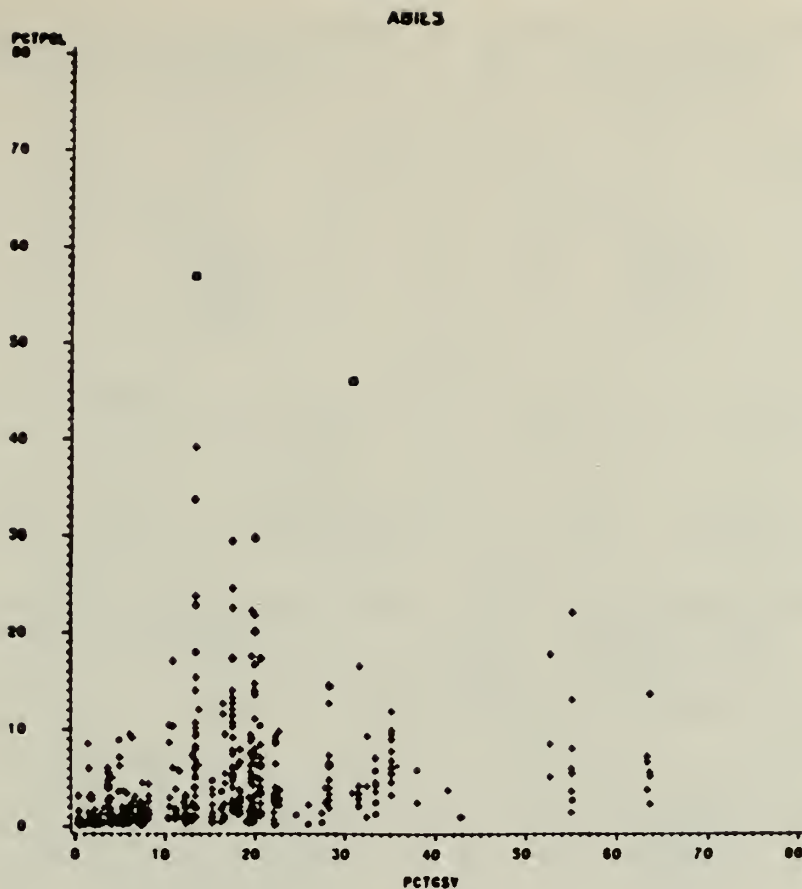


Figure 3.--Scatter plot of percent arboreal pollen (PCTPOL) versus percent growing-stock volume (PCTGSV) for Abies in eastern North America.

$$v_c = \frac{v_a}{\sum v_a} \times 100 \quad (3)$$

We plotted values for recalculated paleovegetation (v) for Picea and Abies for each site on maps (figs. 4, 5) depicting full-glacial (18,000 YR BP), late-glacial (14,000 YR BP), early Holocene (10,000 YR BP), mid-Holocene (6,000 YR BP), late Holocene (2,000 YR BP), and post-EuroAmerican settlement (0 YR BP). On each map (figs. 4, 5), solid dots designate sites with pollen data at the specified time. Open dots indicate locations of additional sites that were used in the study but did not have information for the time indicated on the map. For each time represented, contours were drawn at 10% intervals where dominance values range to 60% or greater. Contours were added at 5% intervals on maps with values of dominance ranging up to 25%. Mapped positions of the marine shoreline, margin of the Laurentide Ice Sheet, proglacial lakes, and postglacial lakes follows Delcourt and Delcourt (1981).

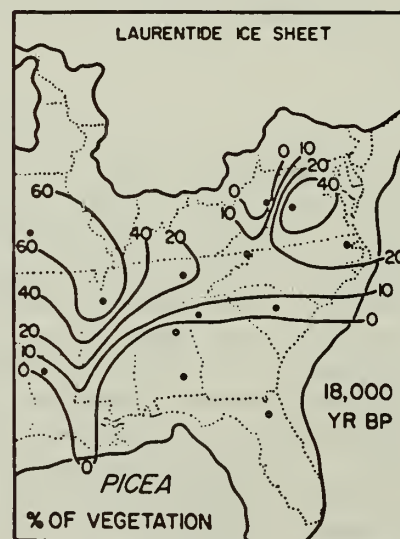
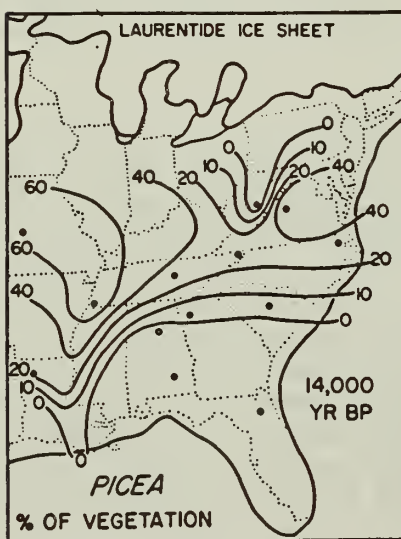
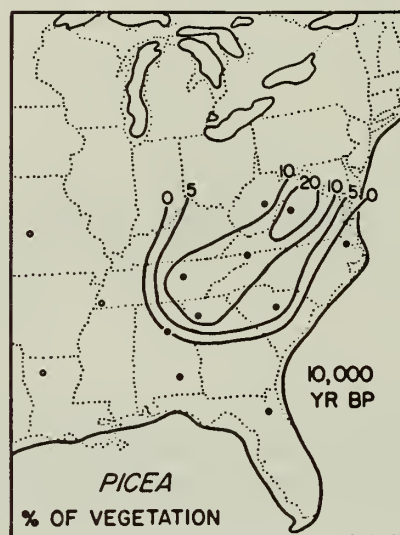
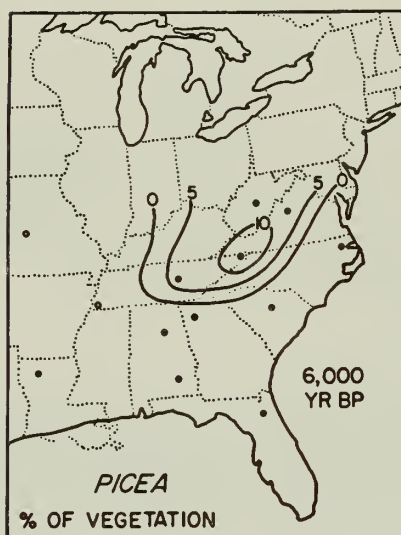
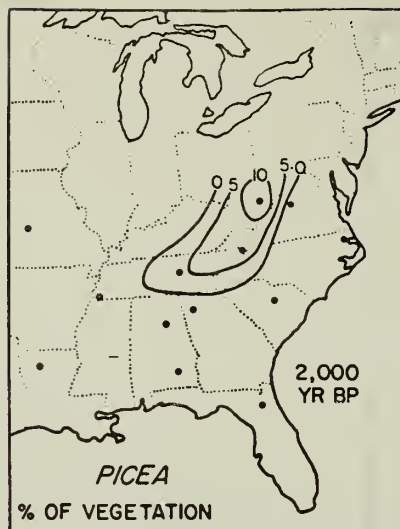
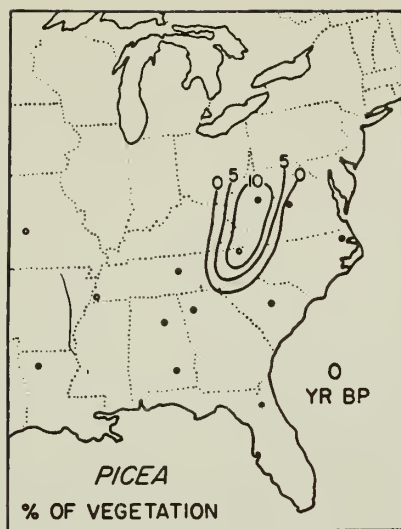


Figure 4. --Dominance maps for Picea in the southeastern United States.

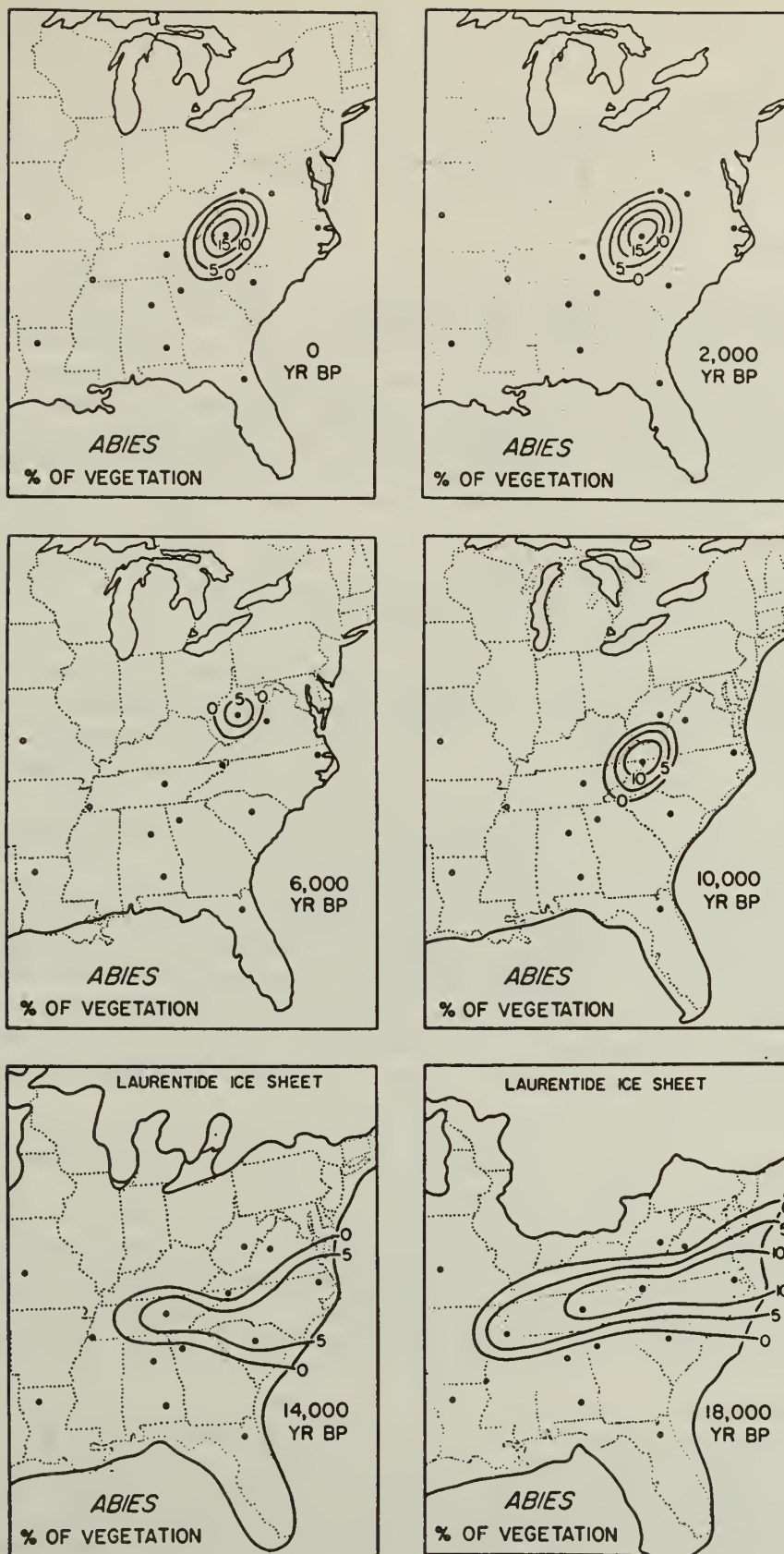


Figure 5.--Dominance maps for Abies in the southeastern United States.

DISCUSSION

Full-glacial (18,000 YR BP)

During the height of the late Wisconsinan full-glacial period, represented by the map for 18,000 YR BP (fig. 4), the distribution of spruce was concentrated in a broad latitudinal belt extending eastward from Missouri across Tennessee and into the Carolinas. Zero values to the north in the Allegheny Mountains of West Virginia and Pennsylvania mark the full-glacial ecotone between boreal forest and tundra (Watts 1979). This boundary is not known with certainty to the west of the Appalachian Mountains, but a narrow zone of tundra probably bordered the Laurentide Ice Sheet along its southern margin (Delcourt and Delcourt 1981). Alpine tundra may also have existed on mountain peaks above 1500 m in the southern Blue Ridge Province, but this speculation (Delcourt and Delcourt 1981) has yet to be tested with appropriate paleoecological sites.

Two full-glacial population centers are evident for Picea (fig. 4). Spruce constituted over 60% of the forests from West Tennessee across Missouri, and spruce also reached up to 40% in the central Appalachian Mountains. Spruce percentages were low in the Interior Low Plateau of Tennessee, where jack pine was dominant in the full-glacial (Delcourt 1979). Eastern populations were probably those of black spruce (Picea mariana (Mill.) B.S.P.) and red spruce (Picea rubens Sarg.) (Watts 1979), whereas western populations were probably mostly white spruce (Picea glauca (Moench) Voss) (Delcourt and Delcourt 1977; Delcourt et al. 1980). As in the modern boreal forests of eastern Canada (Delcourt et al. in press), in the full-glacial spruce was dominant at its northern limit of distribution, and its dominance diminished more gradually toward its southern boundary. As today, the southern limit of spruce 18,000 YR BP coincided with the ecotone between boreal coniferous and cool-temperate deciduous forests.

The distribution of Abies during the full-glacial was even more strongly confined to a narrow east-west belt, constituting up to 10% of the forests in Tennessee and North Carolina at 36° to 37° N latitude (fig. 5). Dominance of fir diminished to zero northward in Virginia and southward in Georgia and South Carolina (fig. 5). Today, balsam fir (Abies balsamea (L.) Mill.) is 10% or more of the growing-stock volume from eastern Ontario to the maritime provinces of eastern Canada (Delcourt et al. in press).

The concentration of both spruce and fir north of 34° N latitude during the full-glacial may have been related to a relatively fixed position of the polar frontal zone at that latitude, separating the relatively cold Pacific Airmass from the warm Maritime Tropical Airmass, and concentrating cold air, cloudiness, and precipitation along and north of that boundary (Delcourt and Delcourt 1983). In that the population centers of spruce and fir were not entirely coincident, edaphic and orographic factors must also have influenced their previous southward migrations, their competitive abilities, and their relative abundances across the region. Overall, however, the variability in composition of

full-glacial boreal forests of the southeastern United States appears to be within that of extant boreal forests of eastern Canada (Delcourt and Delcourt 1983).

Late-glacial (14,000 YR BP)

By 14,000 YR BP, spruce populations had begun to expand along its northern boundary as the Laurentide Ice Sheet receded (fig. 4).

Fir appears to have diminished slightly in dominance and to have begun to contract its total range eastward by 14,000 YR BP (fig. 5). At many sites, however, fir increased briefly between 13,000 YR BP and 12,000 YR BP (not shown in fig. 5).

Early Holocene (10,000 YR BP)

By 10,000 YR BP, white spruce had died out in the southwestern portion of the mapped area, and in general spruce was becoming restricted in the Southeast to the area between the Cumberland and Allegheny Plateaus from Tennessee to West Virginia and the Piedmont of the Carolinas and Virginia (fig. 4). Dominance of spruce diminished to between 5 and 20% in the southern Appalachian region.

Fir was restricted dramatically in range between 14,000 YR BP and 10,000 YR BP (fig. 5). Most of the diminishment in southeastern populations of fir occurred between 12,000 YR BP and 10,000 YR BP (not shown in fig. 5), and it was in that time range that northern populations of balsam fir probably separated from southern populations that are today known as Fraser fir. In the early Holocene, fir migrated northward in the Appalachians at about 250 m per year (Davis 1981).

Mid-Holocene (6,000 YR BP)

By the mid-Holocene, spruce was restricted to higher elevations of the Cumberland Plateau and the Blue Ridge Province (fig. 4).

Of the available pollen records, fir was recorded only in Cranberry Glades in West Virginia at 6,000 YR BP (Watts 1979), thus appearing in this map series (fig. 5) to have migrated northward to the central and northern Appalachians by that time. Fir probably also persisted at highest elevations of mountain peaks in the southern Blue Ridge Province, but this is not yet documented by fossil pollen records.

Late Holocene (2,000 YR BP)

By 2,000 YR BP, red spruce was situated on high-elevation peaks and mid-elevation intermontane valleys in the southern Appalachians. Although locally dominant, overall spruce constituted from 5 to 10% of the forests. Spruce began to expand in the northern Appalachian Mountains about 2,000 YR BP (Davis et al. 1980).

Fir expanded southward and increased in abundance between 6,000 YR BP and 2,000 YR BP, constituting up to 15% of the vegetation of the southern Appalachians.

Post-EuroAmerican settlement (0 YR BP)

Today, spruce remains a dominant of high-elevation peaks and intermontane valleys (fig. 4).

Fir is locally dominant at highest elevations in the southern Blue Ridge Province (fig. 5).

Future research

The available pollen records do not have adequate temporal resolution to reflect well the diminishment of populations of spruce and fir resulting from widespread logging and blight in the 20th century. Sites such as Flat Laurel Gap Bog near Mt. Pisgah and Boone Fork Sphagnum Bog near Grandfather Mountain are appropriate for examining the local effects of logging upon community composition as reflected in the fossil pollen record. Paleoecological sites at lower elevations that record succession during the late-glacial/early Holocene transition from boreal to deciduous forests can give insight into possible changes in forest composition resulting from future elimination of spruce and fir by blight. Paleoecological studies of a series of bogs arrayed along topographic and edaphic gradients in the Southern Appalachian Mountain Region are currently being investigated in order to resolve such fine-scale changes in altitudinal ranges of dominant tree taxa and changes in community composition resulting from changing climate and geomorphic regimes over the past 18,000 years.

CONCLUSIONS

In the northern Appalachians, spruce and fir rapidly colonized newly deglaciated land, then their populations stabilized for most of the Holocene, and spruce has reexpanded in the past 2,000 years (Davis et al. 1980). In the central Appalachians, spruce-fir forest replaced tundra briefly at the late-glacial/early Holocene transition, then was extirpated with Holocene climatic warming, and spruce has recolonized only in the late Holocene (Watts 1979). Only in the southern Appalachians are spruce-fir forests a true relict ecosystem, persisting continuously over at least the past 18,000 years. Over that time span, however, changes have occurred in area occupied as well as in floristic composition. Geographic isolation from northern populations during the Holocene has resulted in elimination of some circumboreal species from the southern Blue Ridge and Ridge and Valley provinces (H. Delcourt unpublished data) and may have promoted speciation in other groups.

Peak warmth of the present interglacial period occurred by 6,000 YR BP. The late Holocene has been characterized by progressive climatic cooling and a trend toward re-expansion of spruce-fir forests. This expansion presumably would have continued if it were not for modern man's widespread alteration of this ecosystem in the southern Appalachians, through extensive logging, inadvertant introduction of pathogens, possible climatic warming following increasing levels of atmospheric CO₂, and potential impacts of acid precipitation. Fine-scale paleoecological studies can help elucidate successional patterns that accompany loss of such dominant species and may provide analogs for future changes in forest composition within the southern Appalachian Mountain Region.

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REVIEW OF THE BIOLOGY AND ECOLOGY OF THE BALSAM WOOLLY APHID
IN SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS

Christopher Eagar^{1/}

Abstract. The balsam woolly aphid (Adelges piceae Ratz.), native to Europe, was introduced into Maine about 1900 and has subsequently spread throughout the eastern fir forests. This insect pest was detected on Fraser fir (Abies fraseri [Pursh] Poir.) on Mount Mitchell in North Carolina in 1957; however, at that time the entire mountain was infested. The aphid was discovered on Roan Mountain in 1962 and in most of the other Southern Appalachian fir communities in 1963. Infestations were not found on Mount Rogers, Virginia, until 1979, but tree core analysis indicated aphid activity since about 1962. Fraser fir on Mount Rogers do not succumb to aphid attack as rapidly as Fraser fir from the other Southern Appalachian stands. Balsam woolly aphid populations consist of wingless females which rely on passive dissemination, with wind currents providing the major vector. Reproduction is parthenogenetic, and fecundity rates are high. The insect inserts its stylet into the bark of the tree and feeds on plant sap within cortical parenchyma cells. During the course of feeding, a substance secreted by the insect is disruptive to nearby cells and tissue. Tree mortality is due to decreased translocation within the xylem, with death occurring in 2-7 years following initial infestation. Aspects of host-pest interactions, as well as the current status and possible air pollution-aphid interaction in the rapid death of Fraser fir, are discussed.

Additional keywords: Abies fraseri, Adelges piceae, Southern Appalachian spruce-fir, host-pest interactions.

INTRODUCTION

Migration of the balsam woolly aphid (Adelges piceae Ratz.) into the Southern Appalachian spruce-fir forests has concerned scientists, resource managers, and recreationalists. This pest is a tiny, sucking insect that feeds on the bark of true firs (Abies spp.), causing mortality much out of proportion to its size. Fraser fir (Abies fraseri (Pursh) Poir.) is easily killed by the balsam woolly aphid, with the time from initial infestation being between 3 and 9 years, depending on the size and vigor of the tree (Amman and Speers 1965). The intensity of the host reaction combined with the phenomenal reproductive potential of the aphid has already created significant changes in the species composition and structure of the Southern Appalachian spruce-fir forests.

The balsam woolly aphid is native to Europe and was first identified in North America in 1908 on balsam fir (Abies balsamea (L.) Mill.) in Maine (Kotinsky 1916). The insect probably arrived in North America prior to 1900 on imported nursery stock, with separate introductions in southern Nova Scotia and Maine (Balch 1952).

^{1/}Biological Technician (Ecologist), Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, TN 37738. I would like to thank R. L. Hay and K. D. Johnson for insight and assistance during initial research activities and preparation of information presented in this paper.

A separate introduction on the west coast of North America resulted in the aphid being identified on noble fir (Abies procera Rehd.) and grand fir (Abies grandis (Dougl.) Lindl.) near San Francisco in 1928 (Annand 1928). Firs in the Willamette Valley were infested by 1930, and by the 1950s the aphid was established throughout the Pacific Northwest from the coast to the summit of the Cascade Mountains (Mitchell 1966).

The balsam woolly aphid was first detected in the Southern Appalachians on Mount Mitchell, North Carolina, in 1957 (Speers 1958). Subsequent surveys revealed that there were 11,000 dead firs and the aphid had spread throughout the entire 3,035 hectares of Fraser fir type on Mount Mitchell (Nagel 1959). High mortality and widespread aphid distribution indicated aphid establishment prior to 1957, perhaps as early as 1940. The Mount Mitchell infestation then spread to the Fraser fir communities throughout the Southern Appalachians.

Balsam woolly aphids could not have chosen to invade a better peak in order to further their population expansion. Mount Mitchell, the tallest peak in the East, is centrally located to all Fraser fir in the Southern Appalachians. The Black Mountains, of which Mount Mitchell is a part, have a north-south orientation in an otherwise southwest-northeast oriented chain. Therefore, Mount Mitchell is a distinctively tall peak in a continuum of tall peaks, providing relatively easy dissemination to the other Southern Appalachian fir stands.

Balsam woolly aphids were detected in 1962 on Roan Mountain (Ciesla and Buchanan 1962), which is located 32 kilometers N 15° E of Mount Mitchell. Grandfather Mountain was found to have aphids in 1963; it is 48 kilometers N 50° E from Mount Mitchell. The same year, aphids were found on Mount Sterling, which is 64.4 kilometers S 85° W of Mount Mitchell (Ciesla et al. 1963). In subsequent years, balsam woolly aphids have been found in all Fraser fir stands.

BIOLOGY AND ECOLOGY OF THE APHID

The balsam woolly aphid has been placed in the order Homoptera, the superfamily Aphidoidea, family Phylloxeridae, and subfamily Adelginae. There are 11 species of adelgids that infest Abies, all of which are holarctic in origin. Two of the 11 species, A. piceae and A. nusslini (Borner), have inadvertently been introduced into North America. A. nusslini, indigenous to Europe, has a limited distribution in North America, where it has not seriously damaged its hosts. In Europe, this species has caused limited economic damage, primarily to Abies alba (Miller) (Bryant 1974). A. piceae is innocuous in Europe but it is extremely damaging in North America. It is believed that A. piceae evolved from A. nusslini following the movement of the latter species from the Caucasion region to Europe. In Europe, the two species apparently occupy different ecological niches, with A. piceae feeding on the trunk and A. nusslini feeding on the twigs and needles (Balch 1952). This pattern has not been observed in North America.

Life Cycle and Development of the Aphid

The fir adelgids exhibit complex polymorphic life cycles which often include alternation of hosts, with spruce (Picea spp.) being the primary host and the true firs (Abies spp.) being the secondary host. Sexual reproduction is associated with the primary host and parthenogenesis with the secondary host.

Throughout its range, the balsam woolly aphid has evolved the capacity to produce successive generations on the secondary host and is not found in sexual or migrant form in North America (Balch 1952). Thus populations of the balsam woolly aphid in North America consist only of females, and reproduction is parthenogenetic.

The life cycle of the balsam woolly aphid consists of an egg stage, three larval instars, and the adult. The following description of each stage is based on examinations made in eastern Canada by Balch (1952) and is consistent with observations I have made in the Southern Appalachians.

Eggs are oval, light purplish-brown, about 0.4 mm long, and are attached behind the stationary parent by a silken thread. As the egg matures, the color changes to orange-brown. The first instar (neosten) is the only form capable of initiating movement. This "crawler" is about 0.4 mm long with an oval, ventrally flattened body. Upon emerging from the egg, its color is light orangish-brown. Once a suitable feeding site is located, the stylet is inserted into the bark and, following a period of diapause, feeding begins. This developing instar becomes purplish-black, and small tufts of wax thread appear on its sides. The insect remains at this location for the rest of its life.

The second instar has a broader body and is about 0.5 mm long. The color remains the same as the first instar; however, the entire body becomes covered with long, curling, white wax threads which give the balsam woolly aphid its characteristic woolly appearance. During this stage the legs and antennae atrophy. The third instar is about 0.65 mm long with all other characteristics similar to the second instar.

Adults have a hemispherical body that is slightly longer than it is wide. The color is still purplish-black and the aphid is about 0.8 mm long. By this time, the wax threads have reached their maximum development and provide easy recognition.

Balsam woolly aphid populations in North America produce a minimum of two generations per year. The overwintering generation is called the *hiemosistens*, and the generation that completes its life cycle during the summer is known as the *aestivosistens*. There is little biological or morphological difference between the two generations.

Hiemosistens. All life stages from eggs to adults have been observed in late autumn; however, only the first instar larvae that have inserted their stylets and become dormant survive the winter. Insect activity begins when the host tree starts its annual growth cycle, but not all aphids begin feeding at the same time. Balch (1952) reported 20 days variation between individuals in the time that aphids broke dormancy on the same tree. In the Southern Appalachians, Amman (1962) found that dormant first instars began feeding as early as April 10 and as late as May 15 during the 1960 growing season.

After feeding begins in the spring, the first adults occur during May and early June. Reproduction begins when the adult is 2 or 3 days old and continues for at least 5 weeks. Eggs require about 9 to 12 days of incubation, but that will vary according to temperature and humidity (Balch 1952, Amman 1968, Greenback 1970).

Aestivosistens. Within a few hours of hatching, the first instar of the *aestivosistens* usually finds a suitable feeding site close to the parent. Two or three days after the stylet is inserted into the bark, the aphid enters diapause

for a duration of 3 to 8 weeks. Aestivosistens complete their metamorphosis during August and September. First instar larvae produced by aestivosistens that are in a dormant stage at the appropriate time in autumn and successfully overwinter make up the hiemosistines of the next growing season.

Reproductive Potential. Balsam woolly aphid reproductive rates are influenced by the weather conditions throughout the entire life cycle of the insect, the vigor and age of the host tree, the amount of protection provided at the feeding site, and the individual aphid (Greenbank 1970; Amman 1970). Balch (1952) reported that the hiemosistens averaged about 100 eggs per adult with a maximum of 248 and that the aestivosistens averaged about 50 eggs per adult with a maximum of 105 eggs. Survival rates will vary with environmental and host factors but average about 60 percent for both generations.

Dispersal of the Aphid. Being wingless and, except for the first instar, incapable of active travel, the balsam woolly aphid is dependent on passive forms of movement. The principal dispersal vector for the balsam woolly aphid is air currents. Crawlers, and occasionally eggs, are readily transported by wind. Balch (1952) found that they were transported more than 90 m by surface winds and several kilometers by vertical air currents in eastern Canada. In the mountainous Southern Appalachians, wind has been responsible for the movement of the aphid up to distances of 64 km (Amman 1966).

In addition to being the primary means of balsam woolly aphid dissemination among the spruce-fir islands of the Southern Appalachians, wind plays an important role in the pattern of infestation development within each islands. Initial infestation on prominent mountain masses in the Great Smoky Mountains was located at the lower elevational limits of Fraser fir. On mountains with a longer history of balsam woolly aphid activity, dead trees occurred at low to middle elevations (1300 to 1700 m). This was followed by a zone of heavy infestation with variable mortality, and then by a gradual decrease in infestation intensity with increasing elevation to the summit (Eagar 1978). Johnson (1977) found that the largest Fraser firs in a stand supported the highest aphid populations. From their tall crowns, these trees provided optimum loci to spread infestations upslope. The behavior of wind in mountain landscapes explains this pattern.

As an air mass approaches a physical obstruction, such as a mountain or large ridge, the air is forced to rise toward the summit. The air mass above the mountain is essentially unaffected by the obstruction and maintains its original speed and direction vector. Thus, air that is forced up by the mountain is restricted to less space, forcing a major air speed increase as the mountain summit is passed. On the leeward side, air pressure is lower, so the speed slows and the air mass falls through a series of eddies. The stronger the wind, the larger the eddy and the more force within the eddy (Schroeder and Buck 1970). During June and September these winds are laden with balsam woolly aphid crawlers and occasional eggs. The wind speed at the windward side at the summit is too great for the deposition of crawlers within the forest canopy. If by chance they should encounter a tree crown, they probably would not survive the collision. However, on the leeward side of the mountain, the aphid-laden air slows within the eddy, thereby providing a high probability of successful insect deposition. If the crawler lands in or near a Fraser fir, a new infestation has begun.

Other means of dispersal are gravity, the primary manner in which fir seedlings and sapling become infested; humans, by unknowing transport of crawlers

or eggs on clothes or vehicles; nursery stock or Christmas tree commerce; and phoresy--transport by animals.

Ecology and Population Dynamics of the Aphid

Environmental Factors. High ambient air temperatures are not fatal to the balsam woolly aphid (Balch 1952). In fact, consistently warmer than normal temperatures within a region would benefit the population. The increased developmental rate induced by the warmer temperature could increase the number of generations per year, which would greatly add to the growth of the population. However, high bark surface temperatures, caused by direct sunlight on a darkened object, are fatal to the adult and all nymphal stages. The cause of death is desiccation (Balch 1952). The second and third instars as well as the adult are afforded some protection from solar radiation by the wool that covers their bodies. Death of aphids due to exposure to direct sunlight is insignificant in terms of overall population dynamics.

Extremely cold temperatures limit population growth in the more northerly latitudes but is not a factor in the Southern Appalachians. All aphid stages except the overwintering first instar are killed by prolonged exposure to temperatures below 0°C and instantly by temperatures below -20°C (Balch 1952, Greenbank 1970). Overwintering first instars require a period of gradual exposure to colder temperatures in order to develop cold-hardiness before they can withstand extremely low temperatures of -25°C to -34°C . Amman (1967) reported that an overnight temperature of -34°C on Mount Mitchell, North Carolina, caused higher than normal mortality, but there was no indication that significant control of aphid populations would result from these rare low temperatures in the Southern Appalachians. Under normal weather conditions, all aphid stages have adaptations which enhance their survival.

Biotic Factors. The balsam woolly aphid in North America is free of damaging parasites and diseases. Introductions in eastern Canada, the Pacific Northwest, and the Southern Appalachians of foreign and native insect predators of the aphid had little effect on population dynamics (Balch 1952, Brown and Clark 1970, Amman 1961, Mitchell and Wright 1967, Amman 1970, Amman and Speers 1971). Ineffective synchronization of predator-prey life cycles, poor searching ability of the predators, the high reproductive capacity of the balsam woolly aphid, and the rapid death of the host tree were all factors in the failure of predators to reduce aphid populations.

The carrying capacity of the host tree is the only biotic factor that significantly affects the upper limits of aphid populations in the Southern Appalachians. This carrying capacity is surpassed in a comparatively short time, resulting in a sharp reduction in the aphid population followed by death of the host (Amman 1970).

Applied Factors. Lindane (gamma isomer of benzene hexachloride) has been the primary chemical for the control of the balsam woolly aphid; however, it is of little practical use in forest conditions since the bole of the tree must be sprayed from within the stand to the point of saturation. Lindane has been used to protect critical high-use recreation areas on Mount Mitchell during the 1960s (Ciesla et al. 1963) and on Roan Mountain beginning in 1971 (Ward et al. 1973; Johnson et al. 1980). At both locations, spraying involved application of 1/8 percent lindane within a 200-foot-wide zone on both sides of the primary

access roads. The use of lindane has come under increased scrutiny by the Environmental Protection Agency due to its persistence within the environment. Nash and Woolson (1967) reported a 10 percent average residue in the soil 14 years after application of 56 and 224 kg/ha for several soil types at Beltsville, Maryland. Lindane is broken down within the soil by microorganisms (MacRae et al. 1967). An evaluation on Mount Mitchell showed high initial concentrations in the litter layer, followed by slow movement into the soil with a peak concentration at 1.5 years after application (Jackson et al. 1974). Tests for lindane in animals and stream water on Mount Mitchell were negative.

Other chemicals which have been shown effective in killing larval and adult balsam woolly aphids under field conditions are propoxur (Baygon), permethrin (Ambush and Pounce), chlorpyrifos (Dursban), and chlorpyrifos-methyl (Reldan) (Hopewell and Bryant 1969; Hastings et al. 1979; Puritch et al. 1980). As with lindane, these insecticides must be applied from within the stand to each individual stem. Most also have limited ovicidal effect, thereby necessitating multiple applications each year. Several of these compounds are toxic to birds and mammals, and their use in natural areas is restricted.

An alternative to the use of highly toxic and/or persistent petrochemicals is the potassium salt of oleic acid (Puritch 1975). Fatty acids are natural constituents of plants and animals, are biodegradable, and, when used properly, are low in phytotoxicity. They have biocidal effect on certain soft-bodied insects, including the balsam woolly aphid. The exact mechanism of death is not certain, but it seems to be associated with the disruption of oxidative phosphorylation within individual cells and the alteration of cell membrane permeability (Puritch 1975). One additional favorable property of potassium oleate for use on the balsam woolly aphid is that it causes the loss of hydrophobic properties of the wax secretions (wool) on the insect's body, thereby allowing better contact with the body. The limiting factors in its use are the mode of application, which is similar to the above, and its lack of residual activity.

Potassium oleate (Insecticidal Soap) is currently being used in Great Smoky Mountains National Park (GRSM) around the Clingmans Dome parking lot and paved trail to the observation tower. The effectiveness of this limited control program is being monitored by 16 permanent plots established throughout the control zone by the GRSM Resources Management Division. Initial observations indicated that high levels of aphid mortality are achieved after each application. However, many trees around the parking lot have died because of several years of heavy infestation prior to control efforts. The U.S. Forest Service is also experimenting with the use of potassium oleate on Roan Mountain, but Lindane continues to be the primary insecticide (Pat Berry, personal communication).

Balsam Woolly Aphid - Fir Interactions

Feeding balsam woolly aphids initiate anatomical and biochemical changes within the host that produce physiological modifications resulting in death of the tree. The anatomical changes have been documented, but the biochemical mechanisms remain less clear. Lack of a culture technique for the insect in the laboratory has delayed analysis of the salivary secretions injected into the tree. Determination of the chemistry of these secretions

is necessary for an understanding of the biochemical basis of damage to the tree.

The reaction of North American Abies to balsam woolly aphid feeding is manifest through microscopic symptoms, which deal with the response of cells near the feeding sites, and the macroscopic symptoms, including growth and form changes.

Microscopic Symptoms. The stylet of the balsam woolly aphid, which is about four times as long as the body, penetrates the bark intercellularly through the phellem and into the phelloderm, where the insect feeds in parenchyma. During feeding, the stylet is partially withdrawn and reinserted; its direction is apparently determined by aphid senses and not solely by the path of least resistance (Balch 1952).

Following the insertion of the stylet, the first instar nymph enters diapause. Prior to diapause, a salivary substance secreted from the tip of the maxillae forms a sheath around the stylet. This salivary substance is also secreted during feeding; its probable purpose is the modification of the feeding site in a manner that facilitates the uptake of needed nutrients (Auclair 1963; Balch et al. 1964; Miles 1968). These secretions also result in damage to cortical parenchyma cells around the feeding site. The saliva produces abnormal cell development around the stylet through either an enzymatic or synergistic action with growth hormones and inhibitors secreted by the aphid or already present in the host tree (Balch et al. 1964). Cortical parenchyma cells are enlarged six or seven times more than normal, cell walls are thickened, and the cell nuclei become larger. This process is closely followed by hyperplasia in the surrounding parenchyma and, sometimes, the formation of a secondary phellogen, which is the initial stage in the wound-healing process (Balch 1952, Saigo 1976). Not all Abies in North America are able to complete this process, whereas European silver fir (Abies alba (L.) Mill.), which has evolved with the aphid, is able to effectively seal off the feeding area with wound periderm before the tree suffers irreversible damage (Kloft 1957).

In a study of the effect of plant hormones on wound periderm formation in Fraser fir, Eagar (unpublished data) found that small wounds in the bark of Fraser fir combined with a one-time injection of two auxin-like compounds (indole-3-acetic acid and naphthaleneacetic acid), a possible component of aphid saliva, required 11 additional days for secondary phellogen formation than the controls of wounding only and wounding and injection of distilled water. Treatments utilizing a gibberellin and a cytokinin formed secondary phellogen at the same rate as the controls. The hypersensitivity of Fraser fir in GRSM may be, in part, due to a disruption of the normal plant defense mechanisms by plant growth substances secreted by the balsam woolly aphid. (See Mullick 1977 for a review of plant defense mechanisms.) Although the chemical content of the saliva of the balsam woolly aphid has not been determined, analysis of the saliva of other parenchyma and phloem feeders has consistently found auxin-like compounds (Miles 1968). The inability of Fraser fir to seal off the feeding site and contain the aphid secretions results in additional plant tissue damage described below.

Diffusion of balsam woolly aphid secretions results in cellular changes within the phloem, vascular cambium, and xylem. The phloem of infested grand

fir (Abies grandis (Dougl.) Lindl.) contained more tangential bands of phloem parenchyma strands and fiber schlaroids and had a high number of traumatic resin ducts and shorter sieve cells than uninfested trees (Saigo 1969). The vascular cambium of infested grand fir contained a wider radial file of cells and increased periclinal and anticlinal division of furiform initials compared to uninfested trees (Smith 1967). The cellular characteristics displayed by the xylem are similar to those of compression wood: short, thick, highly lignified, reddish tracheids; an increase in the number of rays; checks in the secondary cell walls at a larger angle to the longitudinal axis than normal; and a large reduction in the lumen (Balch 1952, Doerksen and Mitchell 1965, Foulger 1968). Abies alba in Scotland did not exhibit these symptoms (Varty 1956).

Balch (1952) and Mitchell (1967) observed that the movement of aqueous solutions of dye through the wood of balsam woolly aphid infested trees was restricted to fewer annual rings and transported slower than in normal wood. Puritch (1971) quantified these differences and found that balsam woolly aphid infestations reduced the permeability of sapwood by 95 percent, a value which approximates the permeability of heartwood. Although some tracheids were aspirated, the main cause of decreased permeability was a reduction in the number of conducting bordered-pit pairs due to encrusting of the perforations on bordered-pit membranes of the sapwood; a condition similar to that of heartwood (Puritch and Petty 1971, Puritch and Johnson 1971). Additionally, the phenolic composition of balsam woolly aphid affected sapwood was similar to normal heartwood (Puritch 1977). Thus balsam woolly aphid infestation causes the formation of premature heartwood which results in greatly reduced translocation of water and minerals to the crown, resulting in water stress and causing death of the tree due to reduction of photosynthesis to near zero (Puritch 1973).

Macroscopic symptoms. Two types of macroscopic changes are associated with balsam woolly aphid attack: those due to infestations being concentrated in the crown, or those on the central stem of the host tree. Crown infestations exhibit the following sequence of external symptoms: (1) swelling at the nodes, (2) shoots becoming thickened and irregularly twisted and often turning downward, (3) tip inhibition, (4) defoliation, and (5) dieback (Balch 1952).

The loss of height growth combined with the slight increase in diameter growth associated with light to moderate infestations produces extreme stem taper. Crown infestations can cause death of the host after 10 to 20 years of aphid activity. Recovery and resumption of normal growth have been reported for balsam fir in Newfoundland (Schooley 1976).

Macroscopic symptoms of stem infestations are not outwardly apparent prior to the death of the tree. Characteristics of stem infestations include a brief period of increased diameter growth followed by 1 or 2 years of reduced diameter growth. The tree dies rapidly, as manifested by the gradual change in foliage color from healthy blue-green to a faded yellow-green, to a bright rusty-red, and finally to dead-brown. The aphid population crashes prior to the completion of change in foliage color (Amman and Talierco 1967,

Amman 1970). This sequence is influenced by the amount and frequency of rainfall during the growing season. Summers with low rainfall or extended periods (2-3 weeks) without rainfall produce the above sequence. However, during summers of adequate rainfall, many aphid infested Fraser fir do not exhibit the final color changes to rusty-red and brown. Instead, the needles stop at yellow-green and fall off throughout the summer.

Fraser fir growing in the Southern Appalachians which are larger than 4 cm dbh have stem infestations. Trees smaller than this exhibit signs of gouting and bud inhibition common to crown infestations. Small Fraser fir saplings and seedlings do not build up large populations of balsam woolly aphids. In examining thousands of small, understory fir in GRSM over the past 8 years, I have not found reproducing adults on trees less than 1.5 m tall.

It is likely, but untested, that young or very small, suppressed, older Fraser fir lack either the proper compounds or sufficient concentration of compounds needed by the insect to produce the moulting and juvenile hormones required for normal development. (See Beck and Reese 1976 and references therein for a general review of the chemistry of insect-plant interactions.). Appreciable mortality of young or small saplings occurs only under heavy overstory infestations. Recovery of young trees does occur, if they have not been too badly damaged, once the overstory dies and the rain of insects to the understory stops.

Patterns of Aphid Infestations

Within an infested stand, canopy position and the degree of stress from competition determine infestation pattern and mortality rates of individual trees (Johnson 1977). Large trees, with their crowns exposed to air currents, are the first to become infested and support large populations for several years prior to death. However, suppressed trees with dbh >4 cm are the first to succumb, although insect numbers on individual trees are constantly low. Trees of intermediate size are the last to die within a stand, probably as a result of becoming infested after the canopy dominates in combination with better vigor than suppressed trees.

Infestation patterns along an individual bole are dependent on the vigor of the tree, stand density, tree size, and morphological features of the bark surface. Vigorous trees with live crown ratios greater than 50 percent will develop insect population along the entire bole, with the highest numbers at the base of the crown. Insect populations on trees growing under average or high stand densities do not develop down low on the bole but occur mainly at the base of and just within the crown. Few insects occur on the portion of the stem in the upper third of the crown, regardless of stand conditions or growth form (Eagar, unpublished data). Thus it is often difficult to detect the presence of balsam woolly aphids by observations made at eye level, particularly in areas of early aphid infestation development. Bark surface features associated with high aphid populations are high densities of lenticels and development of a rough-textured, furrowed bark but not a thick, plate-like bark (Eagar, unpublished data). The balsam woolly aphid apparently cannot physically penetrate the tight, smooth, grey bark of young stems.

The only indication of possible resistance of Fraser fir to balsam woolly aphid attack has been found on Mount Rogers, Virginia. It had been thought that Fraser fir on Mount Rogers were free of balsam woolly aphids prior to detection of two small infestations on Cabin Ridge in 1979 by the USDA Forest

Service, Forest Pest Management Division. Subsequent stem analysis of several trees within the infestation revealed aphid-caused redwood in the annual rings beginning in 1962 (H. Lambert, personal communication). Monitoring of insect populations on individual trees by USDA Forest Service personnel over the next 2 years indicated a pattern of aphid population buildup and collapse. I observed the bark of trees in this stand and found it to be much hardened and having a thicker rhytidome than uninfested trees on Mount Rogers or infested trees in the Great Smoky Mountains. Histological examination of bark tissue from infested trees on Mount Rogers showed numerous small pockets of dead tissue with wound periderm within the cortex, which may have been sealed-off aphid feeding sites. These pockets, the thickened hard rhytidome, and the long history of the infestation without significant spread or mortality suggest a genetically based ability to rapidly form wound periderm around aphid feeding sites which prevents the diffusion of the harmful secretions into the xylem. (NOTE: This mechanism is based on a few observations and should be investigated with appropriate experimental design prior to acceptance.)

CURRENT STATUS AND FUTURE CONSIDERATIONS

The initial wave of balsam woolly aphid caused mortality of Fraser fir in the southern Appalachians is nearly completed. A few small stands with healthy but infested fir are located in the vicinity of Clingmans Dome in GRSM. The fir growing in the protection zones on Roan Mountain (about 162 ha) and Clingmans Dome (about 10 ha) and the fir on Mount Rogers have not been significantly harmed by the aphid. The area that had been protected on Mount Mitchell until 1974 is now heavily infested, and significant mortality is beginning to occur. Without a major breakthrough in development of an inexpensive, fairly specific, aerially applied insecticide, the balsam woolly aphid will continue to be a significant pest in the spruce-fir forests of the Southern Appalachians.

On Mount Sterling in the Great Smoky Mountains, the understory fir that survived the initial infestation and those that have grown from seed since then are now approaching an age that can support balsam woolly aphid populations. Fraser fir outside the control area on Clingmans Dome, located at the opposite end of the fir distribution in the Great Smoky Mountains from Mount Sterling, are just now becoming infested. The prevailing winds blow from Clingmans Dome to Mount Sterling; thus, the return trip will be faster than the initial infestation spread. It seems likely that a cyclic situation will develop: initial infestation → limited recovery and regeneration → reinfestation, etc. The length of time for one complete cycle in the Great Smoky Mountains can only be speculated but appears to be on the order of 35 to 60 years.

In addition to loss of all overstory and a significant part of the understory Fraser fir, Southern Appalachian spruce-fir communities will experience more subtle changes due to secondary responses. The portion of the flora which is adapted to moist, cool, low-light environments will lose a sizable part of its habitat. Boner (1979) sampled stands of various lengths of time since balsam woolly aphid damage and found that in stands with long histories of activity there was a significant increase in blackberry (Rubus canadensis) and a decrease in moss, viburnum (Viburnum alnifolium), and Vaccinium cover. (See DeSelm and Boner, this Proceedings.).

Within GRSM, 131 permanent plots (10 m x 10 m) were established in 1976 and 1977 through a contract with the University of Tennessee (Hay et al. 1978) in order to evaluate forest dynamics in response to aphid-caused disturbance. There are still important components of the spruce-fir ecosystem which are not being evaluated with respect to impacts due to loss of Fraser fir. These areas include mammals, birds, herpetofauna, arthropods, lichens, and fungi. As covered in other papers in this publication, many taxa in these groups have very specific habitat requirements which are unique to spruce-fir ecosystems.

In addition to the community structural aspects of balsam woolly aphid impact in Southern Appalachian spruce-fir forests discussed above, more subtle impacts will probably occur at the functional level. These include alterations in decomposition and mineralization rates (Gorham et al. 1979), disruption of steady state biogeochemical cycles in old-growth forests or reversal of nutrient accumulation in aggrading successional forests (Bormann and Likens 1979), and a net loss of nutrients from the ecosystem. These changes in functional attributes may be much more dramatic in Southern Appalachian spruce-fir forests which experienced significant disturbance from turn-of-the-century logging than in undisturbed old-growth forests. The result in both types of forests would be reduced productivity of subsequent plant communities.

A final consideration of the interaction of balsam woolly aphid with Fraser fir concerns the role of atmospheric pollution. Of particular initial interest are questions of how atmospheric pollutants may predispose or accelerate the death of Fraser fir by balsam woolly aphid infestation. More specifically, interactive effects between pollutant-induced stress of Fraser fir and aphid-caused mortality are suspected but untested.

Information of this nature is particularly relevant since Fraser fir is the most sensitive of North American Abies to aphid attack (Bryant 1974). Balsam woolly aphid infestations in the Northeast and Pacific Northwest have progressed no farther inland than 100 miles from the respective coasts, which are assumed to be the location of initial introduction. Cold winter temperatures in these environments are prohibiting further aphid spread (Balch 1952). These coastal locations also probably experience a diluting of atmospheric pollution by frequent mixing of oceanic and continental air. Prevailing winds in the Pacific Northwest are almost exclusively from the west. Isopaths of weighted average annual pH of precipitation in the East show near normal (5.60) values for New Brunswick and Nova Scotia, Canada (Likens 1976), the regions of highest aphid activity in the Northeast. Of all firs infested by the balsam woolly aphid, only Fraser fir grows in an area which experiences potentially harmful levels of atmospheric pollution (Skelly et al. 1970; Uplands Field Research Laboratory, unpublished data).

Studies based on the hypothesis that air pollutants are involved in the comparatively rapid death of Fraser fir following balsam woolly aphid infestation are currently being investigated at the University of Tennessee, Knoxville (E. E. C. Clebsch and C. Eagar). This study will also seek to determine the sensitivity of Fraser fir seedlings to ozone, sulfur dioxide, and combinations of the two. An understanding of the degree of air pollution impact on Fraser fir seedlings is necessary to evaluate the future probable stand dynamics within the spruce-fir ecosystem, given the potential for cyclic disturbance by balsam woolly aphid infestation.

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UNDERSTORY CHANGES IN SPRUCE-FIR DURING THE FIRST 16-20 YEARS FOLLOWING THE DEATH OF FIR

H. R. DeSelm and R. R. Boner¹

Abstract. One hundred four 0.04 ha plots were used to sample changes in the vegetation following the death of Fraser fir in the Great Smoky Mountains and Black Mountains of North Carolina and Tennessee. Fir death had been caused by balsam woolly aphid infestation. Vegetation changes in the greatest (16-20 year) time class in the Black Mountains provides hypotheses which can be tested in the Great Smokies where fir death is now occurring. The following mostly short-term increases in density or cover have been seen: spruce and yellow birch trees, fir, mountain maple and mountain ash saplings, fir, Menziesia, fire cherry, round leaf gooseberry, Rubus canadensis, R. idaeus var. canadensis, red berried elder subsapling-shrub stems, and ground cover such as certain ferns and mosses.

Additional keywords: Aphid, balsam woolly aphid, Smoky Mountains, Black Mountains, succession.

INTRODUCTION

It is the purpose of this paper to describe the changes in floristic composition and structure of the spruce-fir (Picea rubens Sarg. - Abies Fraseri (Pursh) Poir.) forests following the death of fir after infestation of the balsam woolly aphid (Adelges piceae Ratz.) These changes were advanced to the 16-20 year stage when the field work was done. The early stages are to be found now in the central Great Smoky Mountains where predictions made here from trends found in the eastern Smokies and Black Mountains may be tested.

Fraser fir is a codominant with red spruce in the high forests of southwestern Virginia, East Tennessee, western North Carolina (Little 1975, Pittillo and Smathers 1979, Shields 1962). Above about 1830 m, and in the Great Smoky Mountains above about 1890 m (occasionally lower, Cooley 1954) it is the sole forest overstory dominant (Whittaker 1956). These forests have been called a southern phase (Pittillo and Smathers 1979, Oosting and Billings 1951) of the boreal forest system, but the occurrence of many Southern Appalachian endemics (Harper 1947, 1948, White 1982, DeSelm and Clark 1983), of which some occur in the spruce-fir zone, suggests a period of relative geographic isolation from the main system. The vegetation and environment of the main boreal system has been reviewed by Larsen (1980, 1982).

^{1/} Professor, Botany Department and Graduate Program in Ecology, The University of Tennessee, Knoxville; The Nature Conservancy, Minneapolis, Minnesota, formerly of the Graduate Program in Ecology. The writers acknowledge the support of the Graduate Program in Ecology and permission for study from the National Park Service, the U.S. Forest Service, and the North Carolina Department of Parks.

The balsam woolly aphid was introduced into New England and eastern Canada from Europe about 1900 (Balch 1952). It was seen on Mt. Mitchell in the Black Mountains of western North Carolina at least by 1957 (Speers 1958) and was present earlier (Eagar 1978). It was found on Mt. Sterling in the Great Smoky Mountains in 1963 (Ciesla et al. 1965, Amman 1966) and has been expanding its range southwest in the Smokies since that time. The infestation is now nearly complete (personal communication, C.C. Eagar, July, 1983). The larger trees are first and most severely infected (Johnson 1977, Eagar 1978).

THE STUDY AREAS

Physical Environment

The Great Smoky Mountains (centering 83 30' west longitude, 35 35' north latitude) and the Black Mountains (centering at 82 15' west longitude, 35 45' north latitude) are the study areas. The Smokies contain nearly 50 km² of land area over 1675 m elevation and the Blacks nearly 25 km² of such land - most of this land is spruce-fir or fir dominated (Ramseur 1960). The Smokies are in Blount, Sevier, and Cocke Counties, Tennessee, and Swain and Mitchell counties, North Carolina. The Blacks are in Yancey, Buncombe, and McDowell Counties, North Carolina. Both ranges lie within the Blue Ridge physiographic province (Fenneman 1938).

The climate of the high elevations of these areas is characterized by high precipitation: 238.9 cm (Shanks 1954a, five year study, Great Smokies), and 180.8 cm (Carney 1955, Blacks). Precipitation is well distributed monthly but intense storms in the zones below and above 1220 m vary from 56 to 194 in a 30 year period (Bogucki 1972). Temperatures decline upslope but snowfall does not persist over the whole winter (Shanks 1954a).

Bedrocks of the Blacks are Precambrian metamorphics, gneiss and schist, with fine granitoid layers. The high Smokies are underlain by the Thunderhead Sandstone and the Anakeesta Formation which contains dark, silty to argillaceous rocks altered to slate, phyllite and schist (King, Newman and Hadley 1968). Slopes of 20 to 60 percent are common but some flat areas occur on benches and crests. Soils on coarse textured parent material and a stable surface may be expected to be spodosols, on medium textured parent material or unstable substrate mainly umbrepts, and under heath vegetation spodosols or histosols (Springer and DeSelm 1983). They are usually stoney, acid, shallow and infertile.

The surface organic layer (O-layer), in one study, weighed 97,975 kg/ha and was over 14 X as heavy as the O-layer from the northern hardwood (beech gap) forest adjacent (McGinnis 1958).

Flora and vegetation

Ramseur (1960) found 391 vascular plant taxa in the high elevation communities and 145 taxa (37 percent) in the spruce-fir of the 10 high mountain areas examined. There were 112 taxa in the Smokies and 55 in the Blacks - more intensive sampling will doubtless count more. Interesting floristic elements, as northern taxa occur (Ramseur 1960, Cain 1930), as do endemics (White 1982) and species of national significance because of their rarity (White 1982). Most of these special taxa occur in the understory.

The vegetation of the high Southern Appalachian Mountains was examined from a floristic, ecological, forest crop usage, and land use standpoints by the scientists of the turn of the last century. These observers include Gattinger (1901), Kearney (1897), Harshberger (1903), Ayres and Ashe (1902, 1905) and Pinchot and Ashe (1897). The relative inaccessability of the peaks made scientific study difficult but characterization of the flora and its elements got underway (Gattinger, Kearney, Harshberger). Forests were characterized and the effects of their destruction on soil erosion and downstream flooding were well documented (Pinchot and Ashe, Ayres and Ashe).

Between 1897 (Pinchot and Ashe) and 1935 (Cain 1935) the relative value of the high conifer forests changed dramatically. Pinchot and Ashe state, "Commercially then forests are at present unimportant". In contrast, Cain cites the details of potential log numbers from trees in the Smokies (Champion Fibre Company data from Mt. Mingus). "From the cruise sheets I have found that approximately 50 percent of the trees of 18-22 inch d.b.h. contain four 16 foot logs; of the trees from 24-30 inch d.b.h. approximately 50 percent contain five 16 foot logs; of the trees 32-36 inch d.b.h. approximately 50 percent contain six 16 foot logs while about three percent would cut seven logs." Here is an obvious expression of commercial value. Harshberger (1903) noted in his community ecology comments, non-forest areas, meadows, grassy balds, heath slicks, forest understory "associations" including ones dominated by shrubs, herbs and cryptogams, and forest overstory "black" spruce, Fraser fir and their associates.

The second period of study of this vegetation was initiated by Core (1929) on Spruce Knob, West Virginia, Davis (1930) in the Black Mountains, and Cain (1935) in the Great Smokies. These and subsequent papers now total in number over 52 (DeYoung et al. 1982). Cain's paper is instructive as he departs from the spruce-fir forest type as seen by Harshberger (1903) and Davis (1930) and describes the spruce and fir types separately (see also Ashe 1922, who lists red spruce and southern balsam types, and red spruce with yellow birch and red spruce and hemlock intergradient types; see also Hawley (1932) who describes Southern Appalachian red spruce, red spruce-southern balsam fir and yellow birch-red spruce).

Noted by Cain (1935) in the red spruce type are cover percentages of the six strata, their floristic composition and tree basal area ($76 \text{ m}^2/\text{ha}$). Noted in particular is the dominance of large (girth and height) spruce. Cain notes in the southern balsam fir (Fraser fir) type the much lower heights, the lower basal area ($66.15\text{-}66.99 \text{ m}^2/\text{ha}$) and great cryptogram cover throughout the community. He notes the increased importance of fir upslope - his fir sample stand comes from 1920 m on Mt. LeConte.

Oosting and Billings (1951) sought to sample mixed stands mostly in the middle elevations, often present data one stand at a time and may show absolute and relative data. The Smoky Mountain stands averaged $60.2 \text{ m}^2/\text{ha}$ and varied continuously from mostly spruce to mostly fir. The great tree numbers differential is evident in the 5:12, spruce: fir, total stem ratio (1000 m^2 sample) (compare this to the basal area ratio 34:21). Seedling densities of spruce and fir exceed stems over 2.5 cm d.b.h. by 78X. The seedling spruce to fir ratio was 1:4.1. Among the individual stands, diameters extend to the 34-36 inch (86-91cm) class in spruce and 32-34 (81-86 cm) class in fir but distributions of two inch classes do not fall on a typical inverse J-curve in an arithmetic plot as would be expected (Whipple and Dix 1979) among tolerant taxa (Daniel et al. 1979). It would be instructive to determine the model followed by their

data (Schmalzer 1982). Gaps in diameter sizes in individual stands may represent cyclic reproduction and/or cyclic e. g. blowdown.

Tree growth was also investigated by Oosting and Billings (1951). Spruce to 359 years was found but large spruce were commonly 200-250 years; their plotted relation suggests about 19 inches (48.3 cm) in 200 years. The smaller and younger-at-maturity firs averaged about 12 in (30.5 cm) in 100 years.

Shanks (1954b) resampled the Mt. Mingus spruce-fir stands seen by Cain and Oosting and Billings and reported basal areas for trees over 4 inches (10 cm) d.b.h. : Cain 329.2 square feet (90.0 m²/ha), Oosting and Billings 242.6 square feet (55.7 m²/ha) and his own study 218.5 square feet (50.2 m²/ha), 293.7 square feet (67.4 m²/ha), 293.5 square feet (67.4 m²/ha), and 203.5 square feet (46.7 m²/ha). Other basal areas reported are 34.4-65.6 m²/ha in spruce-fir and 29.1-66.1 m²/ha in fir in the Balsam Mountains (Weaver 1972). Golden (1974) reports 48.1 m²/ha in the Smokies spruce-birch. Boner (1979) reports 161.2-232.0 square feet/acre (37.0-53.3 m²/ha) in Smokies spruce-fir. Crandall (1958) reports 120-232 square feet/acre (27.6-53.3 m²) in the fir forests, 120-361 square feet/acre (27.6-82.9 m²/ha) in spruce-fir stands, 168-368 square feet/acre (38.6-84.5 m²/ha) in spruce types and 120-248 square feet/acre (27.6-56.9 m²/ha) acre in the spruce - hardwood types in the Smokies.

The complexity of the understory has long been of interest. While the possibility of productivity - based site types remains (cf. Heimbürger 1934), understory types were topographically based (Whittaker 1956) with five (valley to ridge) in the spruce, and four (north slope to ridge) in fir stands. This was refined by Crandall (1958) into four fir types, seven types in the spruce and spruce - fir (three also occur in the fir) and three types in the spruce-hardwood (one also occurs in the spruce-fir and fir forests). The prevalence here of cryptograms is notable in this Appalachian vegetation.

Spruce-fir vegetation biomass is heavily concentrated in the overstory tree stratum and amounts to 110-245 metric tons/ha in the Balsams (Weaver and DeSelm 1973), 351 tons/ha (Shanks, Clebsch and DeSelm 1961) or 300-340 tons/ha in the Smokies (Whittaker 1966) and 200-210 tons/ha in the Smokies fir forests (Whittaker 1966). Productivity in the spruce-fir ranges from 580 g/m²/year (Shanks, Clebsch and DeSelm 1961) to 944-1402 g/m²/year in the Smokies fir forests (Whittaker 1966); and 816 g/m²/year in young Balsam Mountain spruce-fir (Weaver 1972). Nutrient cycling studies were initiated in the Smokies (Shanks, Clebsch and DeSelm 1961) and in the Balsams (Weaver 1972) and the current acid rain problem points up the need for continued and extended studies. This third, functional, aspect of this ecosystem was initiated by Shanks, Clebsch and DeSelm (1961), and Whittaker (1961).

METHODS

During the summer of 1974, 104 0.04 ha circular plots (99 plots are reported here) were placed in spruce-fir vegetation in the Great Smoky Mountains National Park and Mt. Mitchell State Park and adjacent Pisgah National Forest. Sampled stands were located using personal reconnaissance, personal communications with appropriate people and information in Speers 1958, Nagel 1959, Ciesla et al. 1965, Aldrich and Drooz 1967,

and Rauschenberger and Lambert 1968, 1969, and 1970. Proposed stands were located on topographic maps so that areas of similar topography between 1560 m and 2010 m could be chosen. Stands were chosen to represent vegetation not modified by balsam woolly aphid attack (Central Smokies) and vegetation with fir dead as long and 20 years (eastern Smokies, Mt. Mitchell, Pisgah National Forests). Although other perturbations were minimized in the stands, plot locations in stands were otherwise random.

Plot diameter was corrected for slope angle (Bryan 1956). All stems greater than 2.5 cm d.b.h. were tallied by species. Stems 2.5 - 12.4 cm (saplings) were counted by species. Stems 12.5 cm and greater (overstory) were counted by species in five cm d.b.h. classes. Two subplots 1.8 m wide were established across the diameter of the plot-totaling 0.008 ha - herein all stems 0.6 m tall to 2.5 cm d.b.h. (subsaplings - shrubs) were counted by species. Also eight subplots 0.3 m x 3.3 m (totaling 0.0008) (ha) were established wherein cover of each taxon less than 0.6 m tall was estimated. Other plot data collected were elevation, slope angle, local slope position, slope form (flat, convex, concave), aspect, surface rock exposed, canopy closure, condition of overstory fir, and probable date of fir death from growth rings. Data were calculated per plot as absolute density, absolute basal area or relative cover (percent). Plots were grouped by elevation and time since opening of the canopy.

Vascular plant nomenclature follows Radford et al. (1968); that for bryophytes follows Crum et al. (1973).

RESULTS

Overstory taxa have responded during time in more than one way (Table I). Fir (Abies), more abundant above 1800 m, has declined (d) greatly in the affected plot groups but by 11-20 years has recruited saplings into the overstory class. The densities of Acer, Amelanchier, Betula lenta, and Prunus have scarcely changed (h) but are present in only certain time classes. The excluded Fagus (e) is special, but all of these have too low densities to conclude that the openings have a profound effect. The densities of Betula lutea and Sorbus, although not present in each age class, seem to be increasing (h-p). Picea is holding its own except at 11-20 years which has declining densities (h-d). Similar behavior appears in the basal areas of the same plots (Table II).

As is usually seen in such data, more taxa occur in the sapling than overstory layers (Table III). Although numbers are low and each time set is confounded with geographic location there are several kinds of reaction to the openings. Acer pensylvanicum, Ilex, Sambucus and Tsuga have invaded the openings (i) and Betula lenta and Viburnum cassinoides have been excluded from the openings (e). Several taxa with low densities throughout peak in the openings, Acer spicatum, Amelanchier, Viburnum alnifolium at 5-6 years, and Sorbus and Prunus at 11-15 years (h-p). Betula lutea, Picea and Rhododendron peak in the 5-10 year period (h-p). Beyond 10 years, fir sapling density increases; by 11-15 years the stem numbers equal those in undisturbed areas (h-p).

Numbers of subsapling-shrub taxa are 26 (Table IV) compared to 15 sapling taxon previously seen. Fir numbers suffer a temporary decline (5-10 years) but by 11-20 years in the Black Mountains the numbers exceed the pre-infestation levels (of the Smokies). Subsaplings of taxa maintaining this density (h) but with low frequency are Acer pensylvanicum, Amelanchier, and Rhododendron sp. Ribes glandulosum, Rubus idaeus

Table 1.--Overstory density of disturbed and undisturbed stands (stem/ha.)

Taxa	Years Since Opening of Canopy					
	0 ^a	0 ^b	5-6 ^c	7-10 ^d	11-15 ^e	16-20 ^f
<i>Abies fraseri</i> (d)	66.2	113.3	1.2		22.9	13.4
<i>Acer spicatum</i> (h)	0.6		0.6	0.9	0.4	
<i>Amelanchier arborea</i> var. <i>laevis</i> (h)	0.8			0.6		
<i>Betula lenta</i> (h)	3.3			0.7		
<i>Betula lutea</i> (h-p)	6.8	0.8	5.8	17.1		
<i>Fagus grandifolia</i> (e)	0.9	0.2				
<i>Picea rubens</i> (h-d)	33.0	26.4	24.3	30.9	10.4	6.6
<i>Prunus pensylvanica</i> (h)	0.6		0.6		0.9	
<i>Sorbus americana</i> (h-p)	1.3	2.8	2.3		6.8	4.1
Total	113.5	143.7	34.8	50.2	41.4	24.1

a/ 27 plots, Smokies, undisturbed, <6000 feet (<1829 m) elevation.

b/ 19 plots, Smokies, undisturbed >6000 feet (>1829 m) elevation.

c/ 8 plots, Black Mts. 5500-6000 feet (1676-1829 m) elevation.

d/ 22 plots, Mt. Sterling, Smokies, <6000 feet (<1829 m).

e/ 10 plots, Black Mts., <6000 feet (<1829 m) elevation.

f/ 13 plots, Black Mts, >6000 feet (>1829 m) elevation.

Table II.--Overstory basal area of disturbed and undisturbed stands (sq. m./ha)

Taxa	Years Since Opening of Canopy ^{a/}					
	0	0	5-6	7-10	11-15-	16-20
<i>Abies fraseri</i> (d)	19.4	32.1	0.1		8.9	4.8
<i>Acer spicatum</i> (h)	0.1		0.1	0.2	0.1	
<i>Amelanchier arborea</i> var. <i>laevis</i> (h)	0.3			0.1		
<i>Betula lenta</i> (h)	2.8			1.3		
<i>Betula lutea</i> (h-p)	2.9	0.6	6.1	9.7		
<i>Fagus grandifolia</i> (e)	0.3	0.2				
<i>Picea rubens</i> (h-d)	27.1	13.8	26.9	17.4	5.8	2.4
<i>Prunus pensylvanica</i> (h)	0.1		0.3		0.1	
<i>Sorbus americana</i> (h-p)	0.2	0.5	0.3		0.9	0.6
Total	53.2	47.2	33.8	28.7	15.8	7.8

^{a/}plot distribution as in Table I.

Table III.--Sapling density of disturbed and undisturbed stands (stems/ha)

Taxa	Years Since Opening of Canopy					
	0	0	5-6	7-10	11-15	16-20
<i>Abies fraseri</i> (h-p)	46.0	37.5	3.5	10.3	42.7	23.7
<i>Acer pensylvanicum</i> (i)			0.6			
<i>Acer spicatum</i> (h-p)	3.4		11.6	1.7	1.3	
<i>Amelanchier arborea</i> var. <i>laevis</i> (h-p)	0.2		3.5	0.2		
<i>Betula lenta</i> (e)	1.1					
<i>Betula lutea</i> (h-p)	3.6	1.9	5.2	7.2	3.2	
<i>Ilex ambigua</i> var. <i>montana</i> (i)			2.3	1.7		
<i>Picea rubens</i> (h-p)	11.9	5.5	9.3	18.8	5.8	4.4
<i>Prunus pensylvanica</i> (h-p)	0.2	0.2		0.2	4.5	
<i>Rhododendron catawbiense</i> (h-p)	0.3			13.1		
<i>Sambucus pubens</i> (i)				0.9	1.3	
<i>Sorbus americana</i> (h-p)	0.3	3.4	2.9	0.2	22.5	5.9
<i>Tsuga canadensis</i> (i)				0.4		
<i>Viburnum alnifolium</i> (h-p)	1.2		2.3			
<i>Viburnum cassinoides</i> (e)	0.2					
Total	68.4	48.5	41.2	54.7	81.3	34.0

a/plot distribution as in Table I.

Table IV.--Subsapling-shrub density in disturbed and undisturbed stands (stems/ha)

Taxa	Years Since Opening of Canopy ^{a/}					
	0	0	5-6	7-10	11-15	16-20
<i>Abies fraseri</i> (h-p)	275.8	225.8	17.4	133.3	359.8	474.7
<i>Acer pensylvanicum</i> (h)	5.3		2.8	3.6		
<i>Acer spicatum</i> (h-p)	15.0		92.5	29.3	6.8	
<i>Amelanchier arborea</i>						
var. <i>laevis</i> (h)	3.8		2.8			
<i>Betula lenta</i> (e)	17.2					
<i>Betula lutea</i> (h-p)	18.7	1.1	28.9	19.2	2.2	
<i>Cornus alternifolia</i> (i)			2.8			
<i>Diervilla sessilifolia</i> (e)		3.2				
<i>Fagus grandifolia</i> (e)	0.8					
<i>Hydrangea arborescens</i> (i)			8.7			
<i>Ilex ambigua</i> var.						
<i>montana</i> (h-p)	3.8		2.8	5.5		
<i>Menziesia pilosa</i> (i)			5.9			59.1
<i>Picea rubens</i> (h)	86.2	10.6	17.4	44.0	8.9	17.2
<i>Prunus pensylvanica</i> (i)				27.5	6.8	1.6
<i>Rhododendron</i>						
<i>catawbiense</i> (h)	2.3	1.1		1.0		
<i>Rhododendron maximum</i>						
(i)				1.0		
<i>Rhododendron</i> sp. (i)						6.3
<i>Ribes glandulosum</i> (i)					6.8	9.3
<i>Ribes rotundifolium</i> (h-p)		2.1	5.9	1.8		35.8
<i>Rubus canadensis</i> (h-p)	151.4	2.1	404.7	477.3	1202.8	364.2
<i>Rubus idaeus</i> var.						
<i>canadensis</i> (i)					384.5	1316.9
<i>Sambucus pubens</i> (h-p)	3.0	13.8	14.4	456.2	72.0	90.2
<i>Sorbus americana</i> (h-p)	12.0	8.5	5.9	32.2	42.5	124.5
<i>Tsuga canadensis</i> (i)				1.0		
<i>Vaccinium erythrocarpum</i>						
(h-p)	175.4	76.7	338.1	103.0	11.3	7.7
<i>Viburnum alnifolium</i>	574.0	104.4	647.5	27.5	4.5	17.2
Total	1144.7	449.4	1598.5	1363.7	2108.9	2524.7

^{a/}plot distribution as in Table I.

Table V.--Percent cover of ground cover taxa of disturbed and undisturbed stands

Taxa	Years Since Opening of Canopy ^{a/}					
	0	0	5-6	7-10	11-15	16-20
<i>Abies fraseri</i> (h)	0.2	0.3	0.3	0.5	0.7	
<i>Acer spicatum</i> (e)	0.1					
<i>Agrostis stolonifera</i> (h)	0.03	0.01			0.1	0.4
<i>Angelica</i> sp. (i)					0.04	0.1
<i>Arisaema triphyllum</i> (h)	0.04	0.01		0.1	0.4	
<i>Aster acuminatus</i> (h-p)	1.0	4.5	6.1	16.0	11.3	20.6
<i>Aster divaricatus</i> (h-p)	0.1	0.02			1.1	2.9
<i>Athyrium asplenoides</i> (h-p)	13.6	25.6	5.4	3.2	38.7	13.1
<i>Atrichum undulatum</i> (i)					1.0	
<i>Betula lenta</i> (e)	0.004					
<i>Brotherella recurvans</i> (h-p)	11.7	3.0	18.6	6.8	1.9	4.5
<i>Carex aestivalis</i> (i)						0.1
<i>Carex brunnescens</i> (h)	0.02	0.7	0.1	0.3	0.03	0.1
<i>Carex debilis</i> var. <i>rudgei</i>	0.03		0.01		0.1	0.3
<i>Carex intumescens</i> (h-p)	0.004	0.02		0.01	1.6	0.02
<i>Chelone lyonii</i> (h-p)	0.1	0.4			4.7	19.7
<i>Cimicifuga racemosa</i> (h)		0.1			0.03	
<i>Circaea alpina</i> (h-p)	0.004		0.1	1.2		
<i>Clintonia borealis</i> (h-p)	1.7	1.6	2.6	0.5	0.8	1.7
<i>Dennstaedtia puncti-</i> <i>lobula</i> (h)	0.3			0.3		
<i>Dicranodontium</i> <i>denudatum</i> (h)	0.5	0.3	0.9	0.7	0.5	0.3
<i>Dicranum fuscescens</i> (h)	0.2	0.5	0.01	0.1		
<i>Dryopteris intermedia</i> (h-p)	15.6	12.7	15.5	29.3	13.0	7.6
<i>Epifagus virginiana</i> (e)	0.004					
<i>Eupatorium rugosum</i> (h)	0.03			0.1		0.2
<i>Glyceria striata</i> (e)	0.01					
<i>Houstonia serpyllifolia</i> (h)	0.02			0.02	0.04	
<i>Hylocomium splendens</i> (h)	11.5	10.4	8.6	11.3	7.3	1.1
<i>Impatiens pallida</i> (h)	0.1	0.9	0.6		1.0	0.8
<i>Laportea canadensis</i> (e)	0.3	0.1				
Liverworts (h)	2.5	2.4	1.1	0.4	0.2	0.3
<i>Luzula</i> sp. (h)		0.01		0.03	0.6	

Table V.--(Continued)

Taxa	Years Since Opening Canopy ^{a/}					
	0 ^a	0 ^b	5-6	7-10	11-15	16-20
<i>Lycopodium lucidulum</i> (h)	2.7		0.1	0.1		
<i>Medeola virginiana</i> (e)	0.01					
<i>Monotropa uniflora</i> (e)		0.01				
<i>Oxalis acetosella</i> (h)	33.8	29.0	39.0	27.9	7.5	4.5
<i>Picea rubens</i> (h)	0.04		0.3	0.04		
<i>Polygonum cilinode</i> (i)				4.7	0.4	0.1
<i>Polypodium virginianum</i> (i)			0.04		0.01	
<i>Polytrichum ohioense</i> (h)	0.5	1.6		0.01		
<i>Ptillium cristacastrensis</i> (e)		0.3				
<i>Rhytidiadelphus triquetrus</i> (h)			0.2		0.05	0.1
<i>Rubus canadensis</i> (h)	0.1	0.01		0.2		0.02
<i>Sambucus pubens</i> (h)	0.02			0.1		
<i>Saxifraga michauxii</i> (h)		0.1				1.2
<i>Senecio rugelia</i> (h)	8.2	12.5		4.2		
<i>Smilacina racemosa</i> (e)		0.01				
<i>Solidago glomerata</i> (h-p)	0.5	0.8			9.2	13.7
<i>Sorbus americana</i> (e)	0.03	0.04				
<i>Sphagnum subnitens</i> (h)	1.2	1.2	2.1	1.5	1.0	3.2
<i>Stachys clingmanii</i> (e)		0.2				
<i>Trillium erectum</i> (h)	0.01			0.01		
<i>Vaccinium erythrocarpum</i> (e)	0.3	0.1				
<i>Veratrum viride</i> (i)					0.1	0.2
<i>Viburnum alnifolium</i> (i)			0.02			
<i>Viola</i> sp. (h)	0.01			0.01	0.01	0.01
Total	107.1	109.7	101.5	104.9	103.5	96.7

^{a/}Plot distribution as in Table I.

var. canadensis and Tsuga. Certain taxa occur in both kinds of stands but their density peaks in the disturbance - some dramatically so (h-p). Taxa which peak in the first 10 years are Acer spicatum, Betula lutea, Ilex, Sambucus, Vaccinium and Viburnum; those peaking at 11-20 years are Rubus canadensis, Sorbus, and Ribes rotundifolium.

Among the ground cover taxa (Table V) the same categories occur. Fir is maintaining its seedling populations in the disturbed area except at 16-20 years-it is not known whether this is a significant loss. A total of 27 are maintaining their populations (h), with variable frequency and cover in the disturbed plots. These include six bryophytes, two tree, two shrub, and 17 herb taxa. Twelve taxa occur in the undisturbed plots but are excluded (e) or have not yet invaded the disturbed areas; these include small trees, a shrub, several herb taxa and a bryophyte. Ground cover invaders (i) not seen in the undisturbed areas include seven taxa: the shrub Viburnum, the bryophyte Atrichum, and several herbs. Ground cover taxa which occur in both kinds of areas but whose cover peaks (h-p) in the disturbed areas number 10, including a bryophyte and nine herb taxa. The cover of the bryophyte taxa peaked early in the 20 year period of change, the two ferns Athyrium and Dryopteris and two herbs Carex intumescens and Circaea peaked in the middle (7-15 years) and the other taxa Solidago, Aster, and Chelone peaked in the 11-20 year period.

DISCUSSION

The underlying assumption of this study that this vegetation is uniform enough to find sampling sites varying only in the time of fir death must be modified to include the variables of unknown past history as consequences of vertical zonal shifts during the hypsithermal period (Billings and Mark 1957), and logging in the Black Mountains and the Smokies Mt. Sterling area (Saunders 1979) although they were not in plot locations of this study. Other variables include the gradient spruce/fir importance change through the spruce-fir zone and the distinctive understory types which Whittaker (1956) related to topographic position. All of these may result in variations in abundance, shown here as presence, density, basal area and cover in a time class. Other factors acting through past history include population genetic makeup shifts in competitors, and changes in past disease and insect predation.

The recovery of Abies from the initial attack of the aphid as evidenced by new overstory stems and partial recovery of sapling stems, the great rise in numbers of subsapling stems strongly suggests the possibility of recovery. However, the paucity of seedlings negates this. At the time of this study these small diameter fir were not being killed.

The invader taxa, not present in the central Smokies undisturbed plots, may indeed be taxa whose propagule mobility allows them to invade open areas - or they may be low frequency overlooked taxa. They include two with winged fruit, seven with pulpy, berry-like fruit, one hooked fruit and taxa two spore-borne. Others are tiny to moderate-sized seed or fruit whose dispersal mechanism is less obvious. Two of these taxa occurred in the seed rain of a spruce and adjacent beech forest (Angelica and Viburnum alnifolium) in the Smokies (Pavlovic 1981). In addition, Prunus pensylvanicum and Sambucus pubens occurred in the spruce stand soil seed bank. While these data are suggestive, that most of the woody taxa are known to at least occur to high elevation (> ca. 1980 m, Stupka, 1964) they indicate that they simply may have too low frequency to have been seen in the undisturbed plots, and their occurrence in disturbed plots places them in the invader class.

The excluded class includes taxa of the undisturbed which do not occur in the disturbed areas. Only two of 14 occur in Pavlovic's (1981) seed rain or spruce stand seed bank (Fagus and Laportea, respectively). The persistence of Fagus and Betula lenta in the disturbed areas, mostly above 1830 m, is limited by the apparent low tolerance of the taxa to elevation extremes (Stupka 1964). It seems possible that the low frequency problem may be affecting the apparent behavior of other taxa.

Most of the taxa of tables I-V are at least maintaining their density or cover through time. Those with particularly low density or cover drop in and out of adjacent time classes (see Acer spicatum Table I, Viburnum alnifolium Table III, Acer pensylvanicum Table IV and Agrostis Table V). Some exhibit what seems to be significant density or cover peaks in the disturbed plots. While the Southern Appalachian spruce-fir has not been shown to exhibit wave destruction (Reiners and Lang 1979), patchwork regeneration following windthrow (Cooper 1913) or even a long term natural disturbance cycle (Lorimer 1977), enough types of natural disturbances are in evidence in these forests (i. e. windthrow, ice storms, insects, debris slides) that it would be a surprise to find the native taxa not positively or negatively adapted to such prevalent changes. These taxa are virtually all perennials but studies of the autecology of the shrubs, herbs and bryophytes are unknown. Such studies would answer many of the questions raised by increased or decreased density or cover, with disturbance, of the understory. The considerable increase in the density of several shrubs raises the possibility of their interference with overstory regeneration and survival of herbaceous taxa. Several taxa are in the sampling category: excluded from disturbed areas. Their continued success in these forests should be examined.

CONCLUSIONS

The differences in concepts of types and their intergrades in the literature suggests that not all types are fully known and not all ecotonal types are described. For example, although spruce-birch is well known, spruce-hemlock and spruce-oak are not well known.

The degree to which our spruce-fir is cyclic is still little understood. The model followed by size or age-class data is unknown.

The relationship of understory type to understory or overstory production is not settled. Probable cyclic reproduction and survival of the overstory and the death of fir makes this difficult to assess now.

Production and nutrient cycling studies need reemphasis in the face of a changing atmospheric environment.

The decimation of overstory fir and its decreased density and basal area is accompanied by differential behavior of other plot tree taxa, some are maintaining their importance, some are losing, and some are gaining in importance.

Sapling and subsapling-shrub size plants may invade, be excluded from, may maintain their approximate numbers, or increase in density or cover on the disturbed plots. Density of Ribes rotundifolium, Rubus canadensis, Rubus idaeus var. canadensis, Sambucus, Vaccinium erythrocarpum, and Viburnum alnifolium exhibit markedly high densities in at least one set of years since opening of the canopy.

Looking at taxa excluded (e) from the disturbed areas, Betula lenta occurs in undisturbed overstory, sapling and ground cover plots but in disturbed plots it is only in the overstory. Viburnum cassinoides occurs in undisturbed sapling plots but in no other smaller size classes anywhere. Diervilla occurs in subsapling-shrub undisturbed plots but in no other smaller size classes. Fagus occurs in undisturbed tree and subsapling plots but in no disturbed plots nor ground cover (reproduction) plots. Of course the parasite Epifagus follows Fagus exactly. Glyceria, Laportea, Medeola, Monotropa, Smilacina and Stachys are herbs which occur in undisturbed but not disturbed plots. It seems that these are the taxa being negatively affected by fir death. Their continued importance in these forests should be examined.

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REGIONAL DIFFERENCES OF SPRUCE-FIR FORESTS
OF THE SOUTHERN BLUE RIDGE SOUTH OF VIRGINIA

J. Dan Pittillo*

Abstract.--A summary of the current available information for the seven ranges that support spruce-fir forests south of Virginia in the high mountains of North Carolina and Tennessee is presented. Literature that pertains to the specific sites is supplemented with comments on some of the species that are characteristic of the given ranges. The isolated nature of the spruce-fir communities that occupy the various range peaks and how each site has its special set of plant species is discussed. Suggestions for research needs, such as the lack of a consistent comparative sampling of all the ranges and investigations of the information available from soil studies in the spruce-fir zone of the southern Appalachians are presented.

Additional keywords: vegetation diversity, grass and heath balds, tundra-like species, soil charcoal, transplants.

INTRODUCTION

Spruce-fir forests in the southern Appalachians represent a relatively minor portion of the native vegetation of the region (cf. to maps by Cooper 1979; Saunders 1980) but because it is attractive to humans, it is a significant component of the region's vegetational diversity. Since the evergreen spruce-fir forest is a series of scattered forest communities within the surrounding deciduous forest, it can be considered as a series of isolated segments or "islands" in relation to the more extensive boreal forest to the north. White, Miller, and Ramseur (1984) have suggested this idea in a recent comparison of the variety of plants that are found in ten areas they studied from Virginia southward.

According to current theory of island biogeography, each island develops its set of native species and the larger the island, the greater its species diversity (MacArthur and Wilson 1967). This would seem a reasonable premise for the isolated units of the southern Appalachian spruce-fir forests.

In this paper we will explore some of the knowledge of each of the isolated segments of the spruce-fir forest south of Virginia. Emphasis will be placed on the differences of these segments, and where indicated, suggestions for areas of research needs will be indicated.

*Professor, Department of Biology, Western Carolina University, Cullowhee, NC.

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APPALACHIAN SPRUCE-FIR FORESTS

Spruce-fir forests extend to sea level in eastern Canada. They occur at about 152 m elevation and upward in Maine and continue as isolated units on mountain peaks southward. Throughout this region red spruce (*Picea rubens*) is the most characteristic tree species. The fir associated with this forest is balsam fir (*Abies balsamea*) as far south as West Virginia; from there southward a closely allied species, Fraser fir (*A. fraseri*) is characteristic (Stephenson and Clovis 1983; cf. Thor and Barnett 1974 for discussion on similarities of the two species). Throughout the range of the spruce-fir forests, spruce dominates on lower elevations and pure stands of fir may be observed at the higher elevations (Stephenson and Clovis 1983).

In the central Appalachians elevations are insufficient to accommodate well developed spruce-fir forests. While comparisons of the northern and southern portions of the spruce-fir have been available for some time (Oosting and Billings 1951), comparisons of the central Appalachian spruce forests with either northern or southern spruce-fir forests were unavailable until recently. In their study, Stephenson and Clovis (1983) found the species composition, except for absence of fir in West Virginia stands, of their study area were not conspicuously different from stands of the Great Smoky Mountains to the south nor the White Mountains to the north. They did suggest, however, that regional compositional differences could be explained by the fact that spruce-dominated communities were extensive enough to encompass distributional limits of many of their associated species.

Very few studies which compare stands of the spruce-fir forest of isolated peaks or between different ranges have been conducted. White, Miller, and Ramseur (1984) have addressed this question for ten areas that are defined by the 5500-foot contour from Virginia southward. They indicate that 342 species have been documented for these areas and find species richness positively correlated with size of the area, number of peaks, maximum elevation, and number of community types present.

Pittillo and Smathers (1979), in a comparison of a vegetational transect across the Balsam Mountains with Whittaker's (1956) vegetational transect in the adjoining Great Smoky Mountains, suggested higher species richness for the Balsam Mountains. In this comparison, Pittillo found 112 species in both areas, 118 species were found in the Balsams only, and 64 in the Smokies only. This is the pattern that is often mentioned in the literature, namely species found only in one area or the other and species common to both areas (cf. Oosting and Billings 1951 for northern and southern spruce-fir forests; Ramseur 1960 for southern spruce-fir forests; and McIntosh and Hurley for northern spruce-fir of the Catskill Mountains).

One of the major difficulties in comparative studies is consistency of the sampling procedures. In comparing the Balsam study above (Pittillo and Smathers 1979) with Whittaker's study, the objectives and sampling procedures are not alike. While the study by White, Miller, and Ramseur (1984) updates Ramseur's work using species lists documented in the literature, a uniform, adequate plot or transect sampling procedure across the range of the spruce-fir forest is needed for definitive comparison. Considering the instability caused by the onslaught of the Balsam woolly aphid (cf. Hay 1980, Johnson 1980), botanists may have passed a time in

which a consistent sampling of the southern Appalachian spruce-fir may be made.

SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS

In this section the ranges that support spruce-fir forests south of Virginia (see Rheinhardt's discussion of the spruce-fir in Virginia elsewhere in this volume) will be briefly discussed along with papers directed specifically to these localized areas. An attempt to compile the appropriate papers is based for the most part on the titles or the knowledge of the paper. There are many papers that entailed studies in many of the ranges, but the title did not suggest the appropriate range. The bulk of the citations are from those by McCrone, Huber and Stocum (1982), Peet (1979), and DeYoung, White, and DeSelm (1982). Papers that dealt with community types within the area of the spruce-fir zone are included in this report. Among them are papers of the spruce-fir communities, fir communities, mixed hardwood/conifer (including spruce or fir of course), the grass and heath bald communities, and ecotones associated with the spruce-fir communities. Not included are the hardwood forest communities such as beech and buckeye gap communities nor northern red oak types ("oak orchards"), etc., though they do fall within the same general zone. Where the natural presence of spruce or fir has been observed by the author, the range is included in the discussion. There are reports of spruce or Fraser fir that are not natural stands in the literature (e. g. Bruce 1977; DeVore 1972) and there are several transplanted populations that may now be reproducing (see discussion under "Transplants" below).

One of the active areas of investigation is the question relating the origin and maintenance of grass balds. While there are a diversity of ideas on the origin of the grass balds (cf. recent papers in the conference volume edited by Saunders 1980), and although investigators differ in approaches to methods of grass maintenance on these balds, all are agreed that there is extensive diminishing of the number and size of southern Appalachian grass balds. Many have emphasized fire as the primary factor in bald maintenance, although this alone does not seem to be completely effective in maintaining the grass against invasion of heath, hardwood trees, nor spruce-fir forest. Recently Garrett Smathers has been looking for the presence of charcoal and has been observing the general characteristics of the soil in grass balds, heath balds, and adjacent northern hardwood and spruce-fir forests. At the Spruce-Fir Workshop in the Great Smoky Mountains National Park research meeting May 20, 1983, we pointed out that charcoal was present in all the community types evaluated (Smathers and Pittillo 1984). It was also pointed out that slopes exceeding 40% generally lacked a B horizon. Thus we indicate that that studies of soils, such as presence of charcoal, horizon characteristics, and the like will likely provide us with clues of the history of communities within the spruce-fir zone and help guide our management procedures for these areas.

Great Smoky Mountains

No segment of the spruce-fir forest has been more studied than that of the Great Smoky Mountains. It would seem logical that this is the case: here is the greatest extent of the spruce-fir forest in the entire southern Appalachian region. This high mountain wilderness was not explored by

botanists until around the turn of the century, unlike the more settled regions to the east. Horace Kephart came to this area in 1904, according to Ellison (1976). Kephart and others realized the value of this wilderness and many people began to make the suggestion that a national park be established here before this entire wilderness was logged. At about the time of the establishment of the park, Gaylon (1928), Cain (1930), Camp (1931), and Sharp (1939) began their studies of the vegetation of the Smokies. So it was in the 1930's and 1940's that we see the appearance of numerous studies of plants and vegetation of the area, including that of the spruce-fir zone (Cain 1935; Cain 1936; Cain 1945; Cain and Miller 1933; Camp 1936; Griggs 1942; Miller 1942; Roberts 1940; Sharp 1941; Wells 1936; Whittaker 1948; and Yard 1942). Studies were somewhat more numerous in the 1950's and 1960's (Bruhn 1964; Crandall 1957; Crandall 1958; Crandall 1960; Crandall 1965; Davis 1966; Hoffman 1959; Gilbert 1954; Griffin 1965; Lambert 1961; MacDonald 1967; Norris 1964; Radford 1968; Rudolph 1963; Schofield 1960; Stephens 1969; Whittaker 1963; and Wolfe 1967) but with the press for protection of the wilderness and the onrush of wilderness experiences by masses of people, renewed studies of the impact of humans and their introduced animals expanded immensely in the 1970's and continues into the 1980's (Bogucki 1970; Boner 1979; Bratton 1974; Bratton and White 1980; Bratton, White, and Harmon 1981; Bratton and Whittaker 1977; DeSelm, Amundsen, and Krumpe 1972; Dey 1978; Eager and Hay 1977; Eager 1978; Fuller 1977; Gant 1978; Golden 1974; Hay 1978; Hay, Eager and Johnson 1976; Huber 1976; Johnson 1977; Lindsay 1976; Lindsay 1977; Lindsay 1978; Lindsay and Bratton 1979a; Lindsay and Bratton 1979b; Lindsay and Bratton 1980; McCracken 1978; Nichols 1977; Pavlovic 1981; Ramseur 1976; Stratton and White 1982; White 1982a; White 1982b; and White, Miller, and Ramseur 1984).

Cowee Mountains

The natural presence of spruce in the Cowees is not generally known. Bruce (1977) in his investigation of pygmy salamanders did not note the red spruce in the Cowee Bald area although the pygmy salamander is normally associated with spruce-fir forests. Unlike most of the spruce stands in the adjacent mountain ranges, the mixed-spruce/hardwood/hemlock stand here occurs in the valley flats north of Cowee Bald peak. Only one other location in our area is characterized by presence of spruce in the valley flats rather than on the slopes and peaks (see the discussion of Long Hope Valley in the Blue Ridge Range below).

Balsam Mountains

Several studies have been conducted in the Balsam Mountains. Most of this work has been carried out during the past decade, after easy access was made possible by completion of the Blue Ridge Parkway. Phil Gersmehl (1970) made a significant study of the establishment of spruce and fir seedlings in the Judaculla Fields on the west side of Richland Balsam. A significant understanding of the dynamics of biomass and nutrient movements within the spruce and yellow birch boulderfield communities was carried out by George Weaver in 1972. Weaver and DeSelm (1973) briefly described this project at the Orono conference. Pittillo and Smathers (1979a) presented a phytogeographic description of the Balsams, outlining the vegetational types encountered on a transect from the French Broad River floodplain up through the spruce fir forest. Larry Barden (1978) investigated the effects of fire

in maintaining grassy balds after prescribed burning. A study on the dispersal of spruce and fir seeds was carried out by Sullivan in 1979 in the same area in which Gersmehl did his studies earlier (Sullivan, Pittillo and Smathers 1980). Lynn Gaines Hortling (Horton and Gaines 1981) described the floristics of the heath communities in Graveyard Fields, comparing these with Flat Laurel Gap further north on the Pisgah Ridge extension of the Balsam Mountains. Very recently Saunders, Smathers, and Ramseur (1983) reported results of their study on secondary succession on Waterrock Knob of the western portion of the Balsams, known as the Plott Balsams.

One of the interesting observations of a species occupying the Balsams as a component of the spruce-fir forest but not found in the Smokies to the west is the presence of pink shell azalea (Rhododendron vaseyi). This rare shrub is rather frequent in the Cashiers vicinity of the Blue Ridge, particularly on Rocky Mountain and to the east (Pittillo 1976). It is also found northward in the Blue Ridge at such places as Flat Rock along the Blue Ridge Parkway (Pittillo 1978). Along the Blue Ridge Parkway of Pisgah Ridge and the Balsams, rather extensive populations have spread from rocky borders into areas that were burned by slash fires of the 1920's to 1940's. The farthest west the species has been observed is on Waterrock Knob.

The Balsams, on the other hand, do not have some species that can be found to the west in the Smokies and to the north in the Craggies. Among them are mountain club moss (Lycopodium selago), spreading avens (Geum radiatum), and perhaps deerhair bulrush (Scirpus caespitosus) (Pittillo 1978; White 1982a; White 1982b). Perhaps involved in this is the lack of cliffside borders where these tundra-like species could find suitable habitats for the past centuries when climates have varied between warmer and drier (hypsihermal period) and cooler and wetter (glacial dominant periods).

Great Craggy Mountains

North of the Great Smoky and Balsam Mountains, the next high mountain elevation mass occurs northeast of Asheville in the Great Craggy Mountains. This ridge lies perpendicular to the highest mountains in the southern Appalachians, the Black Mountains. For some time scientists and others have been curious about the lack of spruce-fir forests on the Craggies despite their altitudes well above the spruce-fir and hardwoods ecotone. This characteristic is quite impressive when one stands on Craggy Pinnacle and looks across Craggy Dome, well above the 1670 m elevation where this ecotone is usually expected, and views the spruce-fir forests of the Blacks at a lower elevation. There are a few scattered Fraser fir trees on the southeast slopes of Craggy Dome but no extensive spruce nor fir forests. There are some scattered spruce trees and a few stands, but historical records and observations indicate all these have either been transplanted here or originated from seeding from planted trees.

There have been a few studies conducted on the Craggies. Kring (1965) addressed the problem of maintaining the rhododendron due to succession by trees such as mountain ash in this famous natural garden. Thomas (1982) further investigated the replacement of the rhododendron by beech. Efforts are underway to continue the studies that deal with the maintenance of the purple rhododendron (Rhododendron catawbiense Michaux) (Smathers 1979).

The Craggies, as implied by their name, are replete with numerous rocky crags and cliffs. Apparently this was a suitable habitat for survival of many of the tundra type of vegetation. As mentioned above, mountain club moss, deerhair bulrush, and spreading avens frequent these habitats. Also found here is a small population of bigtooth aspen (Populus grandidentata, a species not heretofore reported in the literature for this area), a species more common in the ecotonal communities bordering northern prairies or following fires in the northern states. The presence of bigtooth aspen in these areas is generally interpreted as glacial relicts. Likewise, the presence of single-flowered rush (Juncus trifidus var. monanthos, which has been redesignated as J. trifidus subsp. carolinianus recently by Hamet-Ahti, 1980) also reflects this relict characteristic because the species is an "arctic-oroarctic ("arctic-alpine") amphi-atlantic species" (Hamet-Ahti 1980). There are additional rare species for this region that make up a component of this unique area, including Carex biltmoreana, C. misera, Lilium grayi, Prenanthes roanensis, Saxifraga careyana, etc. (cf. Pittillo 1978).

Black Mountains

Scientists have been attracted to this highest southern Appalachian mountain mass since the survey made famous here by Elisha Mitchell in the 1800's. Eggleston (1908) described his early observations he made in the area and with the destructive logging of the Blacks, Pratt and Holmes (1914) questioned whether the spruce-fir forest of Mt. Mitchell could be saved. The vegetation of the Black Mountains was Davis' 1929 dissertation topic (Davis 1929; Davis 1930). The recent balsam woolly aphid infestation and applications of pesticides was followed up by a study of the BHC insecticide movement by Jackson, Sheets, and Moffett (1974).

The spruce-fir forests of the crest of the Black Mountains are primarily comprised of wind-pruned red spruce or Fraser fir. There seem to be fewer rare species, perhaps related to the generally dense spruce-fir stands or to the relatively low diversity of community types (e. g. White, Miller, and Ramseur [1984] note only three types here compared to eight for the Smokies). One notable species of this range is the northern hardwood species, paper birch (Betula papyrifera var. cordifolia). This paper birch population is much larger than the population in the Smokies, which is the only other known for the area under consideration here (White 1982).

Blue Ridge Mountains

The Blue Ridge Mountain Range (the narrow series of ridges of the Blue Ridge Province occurring along the scarp front from the Dahlonga Plateau in Georgia northward to Pennsylvania) has very few peaks that exceed elevations sufficient to support spruce-fir forests. Except for the Grandfather Mountain area and some peaks north and south of it, elevations of this range are below 1525 m.

Abutting against the Black Mountains, there is a scattering of spruce in a mixture of hardwoods and pines that can be observed along the Blue Ridge Parkway (Pittillo 1978). It is farther north in the vicinity of Grandfather Mountain that the spruce become contiguous and along with Fraser fir produce a spruce-fir forest. Since Grandfather Mountain makes a

prominent feature near the Blue Ridge scarp front, earlier explorers, including Andre Michaux (Dugger 1892) and Asa Gray (Gray 1842), were attracted to this location and gave us some of our earliest observations and documentation of the flora for this area.

Grandfather Mountain has been an area of interest to many, in part due to the advertisement it receives from private enterprise. The bulk of the mountain mass remains in natural condition with only the southern tip of the peak developed. This is the basis of its recommendation as a National Natural Landmark (Pittillo 1976). There are numerous cliffs and craigs here and as in the Craggies, there seems to be a complement of tundra-like species. Roan roseroot (Sedum rosea var. roanensis), Blue ridge goldenrod (Solidago spithamea), and Heller's gayfeather (Liatris helleri) are some representative examples (Pittillo 1978).

Further north in the Blue Ridge on a tributary of the New River are some upland bogs that are located within valley spruce forests. These are known as Long Hope Valley bogs, recognized as a National Natural Landmark. The vegetational composition here is unusual in that several northern species have their southernmost populations present. Among them is Canada yew (Taxus canadensis), bogbean (Menyanthes trifoliata), and saxifrage (Saxifraga pensylvanica). Research on the vegetation is presently being carried out by Duke University, University of Tennessee, and Western Carolina University botanists.

Stone Mountains

West of Grandfather Mountain and across the Blue Ridge Province are the Stone and Unaka Mountains. Sometimes Roan Mountain has been referred to the Unakas but it lies farther north and perhaps is most closely associated with the Stone Mountains. Standing as a significant feature of the Blue Ridge Province along the western front, the Roan has likewise attracted many botanists, again with Gray among them (Gray 1842). Once their reports got into the literature, there followed a succession of investigators. Britton (1886) was quickly followed by Scribner (1889) investigating grasses. Initially the presence of open grasslands on these mountain peaks was overlooked since most botanists followed the original pioneer settlers who were grazing cattle on these areas. Here in the 1930's began a controversy of the best explanation for the origin of southern Appalachian grass balds; it has yet to be satisfactorily resolved (cf. Fink 1931; Brown 1938; Brown 1941; Brown 1953; Gates 1941; Oosting and Billings 1951; Mark 1958a; Mark 1958b; Mark 1959; Gersmehl 1969; Gersmehl 1970a; Gersmehl 1970b; Gersmehl 1971; Gersmehl 1973). Specific attention to the spruce-fir forest of Roan Bald is given in Castro's 1969 study.

The cliffy borders on the western exposure of Roan Mountain must have served as habitats for some relict tundra-like species. Spreading avens (Geum radiatum), Roan roseroot (Sedum roseum), bent avens (G. geniculatum), soft three-awned grass (Trisetum spicatum var. molle), Gray's lily (Lilium grayi), Blue ridge goldenrod (Solidago spithamea), and Heller's gayfeather (Liatris helleri) contribute to an impressive list of these tundra-like species.

Transplants

Throughout the southern Appalachians both native and exotic species of spruce and fir are cultivated in yards and on tree farms. The Fraser fir grows relatively well in the valley floors down to 500 m elevation. It does not reproduce here and may be more susceptible to diseases such as spider mite. The red spruce will grow here but not as well. Commonly Norway spruce or cultivars of the white spruce (usually sold as "Colorado blue spruce") are seen instead.

The transplants that are being considered below were those planted with the intent of being allowed to naturalize or establish themselves as a part of the native or man-assisted natural community.

Near the southern terminus of the Blue Ridge Range in Georgia Brasstown Bald has some scattered transplants of Fraser fir. No report of these are known in the printed literature.

In the Nantahala Range west of Franklin, NC, on Winespring Bald is a well established group of Fraser fir transplants. These appear to have been planted here in the 1950's or 1960's.

A report by DeVore (1972) suggested the presence of native Fraser fir in the Unicoi Mountains. However, consultation with U. S. Forest Service officials indicated these were transplants. The tree sizes vary at this site as they might in natural populations, so it is understandable how they might be considered native plants.

Transplants of spruce and fir have been made in other, well established ranges that have native spruce-fir forests. In the Smokies, mature and reproducing Norway spruce (Picea abies) are present on the eastern slopes. In the Balsam Mountains native spruce and fir have been established in the Black Balsam Knob region of the Graveyard Fields. In the Black Mountains transplants following devastating fires of the early 1900's involved many trial plantations, among them spruce and fir. In the Craggies, isolated red spruce and pure stands can be observed at different locations.

Thus, field observations should be checked against the human history of a given location before suggestions of the "naturalness" of a given stand is indicated.

SUMMARY

Spruce-fir forests in the Appalachians generally represent a minor portion of forests of the region, are scattered and isolated segments distributed on increasingly higher elevations southward, and seem to fit the pattern of current theory of island biogeography. In the southernmost portions of the Appalachians the spruce-fir component starts at about the 1675 m contour and since the highest peak is 2038 m, the amount of area is rather limited. Likewise, since the available mass is broken up by peaks of the several ranges that extend above the 1675 m contour, the spruce-fir forest can be thought of as a series of isolated segments or "islands." In this paper we have looked at some of the differences that make up each spruce-fir community of the various ranges and discover some parallels with

the theory of island biogeography. The main point made here is that the various range spruce-fir communities have their expected common species but each one has some unique or restricted species. Evaluation of species diversity, a second major component of island biogeography theory, was not considered here.

Studies that compare spruce-fir stands of the different ranges are very few. This may be particularly unfortunate with the degeneration of the Fraser fir component of the spruce-fir forests. One thing that is especially needed is a consistent sampling procedure throughout the entire range of southern Appalachian spruce-fir forests.

Additionally studies that search for clues of the past history of the communities that make up the spruce-fir zone are needed. The presence of charcoal and lack of a B horizon on steep slopes indicate inadequate previous investigation of available field data.

The discussion of the seven ranges that harbor spruce-fir forests in Tennessee and North Carolina included a listing of literature sources for each of these ranges as well as some of the notable plant species in each. There was extensive literature related to the vegetation of the spruce-fir on some of these while others have not been researched and reported adequately if at all. The Great Smoky Mountains have the most extensive literature (over 50 items are mentioned above) while the one paper dealing with an animal usually associated with spruce-fir is the only paper for the Cowee Mountains. Two of the ranges, Cowee Mountains and the Long Hope Valley of the Blue Ridge, are reported here to contain spruce communities for the first time in the literature; one report of native Fraser fir for the Unicoi Mountains was indicated to be transplants. Finally, a discussion of transplants throughout the southern Appalachians indicated that some species from other regions have been introduced and have naturalized occasionally while the native red spruce and Fraser fir has been established in a number of additional ranges and many additional locations within the natural ranges.

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COMPARATIVE STUDY OF COMPOSITION AND DISTRIBUTION
PATTERNS OF SUBALPINE FORESTS IN THE BALSAM MOUNTAINS
OF SOUTHWEST VIRGINIA AND THE GREAT SMOKY MOUNTAINS

Richard D. Rheinhardt¹

Abstract. The vegetation of subalpine forests in the Balsam Mountains (Mount Rogers and Whitetop) in southwest Virginia were examined and compared to similar forests in the Great Smoky Mountains. Differences in latitude and longitude were considered in comparing zonal distribution patterns.

A spruce-fir (*Picea rubens*-*Abies fraseri*) forest on Mount Rogers is similar in composition and distribution to those of the Great Smokies at equivalent elevations. In contrast to Mount Rogers, Whitetop's subalpine forests are devoid of fir, although the upper 158 m (520') seem environmentally suitable for its growth. It is believed that during the post-Wisconsin xerothermic period, fir was eliminated from Whitetop, but found refuge on the taller Mount Rogers. Although fir has been able to extend its range downward since the xerothermic period, it has been unable to cross the relatively low elevation gap separating the two mountains.

Spruce forests, which were expected to cover slopes between 1190 m (3900') and 1525 m (5000') in the Virginia Balsams, do not extend below 1430 m (4700'). This seemingly truncated distribution might be a result of past human disturbance, but no substantive evidence is available.

The future structure of some aphid-infested spruce-fir forests in the southern Appalachians may be predicted by examining the spruce forests on Whitetop, particularly at elevations which are suitable for the development of spruce-fir forests. Since Mount Rogers' firs appear to be resistant to aphid devastation, the spruce-fir forest there may some day be the only surviving representative of this type of ecosystem. If the resistance to aphid induced death is genetic, and preserving the structural integrity of the spruce-fir ecosystem is deemed important, repopulating aphid-infested areas with fir seeds from Mount Rogers might be considered.

Additional keywords: *Abies fraseri*, *Picea rubens*, southern Appalachians, vegetation, xerothermic period, zonal distribution.

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Biology Department, William and Mary College, Williamsburg, Virginia

INTRODUCTION

The southern Appalachian subalpine spruce-fir (*Picea rubens*-*Abies fraseri*) forests are restricted to seven high elevation mountain areas between Mount Rogers in the Virginia Balsams and Double Springs Gap the Great Smoky Mountains (Ramseur 1960). These isolated forest communities are remnants of a boreal forest ecosystem which was widespread throughout the southern Appalachians during the Pleistocene glaciations. Since the last glacial retreat, ten to fifteen thousand years ago, these subalpine communities have been subjected to different biological and anthropogenic pressures.

Most phytosociological investigations of southern Appalachian subalpine forests have focused on mountain areas south of Virginia: on Roan Mountain (Brown 1951), in the Black Mountains (Davis 1930, Braun 1950), the North Carolina Balsam Mountains (Pittillo and Smathers 1979), and the Great Smoky Mountains (Cain 1935, Braun 1950, Crandall 1958, Whittaker 1956). Although floristic comparisons have been made among southern Appalachian subalpine stands (Ramseur 1960) and between virgin stands in the Great Smokies and the White Mountains of New Hampshire (Oosting and Billings 1957), little in the way of compositional and distributional comparisons between these isolated communities have been attempted. Recently, however, Stephenson and Adams (1984) published data on the northern-most enclave of the southern Appalachian subalpine forest system, those of the Virginia Balsams in southwest Virginia (Fig. 1).

This study compares the composition and distribution of subalpine forests located at the geographic extremes of the southern Appalachian forest system, those located in the southern part of the range (in the Great Smokies) and those located at the northern extreme (in the Virginia Balsams). Because little published information is available on the Virginia Balsams, a description of the area and its forests is presented.

The Balsam Mountains of southwest Virginia include the two tallest and most massive peaks in the state: Mount Rogers (1746 m) and Whitetop (1682 m). These northeast-southwest trending mountains are a geologically complex system of metamorphosed igneous and sedimentary rocks (primarily rhyolite). They are bordered on the north by the Iron Mountains (the first range of the Ridge and Valley Province) and on the south by the Blue Ridge proper.

The high elevation north slopes of the subalpine zones of Mount Rogers and Whitetop are extremely steep and rugged in contrast to their more subdued south slopes. Much of these north slope subalpine forests are believed to be virgin because the extreme topography prevented logging operations there. Most of the rest of the subalpine forests were logged once (circa 1910), although some sections of Whitetop and Cabin Ridge (off Mount Rogers) were logged around 1958 (Shields 1960). Approximately 400 ha of spruce-fir forest covers Mount Rogers and adjacent Pine Mountain and Cabin Ridge, while Whitetop harbors about 150 ha of spruce forest. (Fig. 2).

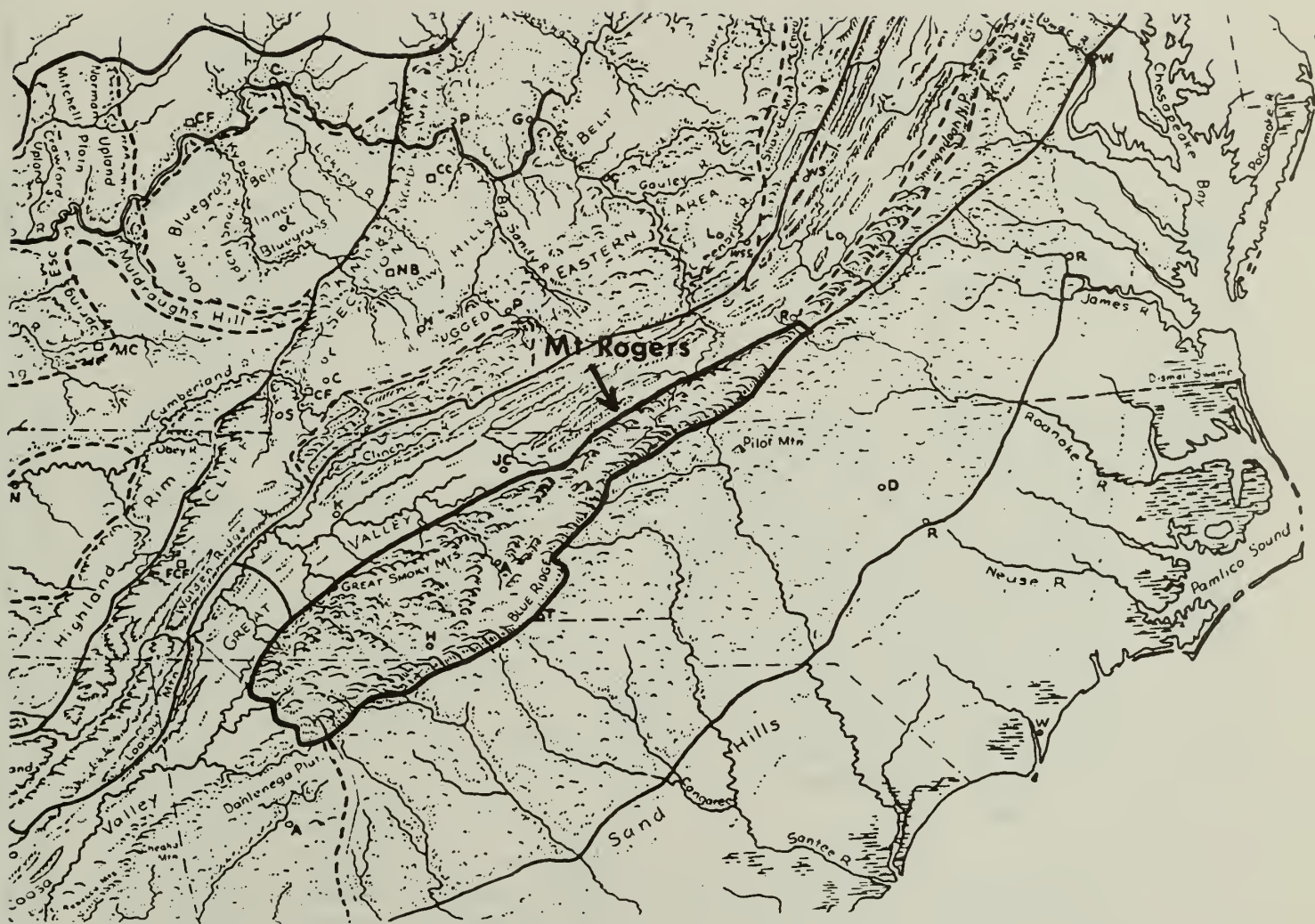


Figure 1. Location of Mount Rogers of the Virginia Balsams in relation to the rest of the southern Appalachians. Reproduced from Braun's (1950) vegetation map of eastern North America.

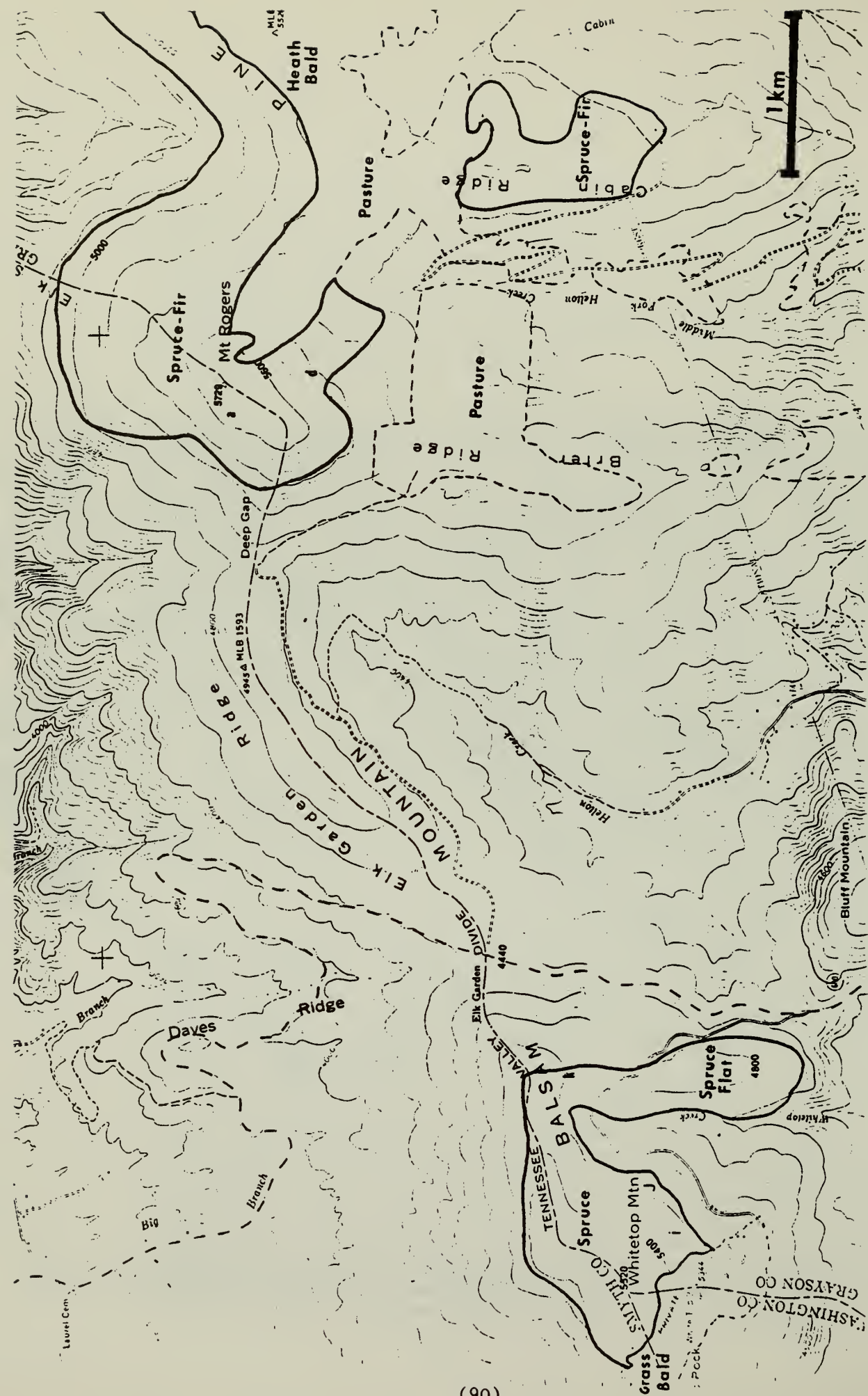


Figure 2. Approximate distribution of subalpine forests on Whitetop and Mount Rogers. The letters a, d, i, j, and k depict the topographic locations of stands quantitatively described in Tables 1, 2, and 3.

Since the Virginia Balsams are located approximately 170km northeast of the Great Smoky Mountains, equivalent topographic-climatic conditions in the Virginia mountains should be about 183 m lower than in the Great Smokies (Hoptkins 1938). This value is only approximate since vegetation patterns are affected not only by climate and topography, but by precipitation regime, humidity, history of use, and possibly by the heights of the mountains being compared.

METHODS

Quantitative information presented on the Virginia subalpine forests are a synthesis of data collected by the author and other investigators (from Shields 1960 and unpublished data of Adams 1982). Data presented on the Great Smoky Mountains are primarily derived from earlier (pre-1960) ecological studies by Cain (1935), Crandall (1958), Ramseur (1960), and Whittaker (1956), although some recent data collected by the author are included. In order to make a more accurate comparison between stands, measurements were standardized to relative basal areas whenever possible. It should be noted that comparisons can only be of a general nature since sampling methods vary. Taxonomic nomenclature follows Radford et al. (1968), except that the taxon treated as Amelanchier arborea var. laevis is here reported as Amelanchier laevis Wiegand.

RESULTS

Quantitative data on the composition of subalpine stands on Mount Rogers and in the Great Smokies are presented in Table 1. Stand A on Mount Rogers' summit is believed to be virgin. Note its similarity to stand F in the Great Smokies. On Mount Rogers, spruce and fir generally share dominance at about 1646 m (note stand C). This coincides with the 1830 m average isocline of equal basal area described by Whittaker (1956) for the Great Smokies. As is the case in other southern Appalachian subalpine forests, fir exhibits an increase with respect to spruce toward higher elevations, while the total basal area of the forest declines. Also, as Whittaker (1956) found in the Great Smokies, fir exhibits a greater relative dominance toward more mesic sites. Note that in stand D (near a high elevation stream) fir shows a much higher relative dominance in comparison to spruce even at an elevation well below 1646 m.

Most quantitative data for the Great Smokies were collected prior to 1960. Since 1960, Balsam wooly aphid-infestation has dramatically altered the structure of many subalpine forests by killing large numbers of canopy-sized Fraser firs. A recently (1983) sampled stand on Mt. LeConte in the Great Smokies (stand M, Table 2) exemplifies this structural change. Numbers in parentheses include counts of standing dead timber, most of which are fir killed by the aphid. This forest now resembles the spruce forests on Whitetop in composition (note stand K), except that the canopy is more open in aphid-infested areas. Surprisingly, Fraser fir on Mount Rogers has not been affected by the aphid, although the organism has been present there for over 20 years (C. Eager, personal communication).

Table 1. Composition of spruce-fir stands on Mount Rogers, Virginia (A,B,C,D) and the Great Smokies (E,F,G,H). All values are relative. Elevations in parentheses are equivalent elevations for Mount Rogers (MR) and the Great Smoky Mountains (GRSM). The presence of species with less than 1% coverage are denoted with a "p". Data source indicated below.

Stand Elevation (m)	MR GRSM (1920)	Mount Rogers			Great Smokies				
		A 1737 (1959)	B 1692 (1959)	C 1646 (1829)	D 1591 (1774)	E (1737) 1920	F (1737) 1920	G (1612) 1795	H (1594) 1777
<i>Abies fraseri</i>	78	55	43	42	89	82	29	38	
<i>Picea rubens</i>	13	31	36	25	5	17	54	38	
<i>Betula lutea</i>	-	11	10	31	2	-	?	?	
<i>Sorbus americana</i>	9	2	6	-	1	1	?	?	
<i>Amelanchier laevis</i>	-	-	p	-	-	-	?	?	
<i>Aesculus octandra</i>	-	-	1	1	-	-	?	?	
<i>Acer pensylvanicum</i>	-	-	p	1	-	-	?	?	
Other	0	1	3	0	3	0	18	24	

Stands A, B, and D: Data from Rheinhardt (1980); values are relative basal areas.
 Stand C: Data from Shields (1960); values are relative basal areas based on six transects between 1616 m and 1676 m.
 Stand E: Data from Cain (1935); values are average relative basal areas for two stands.
 Stand F: Data from Crandall (1958); values are relative densities.
 Stands G and H: Data from Oosting and Billings (1951); values are average relative basal areas for two stands.

Table 2. Canopy composition of spruce forests on Whitetop Mountain, Virginia (I,J,K) and on Inandu Mountain and Mt. LeConte in the Great Smokies (L,M). Elevations in parentheses are equivalent elevations for Mount Rogers (MR) and the Great Smoky Mountains (GRSM). Data source indicated below.

Stands	I	J	K	L	M
Elevation (m) MR	(1609)	(1555)	(1481)	1311	1556
GRSM	1792	1737	1664	(1495)	(1740)
Basal area (m /ha)	34	40	33	56	30 (51)
<i>Abies fraseri</i>	-	-	-	-	3 (33)
<i>Picea rubens</i>	73	76	46	66	43 (31)
<i>Betula lutea</i>	21	14	21	14	23 (14)
<i>Tsuga canadensis</i>	-	-	-	11	-
<i>Fagus grandifolia</i>	6	-	21	-	-
<i>Acer saccharum</i>	-	-	9	-	-
Other	0	10	3	9	30 (22)

Stands I, J, and K: Data from Rheinhardt (1980); values are relative basal areas.

Stands L and M: Unpublished data collected by Rheinhardt and Adams (1983); values are relative basal areas. Compositional data in parentheses includes standing dead stems (most dead firs were killed by the Balsam wooly aphid).

Another interesting difference between the subalpine forests of the Great Smokies and those of Mount Rogers is that on Mount Rogers, spruce is the overwhelming conifer dominant only in a narrow transition zone between subalpine and northern hardwood forests. Thus, spruce occurs primarily above 1463 m on Mount Rogers, in contrast to the Great Smoky Mountains where spruce forests sometimes extends to as low as 1372 m (the equivalent of 1190 m in the Virginia Balsams).

In contrast to Mount Rogers, Whitetop's subalpine forests are devoid of fir, although the upper 158 m seem environmentally suitable for its growth. Red spruce is the sole conifer dominant in subalpine forests above 1555 m (Fig. 2). Note stands I and J (Table 2) on Whitetop, which are at elevations high enough to support fir. Note also the similarity between stand K on Whitetop and stand M on Mt. LeConte (stand M is the former spruce-fir stand which lost almost all of its fir to aphid-infestation).

As is the situation on Mount Rogers, spruce forests on Whitetop do not extend to as low an elevation as one might expect based on its lower distribution in the Great Smokies. The lower limit of spruce forests on Whitetop is 1400 m (along a high elevation flat), which is more than 200 m above its predicted limit based on the lower range of spruce in the Great Smoky Mountains.

The herbaceous stratum of subalpine forests of the Balsams are similar floristically to those of the Great Smokies. The Virginia Balsams, however, lack many of the site-types described by Crandall (1958) for the Smokies because subalpine forests in the Balsams are less topographically diverse than the Smokies. Open slopes of Mount Rogers' subalpine forests are dominated by Oxalis acetosella and Dryopteris campyloptera (Table 3). Towards less mesic sites, the relative importance of Oxalis and Dryopteris decrease as Carex spp. increase. Other herbaceous species include Aster divaricatus, Clintonia borealis, Arisaema triphyllum, and Lycopodium lucidulum.

Whitetop's herbaceous vegetation differs somewhat from Mount Rogers in that Maianthemum and Thelypteris noveboracensis are relatively more important (stand I, Table 3) on Whitetop. When Shields (1960) found Maianthemum to be more important in the spruce forests of nearby Beartown Mountain than on Mount Rogers, he concluded that Beartown was more closely related to more northern subalpine forests (this was because Oosting and Billings (1951) included Maianthemum in their list of species for the White Mountains, but not for the Great Smokies). A more detailed study of Whitetop's herbaceous vegetation should be made to determine its position in the vegetational mosaic of the Appalachian subalpine system.

Table 3. Herbaceous composition of subalpine forests in and the Great Smokies (N,O,P). Elevations in parentheses are equivalent elevations for the Virginia Balsams (VB) and the Great Smoky Mountains (GRSM). Data source indicated below. Sp-F = Spruce-fir forest and Sp = Spruce forest.

		Virginia Balsams			Great Smokies			
		A	B	D	I	N	O	P
Elevation (m)	VB	1737	1734	1591	1600	(1737)	(1509)	(1509)
	GRSM	(1920)	(1917)	(1774)	(1783)	1920	1692	1692
Forest-type		Sp-F	Sp-F	Sp-F	Sp	Fir	Sp-F	Sp
Oxalis acetosella		70.4	51.3	42.0	12.7	43.0	54.9	65.9
Dryopteris campyloptera		25.7	35.5	16.5	35.6	22.8	23.2	13.5
Aster acuminatus		3.9	4.0	10.4	—	8.2	0.1	0.4
Carex spp.		—	7.7	10.4	—	—	—	—
Clintonia borealis		—	1.1	—	—	1.7	0.4	0.2
Arisaema triphyllum		—	0.6	4.2	—	—	—	—
Lycopodium lucidulum		—	—	8.6	—	—	0.1	1.8
Other		0.0	0.0	7.8	51.7	24.3	21.3	18.2

Stands A,D, and I: Data from Rheinhardt (1980); values are averages of relative coverage and frequency.

Stand B: Unpublished data collected by Adams and Stephenson (1982); values are averages of relative coverage and frequency.

Stands N,O,P: Data from Crandall (1958); values were converted from relative coverages converted from absolute coverages.

Includes Rubus canadensis (13.4), Thelypteris noveboracensis (15.9), and Maianthemum canadense (14.4).

DISCUSSION

A comparison of the composition of spruce-fir forests of Mount Rogers and the Great Smoky Mountains indicate a close affinity between the two areas. The Smokies and the Virginia Balsams differ in that the lower distribution of spruce is truncated in the Balsams and fir is absent on Whitetop Mountain.

Mark (1958), in his study of southern Appalachian grass balds, found an inverse relationship between the height of a mountain and the lower limit of its coniferous forest. He suggested that after the xerothermic period, lower elevation mountains were left with smaller and more "biotype depleted" conifer populations which might be relatively poorly adapted to invade downward. If correct, this could explain why spruce is restricted to higher elevations in the Virginia Balsams in comparison to the mountains of the Great Smokies. However, if the spruce population became genetically impoverished during the xerothermic period fir must have become even more so. Yet, the lower distributional limit of fir is as would be expected if regional climatic differences are considered.

Another possible explanation is that spruce's present distribution is related to disturbance history. On the basis of timber extraction records and climatological data, Pielke (1981) concluded that spruce was once much more extensively distributed in Virginia prior to the large scale logging operations of the late 1800s and early 1900s. Further, he believes that the commonplace burning of logging debris destroyed favorable microclimate and soil conditions necessary for the successful germination and growth of spruce. He believes large areas of Virginia (above 900 m) were once spruce forests, but are now dominated by hardwoods.

Pielke's conclusions have been met with some skepticism since old logging records are unreliable, and often hemlock (*Tsuga canadensis*) and fir were recorded as spruce (Shields 1960). Also, in the Virginia Balsams, there is no evidence that spruce is increasing in importance in the higher elevation hardwood forests as might be expected. More in depth investigations are needed before it can be determined with any reasonable certainty whether or not spruce was once more extensively distributed in the Virginia Balsams or in the rest of Virginia.

A possible explanation for the lack of fir on Whitetop is that a slight shifting in ecotonal boundaries upward during the last post-Wisconsin xerothermic (or hypsithermic) period may have led to the elimination of fir from Whitetop (Fig. 3). but not spruce (which extends to lower elevations than does fir throughout the southern Appalachians). Fir might have been able to find refuge on the higher summit of Mount Rogers during the xerothermic period.

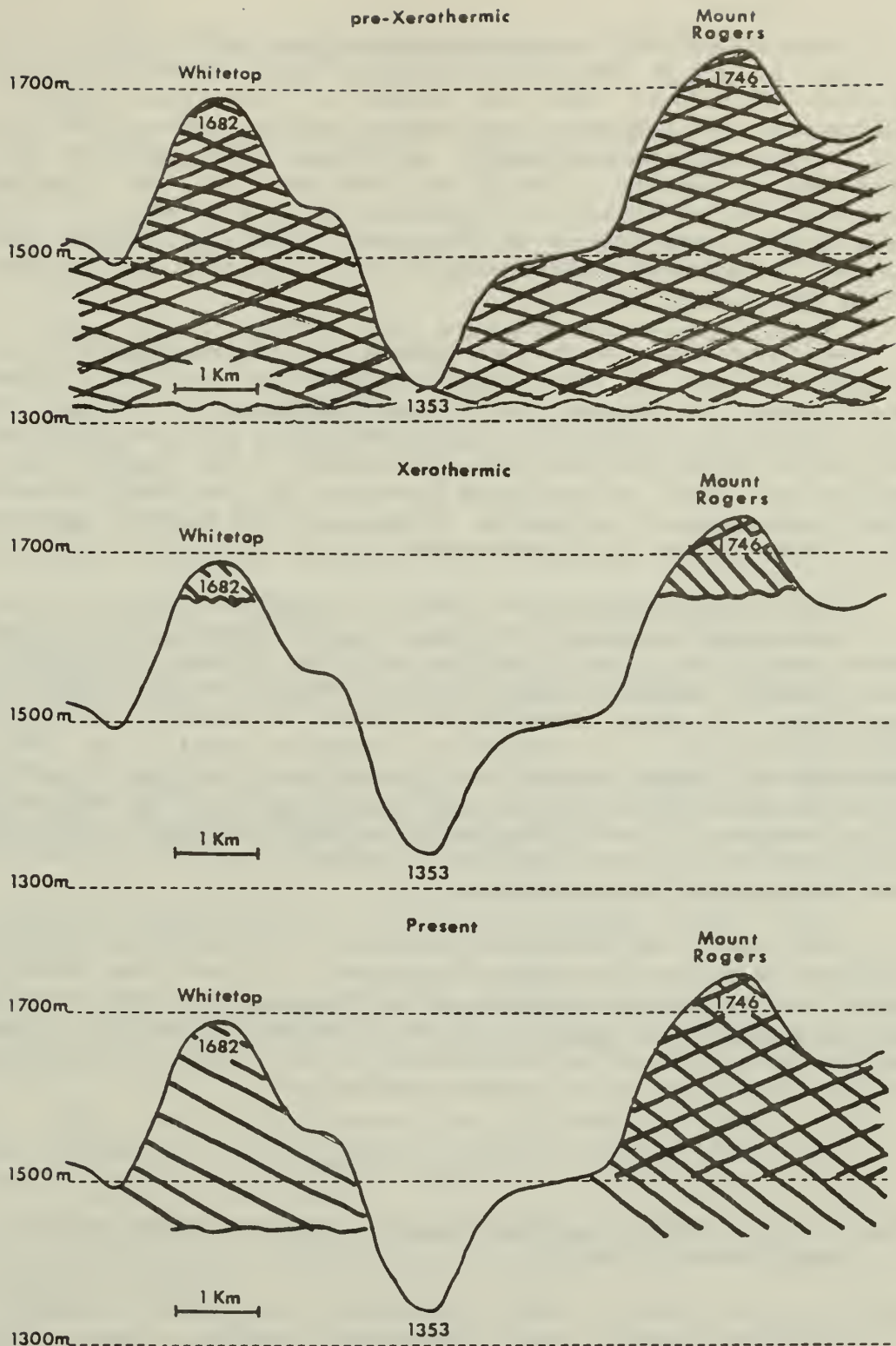


Figure 3. Presumed changes in the distribution of subalpine forests on Whitetop and Mount Rogers caused by climatic conditions of the post-Wisconsin xerothermic (or hypsithermic) period about 4,000 years ago. Single diagonal lines delimit the distribution of spruce forests while cross-hatching represents the distribution of spruce-fir forests.

Then, when global temperatures again began cooling, fir must have extended its range down the slopes of Mount Rogers to its present position (182 m lower than the height of Whitetop's summit). It appears that fir has been unable to reoccupy the highest elevations of Whitetop Mountain, where climatic conditions seem suitable for its establishment, because it could not cross the fairly low elevation gap (elevation=1347 m) separating Whitetop from Mount Rogers. A similar scenario was hypothesized by Whittaker (1956) as having possibly occurred in the Great Smokies with respect to both spruce and fir versus hardwoods on peaks.

Subalpine spruce forests on Whitetop are compositionally similar to other forests in the southern Appalachians which were spruce-fir forests prior to Balsam wooly aphid-infestation. The primary difference between Whitetop's subalpine forests and the others is that Whitetop's forests have had more time (about 4,000 yrs.) to reach equilibrium. Thus, the subalpine forests of Whitetop may represent the future structure of spruce-fir forests in the southern Appalachians after recovery from aphid destruction.

Mount Rogers appears to be unique in that its Fraser firs are able to tolerate aphid stress. Perhaps as was during the xerothermic period, when the fir population was very low (founder population) that an ability to withstand aphid-induced stress became fixed in the population. It might therefore be prudent to determine whether or not aphid resistance is a genetically acquired trait. If the fir population on Mount Rogers does indeed have a genetic propensity to withstand aphid-induced stress, and preserving the structural integrity of the ecosystem is deemed important, it might be worth investigating the possibility of repopulating aphid-infested areas with seeds derived from firs growing on Mount Rogers.

Fortunately, the subalpine forests of the Virginia Balsams are currently protected from human disturbance. Not only does Mount Rogers harbor the northern-most enclave of the Southern Appalachian spruce-fir forest ecosystem, but the firs there may contain a reservoir of genetic material which may one day prove useful in re-establishing this species in areas from which they are being eradicated.

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RECREATIONAL IMPACTS IN THE SOUTHERN APPALACHIAN SPRUCE-FIR ECOSYSTEM

Paul Richard Saunders¹

Abstract.--Research in the Southern Appalachian spruce-fir forest ecosystem has shown forests are damaged by fire and windthrow; recreation has led to the introduction of exotic species and reduction of species cover and diversity, and effects of mule-logging on forest regeneration, floristics, and vegetation are minimal. Areas for research in Great Smoky Mountains National Park include the impacts of firewood gathering, windthrows at shelters and campsites, effect of diseases on tree vigor, recovery of balsam woolly aphid infested recreation sites, soil erosion at recreation sites, reduction and rehabilitation of illegal campsites, and water quality monitoring and protection.

Additional keywords: Backcountry use, dispersed recreation, wilderness.

INTRODUCTION

Southern Appalachian Mountain red spruce-Fraser fir (*Picea rubens-Abies fraseri*) forests (scientific nomenclature for vascular flora follows Radford, et al. 1968) are a small disjunct, remnant ecosystem located above 1670 meters on the higher mountain peaks of eastern Tennessee, western North Carolina and southwestern Virginia (see figure 1). While the area ranges from Mt. Rogers on the north to the Balsam Mountains on the south, most of the discussion will focus on the Great Smoky Mountains.

Primarily as a result of logging followed by slash and successive fires, these forests have been reduced over 50 percent from 13,875 hectares of spruce-fir and 402ha of spruce to 6831ha of spruce-fir and 50ha of spruce (see table 1). Much of the area currently mapped as spruce-fir or spruce is not dominated by closed canopy forests.

Recreation

Today, recreation activities such as backpacking, nature walks, picnicking, photography and driving for pleasure are the principal uses of the remaining spruce-fir forests. With the exception of the Plott Balsam and Grandfather Mountains, most of the spruce-fir zone is in federal or state ownership. Portions of privately owned Grandfather Mountain are developed for tourists, where approximately 250,000 persons annually pay to see the exhibits and view from atop Grandfather Mountain (Steve Hart, personal communication, 1976). Except for the narrow corridor of the Blue

¹ Associate Professor of Wildland Recreation Management, Department of Forest and Range Management, Washington State University, Pullman, Washington, 99164-6410. This is Scientific Paper 6627, Agriculture Research Center, Washington State University, Project 0596.

Figure 1. Location of the one spruce and seven spruce-fir forests in the Southern Appalachian Mountains. Named mountains have or may have had a few native spruce present, or spruce or fir planted. The boundary of Great Smoky Mountains National Park and the location of the Blue Ridge Parkway and Appalachian Trail are also shown.

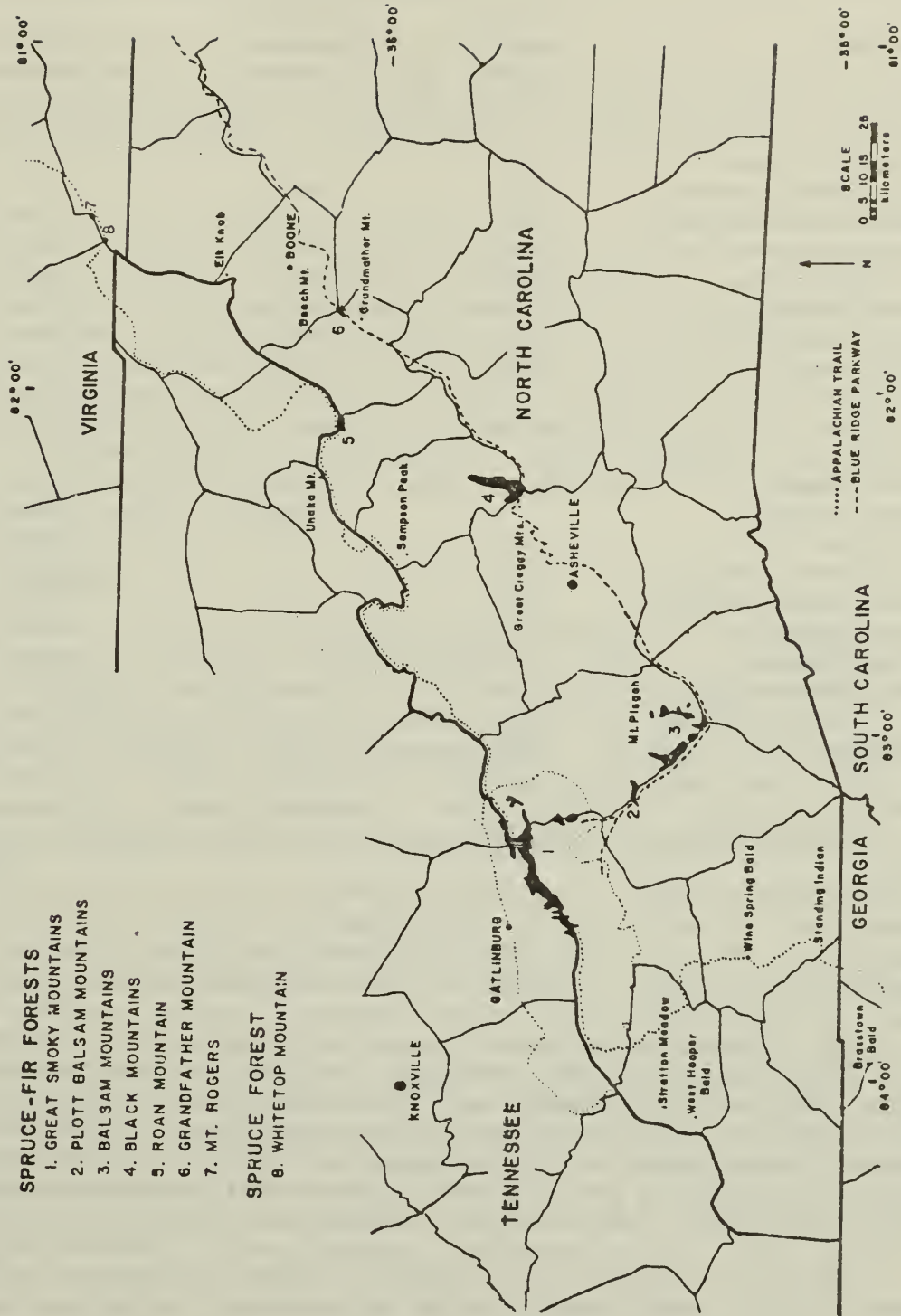


Table 1. Extent of the Southern Appalachian spruce and spruce-fir forests prior to and after logging. Area is in hectares.

Location	probable past extent	currently spruce-fir or spruce	% of change
Spruce-Fir Forests			
Great Smoky Mountains	6013	3665	-39.0
Plott Balsam Mountains	662	193	-78.9
Balsam Mountains (N.C.)	3127	614	-80.4
Black Mountains	2524	1457	-42.3
Roan Mountain	896	355	-60.4
Grandfather Mountain	247	220	-10.2
Mt. Rogers	406	326	-19.7
Subtotal	13,875	6831	-50.8
Spruce Forests			
Beech Mountain	1	0.1	-90.0
Elk Knob	79	-	-100.0
Grandmother Mountain	13	5	-61.5
Great Craggy Mountains	200	10	-95.0
Sampson Peak	15	-	-100.0
Unaka Mountain	59	-	-100.0
Whitetop Mountain	35	35	-
Subtotal	402	50.1	-87.5
Total	14,277	6881.1	-51.8

Ridge Parkway, there are no public recreation areas in the Plott Balsam Mountains. The only lodge or hotel remaining in operation within this ecosystem is Mt. Le Conte Lodge, a private concession, accessible only by foot or horse, on Mt. Le Conte in Great Smoky Mountains National Park.

Mt. Mitchell State Park is accessible to the public only from the Blue Ridge Parkway, or the steep Commissary Ridge - Mount Mitchell Trail which originates 9 kilometers east of the park at 915 meters. The principal attraction is the view from the tower atop Mount Mitchell (2038 meters), the highest peak east of the Black Hills and Rocky Mountains. Annual visitation is slightly over a quarter million visitors who participate in activities such as hiking, camping, picnicking and photography.

The only spruce-fir area under jurisdiction of the U.S. Forest Service (USFS) where visitor use is monitored is Shining Rock Wilderness Area in Pisgah National Forest. Annual visitation to the 5425 hectare area is over a quarter million visitor days per year (one visitor day is any combination of people and times equal to 12 hours). The mean use of 47.4

visitor days per hectare makes it one of the most heavily used wilderness in the country. The USFS also has jurisdiction over spruce-fir areas near the wilderness, Mt. Rogers in the Balsam Mountains of Virginia, Roan Mountain, and most of the Black Mountains north of Mt. Mitchell State Park.

The National Park Service (NPS) administers Great Smoky Mountains National Park (GSMNP) and the Blue Ridge Parkway (BRP) which passes near or through all spruce-fir areas (see figure 1) except Roan Mountain, Mount Rogers and Whitetop Mountain. Annual visitation along this 751 km roadway from GSMNP to Shennandoah National Park exceeds eleven million people.

Over half of the remaining spruce-fir forests are within GSMNP, most of them virgin. The spruce-fir zone in the park accounts for 1.8 percent of the park area, yet has 10.8 percent (129 kilometers) of park trail distance, receiving approximately two-thirds of park day hikers (186,000 visitors) and about 15 percent of overnight backcountry use (15,000 visitors) annually. Nearly half of the 113 kilometer Appalachian Trail within GSMNP lies within the spruce-fir zone. This is a popular trail because of its system of shelters, and its key location, thus about half of the backpackers (50,000) hike through spruce-fir forests annually. Adding to this area's high use is the paved Clingman's Dome trail with several hundred thousand annual visitors.

Balsam Woolly Aphid

The balsam woolly aphid (Adelges picea Ratzenburg) is an insect introduced into this country from Europe prior to 1908. It attacks all true firs or Abies, of which Fraser fir is the most seriously infested of the nine North American species (Mitchell 1966). The aphid was first discovered on Mt. Mitchell in 1957 (Speers 1958). By 1962 it had spread to Roan Mountain and in 1963 was detected in Great Smoky Mountains and on Grandfather Mountain (Amman and Speers 1965). Today all southern spruce-fir areas are infested with the balsam woolly aphid, some have suffered heavy losses.

METHODS

The field research on which this discussion is based was conducted in all spruce-fir areas and the all-spruce forest on Whitetop Mountains from 1975 through 1982. Study was also made of mountains with planted spruce or fir; areas with historical (but not always accurate) accounts of past spruce or spruce-fir forests (Ayres and Ashe 1902a, 1902b, and 1905; Holmes 1911; Pinchot 1897); and areas of sufficient elevation which currently, and perhaps historically, lack the fir component. All virgin, second-growth, logged, and balsam woolly aphid infested forests were sampled using a series of random 10x10 meter quadrats to provide baseline data on virgin and disturbed spruce-fir forest canopies and understories. A 2x2 meter nested quadrat was used to sample understory vegetation strata in the (1) ground layer - less than 5 centimeters tall, (2) herb layer - all other nonwoody herbs, and (3) shrub layer - all shrubs and trees less than 2.5cm dbh regardless of height.

All recreation sites (hiking and nature trails, overnight campsites, overnight shelters and picnic areas) were sampled using a set of 3 meter

wide transects beginning in the center of the trail or campsite, or at the edge of the shelter or picnic table and of sufficient length (10-75 meters) to terminate within the forest. Percent cover was measured for each species at one-quarter or one-half meter intervals in the three vegetation strata. Overstory basal area was also measured. A spruce-fir and an all-spruce wind throw were sampled using the transect procedure. Sampling was designed to permit comparison of species presence and cover for all possible natural and human disturbances whether using plots or transects. To prevent additional complications, sampling was not done in human disturbed areas that had also been heavily infested by the balsam woolly aphid.

RESULTS

Transects used to measure the recreation disturbances were of different lengths, therefore the transects were divided into four vegetation zones to permit comparisons between disturbance types. The spatial location of the four zones for each type of disturbance is shown in Figure 2.

The bare vegetation zone was always the site of the disturbance, being devoid of all but protected pockets of vegetation, generally lacking a litter layer, or containing a mosaic of bare soil and forest litter.

The disturbed vegetation zone was located beyond from the bare vegetation zone and was also actively used for recreation. The disturbed zone was dominated by a forest litter layer and often contained plant species more resistant to human trampling.

The transition vegetation zone was adjacent and beyond the disturbed zone and was used for recreation but with less intensity than the disturbed or bare zones. This zone contained a variety of herbs, shrubs, and trees with briars and tree reproduction the most important feature.

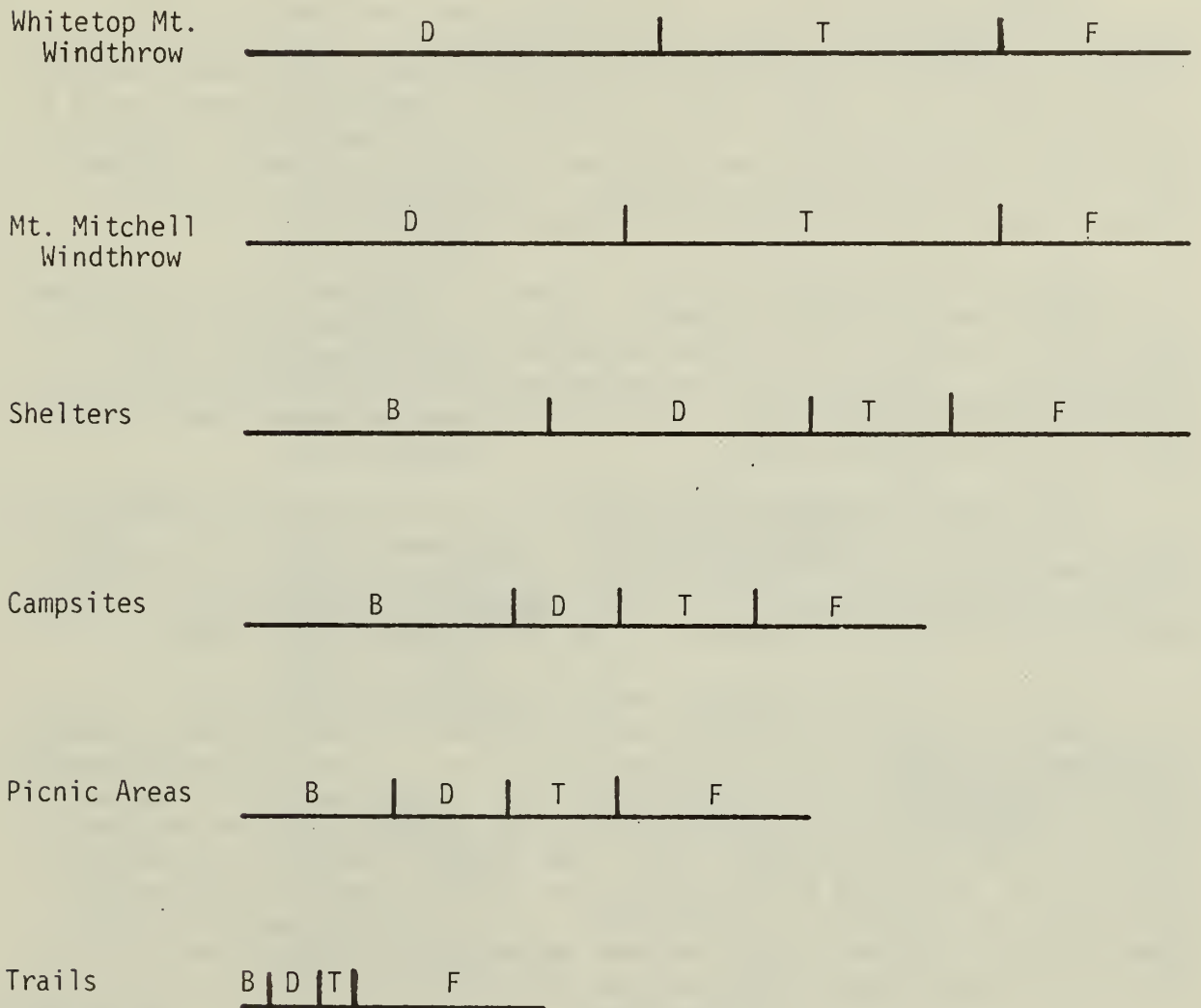
The forest vegetation zone was farthest from the recreation disturbance. It was infrequently entered by man, and was either virgin or second-growth stands.

Windthrows showed all but the bare vegetation zone and were infrequently entered by man, being almost impenetrable for recreation or sampling. However, they provide a comparison of natural disturbance and recovery against which human disturbance and recovery can be compared. Both windthrows, one of natural origin (Mt. Mitchell) and one of man-made origin in an all-spruce forest (Whitetop Mt.) are shown separately in Figure 2. The two windthrows are quite similar as neither has a bare vegetation zone. In comparison, all recreation disturbances have a bare zone radius of nearly 1 meter for trails, to 4 meters at picnic areas, 7 meters at campsites and 8 meters at shelters. Trails represent a narrow corridor of disturbance, whereas picnic areas, campsites and shelters are much larger disturbances, with shelter creating a disturbance and canopy opening at least as large as windthrows.

In order to better understand species response to disturbance, species response categories were defined using the vegetation zones. Categories were based on where each species had its highest mean cover and

Figure 2. Location of the four vegetation zones in the disturbances sampled with transects. Distance is from the center of the disturbance. B=bare vegetation zone, D=disturbed vegetation zone, T=transition vegetation zone, and F=forest vegetation zone.

Type of
Disturbance



0 5 10 15 20 25

Distance in Meters

other zones in which the species was present. The eight categories were (1) only in the forest zone, (2) only in the transition zone, (3) only in the disturbed and bare zone, (4) highest in the disturbed zone but also in the transition zone, (5) highest in the transition zone but also in the forest zone, (6) highest in the forest zone but also in the transition zone, (7) uniformly found in all zones, and (8) an irregular distribution or in all zones. Examination of the data found no species had a uniform distribution (#7), thus only seven response categories were found in the field.

Species most sensitive to disturbances such as trampling, soil compaction, increased sunlight, greater temperature fluctuations, and other microenvironmental changes should be farthest from the disturbance or only in the forest zone. Species least effected by these disturbances would be in disturbed and bare zones. Exotic or nonnative species were frequent in these zones. Every species was not found in the same response category at each recreation or windthrow disturbance, thus discussion is based on average response for each species as shown in Table 2.

Species found only in the forest zone occur primarily in the spruce-fir forest community (Ramseur 1960). Species listed in Table 2 were found near trails or smaller, less used campsites, but not near the larger disturbances. The species are not especially common or of higher cover in virgin or second-growth stands. They are assumed to be most sensitive to human and other disturbances.

Only transition zone species do best in partial to full sunlight where trampling is minimal. The exotic Festuca spp. primarily F. rubra, was present due to recent seeding along a nature trail. Its survivability in this environment remains to be seen. Diervilla sessilifolia is the most prevalent transition zone species at the Mt. Le Conte Lodge, GSMNP.

Nearly all of the disturbed and bare zone only species were exotics, introduced at shelters, campsites, and picnic areas through direct seeding by managers, on boot soles of recreationists, and in horse droppings and horse feed horsepackers are required to carry. These species occurred at the most intensively used and disturbed sites studied, and are the same species frequenting roadsides, yards, and fields. The only tree reproduction species listed was B. papyrifera var. cordifolia, found in the disturbed zone of the spruce-fir windthrow. It is an important tree in the regeneration of natural windthrows and burned areas, through few saplings survive to become mature trees (McLeod 1977, Sprugel 1974).

The fourth category includes species with their highest cover in the disturbed and transition zones. Most are exotics introduced to the recreation sites. The native Houstonia serpyllifolia occurs where trampling is minimal along trail edges in both spruce-fir and hardwood forests. Rubus idaeus var. canadensis was found in both windthrows and picnic areas. Its seed longevity, possibly sixty-five or more years (Harrington 1972), makes it an important component of reestablishing the 50-75 year Southern Appalachian spruce-fir windthrow cycle.

Table 2. Species response to recreation and windthrow disturbance using seven response categories and ground/herb, shrub, and tree reproduction strata. Response class with highest cover is listed first. Exotic species are denoted by an asterisk(*) and species found only in windthrows by a(w).

Response Class	Species by Strata		
	Ground/Herb	Shrub	Tree Reproduction
Forest Zone Only	<u>Lycopodium lucidulum</u>	<u>Viburnum cassinoides</u>	<u>Amelanchier arborea</u>
			var. <u>laevis</u>
	<u>Asplenium montanum</u>		<u>Illex ambigua</u> var.
			<u>montana</u>
	<u>Polypodium virginianum</u>		
	<u>Carex communis</u>		
	<u>Veratrum viride</u>		
	<u>Uvularia perfoliata</u>		
	<u>Streptopus roseus</u>		
	<u>Mediola virginiana</u>		
	<u>Trillium erectum</u>		
	<u>T. undulatum</u>		
	<u>Circaea alpina</u>		
	<u>Diphylleia cyomsa</u>		
	<u>Monotropa uniflora</u>		
Transition Zone Only	<u>Galax aphylla</u>		
	<u>Stachs clingmanii</u>		
	* <u>Festuca</u> spp.	<u>Diervilla sessilifolia</u>	
	<u>Stellaria pubera</u>	<u>Vaccinium corymbosum</u>	
	<u>Fragaria virginiana</u>		
	<u>Hypericum mitchellianum</u>		
	<u>Viola rotundifolia</u>		
Disturbed and Bare Zone Only	<u>Eupatorium rogosum</u>		
	* <u>Achillea millefolium</u>		
	* <u>Poa</u> spp.		w <u>Betula papyrifera</u> var.
	<u>Carex aestivalis</u>		<u>cordifolia</u>
	<u>Smilax herbacea</u>		
	* <u>Polygonum coccineum</u>		
	<u>P. cilinode</u>		
Disturbed and Transition Zones	* <u>Ranunculus acris</u>		
	* <u>Taraxacum officinale</u>		
	* <u>Poa annua</u>	<u>Rubus idaeus</u> var.	
	<u>P. alsodes</u>	<u>canadensis</u>	
	* <u>P. pratensis</u>		
	* <u>Stellaria graminea</u>		
	* <u>Trifolium repens</u>		
	* <u>Plantago lanceolata</u>		
	<u>Gallium triflorum</u>		
	<u>Houstonia serpyllifolia</u>		

Table 2. Cont'd.

Response Class	Ground/Herb	Species by Strata	
		Shrub	Tree Reproduction
Transition and Forest Zones	<u>Athyrium asplenoides</u>	<u>Ribes rotundifolia</u>	<u>Abies fraseri</u>
	<u>Dryopteris campyloptera</u>	<u>Rubus canadensis</u>	<u>Picea rubens</u>
	<u>Carex debilis</u>	<u>Menziesia pilosa</u>	<u>Sorbus americana</u>
	<u>C. normalis</u>	<u>Vaccinium</u>	
	<u>C. brunnescens</u>	<u>erythrocarpum</u>	
	<u>Cimicifuga americana</u>	<u>Viburnum alnifolium</u>	
	<u>Podophyllum peltatum</u>		
	<u>Saxifraga michauxii</u>		
	<u>Viola macloskeyi</u> var.		
	<u>pallens</u>		
	<u>Angelica triquinata</u>		
	<u>Aster acuminatus</u>		
	<u>A. divaricatus</u> var.		
	<u>chlorolepis</u>		
Forest and Transition Zone	<u>Bryophytes</u>	<u>Rhododendron</u>	<u>Fagus grandifolia</u>
	<u>Carex intumescens</u>	<u>catawbiense</u>	
	<u>Clintonia borealis</u>		
	<u>Claytonia caroliniana</u>		
	<u>Oxalis acetosella</u>		
	<u>Solidago glomerata</u>		
Irregular Distribution	<u>Glyceria melicaria</u>	<u>Ribes glandulosum</u>	<u>Betula lutea</u>
	<u>Cinna latifolia</u>	<u>Sorbus melanocarpa</u>	<u>Prunus pensylvanica</u>
	<u>Carex</u> spp.	<u>Sambucus pubens</u>	<u>Acer spicatum</u>
	<u>Arisaema triphyllum</u>		<u>A. saccharum</u>
	<u>Luzula acuminata</u>		<u>Cornus alternifolia</u>
	<u>Maianthemum canadense</u>		
	<u>Erythronium americanum</u>		
	<u>Laportea canadensis</u>		
	<u>Cardamine clematitis</u>		
	<u>Impatiens</u> spp.		
	<u>Viola</u> spp.		
	<u>Cuscuta rostrata</u>		
	<u>Monarda didyma</u>		
	<u>Chelone lyoni</u>		
	<u>Rudbeckia lacinata</u>		
	<u>Senecio rugelia</u>		

The fifth category of species had their highest cover in the transition zone, but continued with fairly high cover into the forest zone. When present in the bare or disturbed zone they were in well protected areas, such as next to the shelter or among tree roots. Many of these are shrub species, however spruce-fir forests usually do not have a well developed shrub stratum unless there has been windthrow, dying of canopy trees, or balsam woolly aphid infestation. Shrubs and tree reproduction occurred in a ring at the edge of the disturbance, an area not usually entered by recreationists.

The sixth category of species had their highest cover in the forest zone, had considerable cover in the transition zone, and were rarely present in the disturbed zone. These shade tolerant species are not resistant to trampling. Combining the species in this and the previous category accounts for a majority of the typical Southern Appalachian spruce-fir forest species (Oosting and Billings 1951, Ramseur 1960, Saunders 1979, Schwarzkopf 1974, Whittaker 1956).

The final category of species had an irregular distribution or were present in all vegetation zones, but were not prevalent in one zone or lacked sufficient data for their preferred location to be ascertained. None of these species are exotics and none, with one exception, are regarded as primarily spruce-fir forest species. The exception, Senecio rugelia, is principally a spruce-fir forest species and endemic to the Great Smoky Mountains. It occurred in the forest zone and transition zone at shelters and along trails, but did not do well when trampled. Prunus pensylvanica, like Rubus idaeus var. canadensis is a disturbance species capable of revegetating severe disturbances such as fire and logging, but it is not common in windthrows. Its presence is dependent upon a mineral seedbed, and a seed source or buried seed longevity. Once established the saplings survive trampling.

DISCUSSION

This discussion of spruce-fir ecosystem management will first address what is known about spruce-fir forests and dispersed recreation and secondly, identify recreation impacts that are not well known and how they might be studied.

Known Impacts

The literature (Brown 1941, Davis 1930, Korstian 1937) and recent research (Saunders, et al. 1981 and 1983) show fire to be a serious hazard in these forests. While there have been some dry years, annual precipitation of 150-220 centimeters usually is evenly distributed throughout the year, (Hardy and Hardy 1971, Data Services Branch 1976), making lightning fires a rarity (Bardens and Woods 1973). The major destructive fires were man-caused and followed large scale clearcut logging and improper slash disposal. Only one campfire which burned out of control caused much damage (Saunders, et al. 1983). It burned one hectare and like other fire sites, has been slow to recover, probably due to destruction and erosion of the highly organic soils.

Spruce-fir forests are inherently susceptible to windthrow, especially on exposed sites or when the canopy is opened. Soils are generally 30-60 centimeters thick over bedrock (McCracken, et al. 1962, Wolfe 1967). Both spruce and fir are shallow rooted trees. Most windthrow occurs in mature stands during high winds (95-300 kilometers per hour) in February, March and April when thawed soils permit trees to be easily blown down. Older firs are susceptible to bole breakage during high winds due to rotten or hollow boles. There is evidence of a growing windthrow at the Mt. Collins Shelter, GSMNP, in a stand of 200+ year old spruce. Clearing for construction of the shelter in 1960 created an opening in the forest canopy.

Exotic species are present at the more heavily used recreation sites, or where managers have attempted seeding nonnative (exotic) plant materials. To date, exotics have not been found within the forest, presumably because they compete best in the open bare and disturbed zones and poorly in the denser shaded transition and forest zones. The most important vector of exotics may be horses. At non-GSMNP spruce-fir recreation sites where horses rarely if ever are present, exotics were absent. Using sterile horse feed or prohibiting horses may help keep these species out of other recreation sites. The major problems with the introduced species is their ability to out compete native spruce-fir species, creating potential for escape into this ecosystem, and their disruption of site visual appeal.

As shown in Table 2, most of the common spruce-fir species respond to recreation impacts, primarily trampling and the resultant soil compaction in a fairly predictable manner. Other factors influencing species response include increased sunlight in forest openings and increased microclimatic fluctuations and temperature and moisture extremes. None of the native species are well adapted to this kind of impact, thus the large bare and disturbed zones surrounding shelters (707 square kilometers) and campsites (314 sq km), and the presence of exotic species. Given reduced vegetation cover and increased soil erosion, openings and impact sites should be kept as small as possible. Not only will this improve site vegetation and soil conditions, but also the site aesthetics.

A firewood logging operation has been conducted to supply the Mt. Le Conte Lodge, GSMNP, since its origin as a tent camp some 75 years ago. Logging was halted in July 1976. Examination of this mule-logged area found it to have a floristic composition similar to that of virgin stands, although fewer species were present and species cover values were different. The mule-logged stand contained more shrub cover and denser tree reproduction. Soil erosion appeared minimal because of the narrow skid trails and absence of roads. Site recovery was excellent, especially when compared to recent machine-logged stands and a closed canopy spruce-fir forest should result.

Unknown Impacts and Monitoring

One spruce-fir recreation problem for which there is no answer is the impact of firewood gatherings on vegetation trampling, nutrient cycling, and careless or deliberate cutting of live trees and saplings. There are hikers who persist in using fires for cooking purposes, leading them to cut live trees because they were conveniently close. The campfire impact

should be studied using an available fuels and vegetation comparison between areas with and without wood gathering.

Windthrows are a natural disturbance mechanism in spruce-fir forests, but they also occur when man opens the forest canopy. Long term study is needed at several GSMNP shelters, especially Mt. Collins and Tricorner Knob, to determine if canopy openings will stabilize or continue enlarging. Study is also needed on how these areas which receive recreation use, will recover relative to other natural, undisturbed windthrows.

Fungi and disease are known to weaken the trunks of fir, and probably spruce. Injury of these and other thin barked trees from axes, and scuffing of roots by hikers and horses provides an easy entrance for diseases. Research has not been done on what diseases are present, individual species resistance, and what portion of trees at recreation sites compared to undisturbed sites are infected.

The balsam woolly aphid infestation has spread widely, especially in GSMNP, since this recreation impact study began nearly a decade ago. As a result several recreation sites have lost and more are losing their fir canopy. Since use is still occurring at these sites, questions needing answers are how well will these sites recover, and will the reduced canopy and increased sunlight permit exotic species to invade the spruce-fir forest. Woody exotics are a problem in GSMNP in lower elevation successional deciduous forests (Baron, et al. 1975).

Soil erosion is a problem with the thin, organic soils on these often steep sites. The rate and amount of soil erosion at recreation sites has not been quantified. Soil cores from some shelters show a complete loss of the A horizon. Some trails on ridge faces have become major drainage ways, eroding to depths of a meter or more. Many trail sections have exposed tree roots (an entry for disease) and exposed bedrock or C horizons. This research should focus not only on what soil erosion is occurring, but also on how to control it.

Illegal campsites are a problem along all trails, especially the Appalachian Trail in GSMNP. The backcountry permit system was begun over a decade ago to eliminate this problem by designating overnight sites and controlling the location and number of people at all backcountry overnight campsites and shelters. Late visitors to the park often do not obtain a permit and other users simply ignore the posted regulations at all trail-heads. Such users either cause overcrowding at legal sites, or they as well as users with permits go to illegal sites to avoid crowded conditions. Most illegal campsites are small, but their presence is obvious and a signal to other backpackers of a possible campsite. Elimination and rehabilitation of these sites may discourage use and prevent some trail sections from looking like a continuous series of campsites. In addition, an education program for all GSMNP backcountry users explaining the reasons for the permit system may help reduce this problem.

All backcountry users and their livestock need to eliminate body wastes periodically. The location and methods of waste disposal is critical to the health of all users and the environment. Recent research

(Temple, et al. 1980) has shown that the recommended method, shallow burial in holes 5-20 cm deep, does not kill bacteria even after 3 years. All overnight sites are located near springs, which are not common in the spruce-fir forest. Water quality needs to be continually monitored at these sites as well as studies undertaken to determine the safest means of waste disposed by both humans and livestock.

CONCLUSIONS

Research in the Southern Appalachian spruce-fir forest ecosystem has shown that (1) the forests and soils are easily damaged by fire, (2) windthrow is a natural perturbation which also occurs when the forest canopy is opened by man, (3) exotic species are prevalent in recreation disturbed sites, (4) native spruce-fir species cover and diversity is severely reduced by recreation activity into four distinguishable vegetation zones, and (5) mule-logging does not damage the soil or reduce species richness nearly as much as recent machine-logging. Research needs associated with dispersed recreation in this ecosystem are (1) the impact of firewood gathering on vegetation and nutrient cycling, (2) if canopy openings for shelters and campsites will stabilize or expand as a result of subsequent windthrow, (3) effect of tree diseases introduced by root and trunk injury on individual tree and canopy health, (4) effect of continued recreation use on recovery of balsam woolly aphid infested stands, (5) amount of soil erosion at recreation sites and along trails, (6) reduction and rehabilitation of illegal campsites, and (7) monitoring water quality and developing safe means of human and animal waste disposal. Research and management problems were not prioritized, but the issue of water quality is probably the most important to the users of these forests.

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PRE-PARK DISTURBANCE IN THE SPRUCE-FIR FORESTS
OF GREAT SMOKY MOUNTAINS NATIONAL PARK

Charlotte Pyle¹

Abstract. The major pre-park disturbances in the spruce-fir zone of Great Smoky Mountains National Park were mechanized logging and logging slash fires. Estimates by previous authors of prelogging and postlogging spruce-fir areas in the Southern Appalachians as well as in the national park were reviewed. Area of spruce-fir extant in the park following logging was estimated by means of a dot grid laid over the "spruce" portions of the Miller vegetation type map of the park. Miller's "spruce" was analogous to what I have called "spruce-fir" for this analysis. Spruce-fir was broadly defined to include three cover types of the Society of American Foresters (red spruce-yellow birch, red spruce, and red spruce-Fraser fir) as well as spruce with a rhododendron understory and stands dominated by Fraser fir alone. Estimated spruce-fir area prior to logging was based on early maps and timber estimates found in the Park Archives. The difference in the prelogging total (17,910 hectares) of spruce-fir versus postlogging total (13,370 hectares) was attributed to destruction of habitat following fire. The possibility of additional loss of spruce due to failure of cut-over spruce to regenerate in stands that were originally a mixture of spruce and hardwoods was also discussed.

INTRODUCTION

The spruce-fir zone in Great Smoky Mountains National Park (GRSM) is found in the highest elevations in the park, along the North Carolina/Tennessee state line west from Cosby Knob to about Double Springs Gap. Major spruce-fir ridges extending from the state line are (1) from Tri-Corner Knob southeast to Big Cataloochee Knob and on in a southerly direction, as well as east to Mount Sterling; (2) from Mount Kephart out the Boulevard to Mount LeConte; and (3) Mingus Ridge. In addition, Raven Fork is unusual in the park, with spruce covered coves as well as ridges extending down to 4500 feet elevation and below throughout the watershed. An outlying population of spruce is found west of Double Springs along Miry Ridge.

The major prepark disturbances in the spruce-fir zone were mechanized logging and slash fires. Prior to acquisition for the park, ownership of the spruce-fir zone was divided among several timber companies who sought spruce for lumber and pulp. This corporate ownership reflects the fact that, unlike other forest types in GRSM, the spruce-fir offered little to farmers and livestock herders; consequently, the type as a whole was little impacted by farming activities. Extremely limited use of the GRSM spruce-fir zone by stockholders (e.g., on Andrews Bald or Mount Sterling) is in contrast to the situation reported by Hopkins (1899) for West Virginia spruce-fir, where herders girdled trees and subsequently burned large areas for pasture. Hopkins discussed several other disturbances in the spruce vegetation of West Virginia. Of these disturbances (logging, fire, clearings, roads, commercial railroad construction, bark beetles, and windfalls), only logging and slash fires were important in GRSM during the prepark era. Although there do exist

1. Biological Technician, Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, Tennessee.

records of "blowdowns," disturbance to spruce-fir vegetation by windfall prior to park establishment was insignificant in relation to the total area of this vegetation type.

LOGGING HISTORY

Because spruce is a high elevation species, and the high elevations of Great Smoky Mountains were quite inaccessible, the spruce-fir zone in GRSM was not affected by the early small-scale and technologically simple logging operations of local people. An example of the prevalent logging technology associated with early logging in GRSM was the use of horse teams in accessible hardwood coves to drag logs to a portable mill set up on the site, from which cut lumber was hauled by wagon to market. Following the development, in the early 1900s, of highly mechanized technology in logging as well as improved methods of wood processing, commercial corporations became interested in the remote spruce-fir zone of the Smokies (Lambert 1958). These well financed outside operators built large mills and used mechanized skidders plus railroads to bring logs long distance to the mills (Lambert 1958).

Loggers' demand for spruce was related to its physical properties--strong and lightweight wood and ability to be pulped by the sulfite process (which had been reintroduced into the United States in 1887; Panshin et al. 1962). The heyday of spruce cutting in GRSM was during the first World War, at which time not only was the timber cut for pulp but also for wood to be used in aircraft construction. In 1918, Suncrest Lumber Company was receiving a U.S. government subsidy (in the form of 200 "army men") for extraction of spruce from Big Creek watershed (Hardwood Record 45:39, 8/25/18, located in GRSM Archives). At the end of World War I this aid was cut off. A million and a half board feet of spruce logs were left lying on the ground, signaling the end of an operation that was no longer profitable (Lambert 1958). The demand for spruce pulp was expected to be more or less continuous after the completion of a pulp and paper mill in 1905 in Canton, North Carolina (Champion Fibre Co. records, "Expect to Prove: History," located in GRSM archives). It was for this expected demand that Champion Fibre Co. in particular had acquired such a large reserve of spruce-fir forest in GRSM. However, before Champion and the other timber corporations were able to log all the spruce-fir zone, condemnation proceedings began for the proposed Great Smoky Mountains National Park. In conjunction with this, Champion's cutting of spruce in GRSM ceased in 1927 (Champion Fibre Co. records, "Expect to Prove: History").

SOURCES OF INFORMATION ON SPRUCE-FIR DISTURBANCE HISTORY

Following condemnation, the timber companies were interested in getting a maximum price for their holdings. As a consequence, transcripts of the condemnation proceedings contain many differing opinions as to exactly the quantity and value of the timber that was left within a company's boundary. Furthermore, because concern was with how much, not where, testimony was often vague as to actual location of cut versus uncut areas. For the most part, rather than written records, the best parkwide source of information on logging impacts in the spruce-fir zone is a map made by Frank Miller, a National Park Service (NPS) forester in the 1930s. Miller's map shows vegetation types, including a "spruce" type plus

a "cut over" line and a "burned" designation. The cut-over line delineates logging that altered the area enough to present a fire danger different from the adjacent noncut-over tracts. Such logging is called "heavy cut" by other anonymous map sources in the GRSM Archives. The boundaries of "cut over" or "heavy cut" do not include areas where a few big trees were selectively removed from a stand.

A second source of mapped information on logging impacts in the spruce-fir is the type maps made in the 1930s by the Tennessee Valley Authority (TVA). For GRSM, the TVA generated vegetation type boundaries and stocking are based entirely on ocular estimation in contrast to Miller's types and stocking based on 1/5-acre plots in addition to ocular estimation.

A third vegetation typing method was employed by Chris Eagar of Uplands Field Research Laboratory, who made a parkwide set of spruce-fir type maps based on interpretation of recent aerial photographs (C. Eagar, unpublished maps, Uplands Field Research Laboratory). Areas of spruce-fir forest where effects of fire or logging could be recognized in the air photos were mapped.

Although written records of spruce-fir distribution prior to and following logging were generally not site specific, certain references are useful in consideration of the probable original effects of logging on spruce-fir vegetation. Buckley (1859), Hopkins (1899), Whittaker (1956), and Saunders (1979) discussed general placement of a lower elevational boundary for spruce or the spruce-fir type. Ayres and Ashe (1902) discussed Southern Appalachian spruce in general terms and also (1905) gave watershed descriptions that included mention of percent spruce present. Korstian (1937) and Minckler (1940) described problems with spruce regeneration following logging in the Southern Appalachians. Lambert's (1958) unpublished report available at GRSM library), although lacking in information mappable at the 1:24,000 scale, contains a detailed written compilation of information concerning logging operations specific to GRSM. Finally, the GRSM Archives houses a variety of documents representing most of the logging companies in operation at the time of park land acquisition.

METHODS

Location and areal measurements of spruce and/or fir vegetation types were based mainly on the maps described above. Air photos were superficially examined as a check on reasonableness of maps of current spruce-fir vegetation. Because field work was beyond the scope of this present work, reliance was placed also on written records of estimates of total prelogging era spruce-fir acreage in certain watersheds. Use of historic estimates of spruce area allows for calculation of loss of area of the spruce forest type but does not confer knowledge concerning actual location of extirpated spruce beyond the major watershed unit.

Because it was based on field plots and extensive field reconnaissance, the Miller map was used as the main source of information on existing spruce-fir in GRSM. A dot grid (64 dots per square inch) was used to estimate area after it was found that the uneven surface of the map was not conducive to planimetric estimates. A second dot grid estimate was made as a check of the first, and the small differences in the two were averaged to produce the final spruce-fir area estimate used for each watershed. Number of hectares total in each major watershed were taken from estimates of area based on the National Park Service Denver Service Center digitization of

watershed boundaries marked on 7-1/2 minute topographic sheets.

To estimate spruce-fir area lost following logging, several methods were used, depending on watershed history and available information. In the upper reaches of the Oconaluftee River, a small area believed to have been partially covered by spruce had been burned in 1925. The method used for this watershed started with derivation of expected extent of spruce forest type based on estimating the average elevation of spruce in the adjacent Bradley Fork watershed as shown on the Miller map. Bradley Fork was not logged at high elevation and has much the same general aspect, topography, and relief in relation to surrounding landforms as does the upper Oconaluftee River. In Bradley Fork, the average boundary of spruce was 4500 feet elevation on the the ridges and, in draws, 5350 feet. The difference in area of present spruce zone versus expected area was estimated with a dot grid placed over the Miller maps. Dots were counted between Miller's marked boundaries and the expected boundaries of 4500 feet on ridges and 5350 feet in draws.

Although Bradley Fork was not logged at high elevations, in 1925 a large logging slash fire in the Oconaluftee River watershed overlapped into uncut spruce-fir in Bradley Fork as well as across the state line divide into the Middle Prong around Charlies Bunion. An arbitrary elevation of 4500 feet was taken for the original boundary of spruce on the widely convex ridge extending into the Middle Prong from Charlies Bunion. In Bradley Fork, the position of extant spruce on Richland Mountain (adjacent to the burned area) very nearly defined the prefire extent of spruce.

Although Straight Fork and Bunches Creek were heavily logged, there were no major fires at high elevation. Therefore, as will be discussed later, no nonspruce areas were construed as having supported spruce-fir forests prior to logging.

In contrast, in the Cataloochee watershed there was high elevation logging followed by fire. Both written records and maps give reason to believe that the burned area south of Mount Sterling Ridge now forested in hardwoods once supported spruce vegetation. In a letter to the North Carolina Park Commission dated December 7, 1929, J. F. Green and others wrote, "We followed most of the high line of railroad constructed by the Ravensford Lumber Company from Pin Oak Gap around to the head of Little Cataloochee, a distance of 18 miles. We found this line followed about the lower edge of the spruce belt...We find the spruce had been taken below the railroad for a distance of 1500 to 2000 ft and the hemlock left standing.... Also...this cut over land has since been burned over and everything destroyed." The catastrophic burn is documented on Miller's map. Based on the information contained in this letter, the boundary of "spruce lands" from a small scale prelogging era map in the GRSM archives (Uplands Lab Map Index No. 81) was transferred freehand to a USGS 1:2400 scale topo sheet. This boundary corresponded very well to the old railroad grade shown on the current USGS map. Miller's fire boundaries extend some 1000 to 2000 feet farther downslope of this railroad grade, further corroborating Green's observations.

In order to estimate area once covered by spruce vegetation in this part of the Cataloochee watershed, arbitrary prelogging boundaries were created based on the assumption that the railroad grade was indeed in the vicinity of the lower boundary of spruce and that the local pattern of spruce distribution included spruce fingers extending down ridges and hardwood inroads up draws. Additionally, based on the same map source

(map 81), an arbitrary boundary of prelogging spruce forest was created for a small area within the burn on Shanty Mountain, which is also in the Cataloochee watershed. Burned area on Shanty Mountain was estimated with a dot grid laid over a marked xeroxed copy of the Miller map. Area of burned spruce marked on the 1:24000 scale was estimated by taking the average of three planimetric determinations.

In the other two GRSM watersheds where much of the spruce-fir vegetation type was destroyed by fire (Forney Creek and Big Creek), no attempt was made to reconstruct prelogging spruce boundaries due to the fact that no prelogging spruce-fir maps could be located. However, a general estimate of the area of spruce removed was made based on written records of prelogging spruce-fir acreage. The Big Creek watershed was one of the most extensively burned watersheds in the park. Its upper reaches are rather remote, and little was known about its prelogging vegetation. Ayres and Ashe (1905) did not even list spruce as a component of the vegetation, although Mount Guyot and Tri-Corner Knob, which are a part of the major mountain mass of spruce-fir zone in the Great Smoky Mountains, serve as boundaries of the watershed. It appears, however, that by 1911 the area was becoming better known. The October 1911 issue of American Lumberman contained an article that included: "It will require five switchbacks on some of the mountains in order to reach the spruce which is found above 4500 feet." Also in 1977, the Lemieux Brothers and Company (timber estimators) estimated that there were 4850 acres of spruce land in the Big Creek watershed. It is not clear whether this estimate includes what was then known as Upper Baxter Creek (now Sinking Creek).

Given that little sign of past presence of spruce (other than the occasional spruce crown seen emerging from the numerous rhododendron thickets) is visible on current aerial photography, and that Miller in the 1930s typed very little area as spruce, one might conclude the reports of spruce in Big Creek were greatly exaggerated. If one takes Camel Gap on the North Carolina/Tennessee border as the easternmost boundary of continuous spruce-fir of the northern edge of the Big Creek watershed and uses, for the lower limit of spruce, a consistent 4500 feet contour around the watershed to the unlogged area near Mount Sterling, then the estimated total area of spruce-fir in Big Creek is considerably more than 4850 acres. However, if one hypothesizes a spruce boundary that falls as low as 4500 feet on ridges and as high as 5500 feet in draws (a pattern similar to that in the unlogged Bradley Fork spruce-fir forest), then the total estimate of 4850 acres of spruce is within the realm of reason. Given that no better information was found, the Lemieux Brothers and Company estimate of 4850 acres (1963 hectares) was taken for the prelogging area occupied by spruce-fir.

Because the spruce-fir type remaining in the Big Creek watershed is small and in disjunct patches, it was not suited to areal estimates by dot grid on the 1:62500 scale. However, Miller's plot records (in the GRSM Archives) included area estimates made from a no longer available set of 1:24000 scale maps showing Miller's type boundaries. These estimates of cut-over and virgin spruce were used. The difference between Miller's area estimate and the Lemieux Brothers and Company estimate was accepted as the amount of spruce-fir forest lost due to logging fires. This does not correspond mapwise to the area shown by Miller as burned in 1925. However, there are records in this watershed of earlier spruce-fir fires not recognized in Miller's mapping (e.g., Lambert 1958; Anonymous Lumbering Map made circa 1928-1930, Uplands Lab. Map Index No. 58, in GRSM archives).

Lambert (1958) reported that prior to logging by the Norwood Lumber Company, there was an estimated 30,000,000 board feet of spruce in the Forney Creek watershed. He gives the average cut as 15,000 board feet per acre. This works out to an original spruce-fir zone of 2000 acres ($\approx$ 809 hectares). Close examination of current air photos does not show a great abundance of spruce in the watershed. Proposed reasons are that spruce was decimated in the logging slash fires of the 1920s; or that Forney Creek, being on the westernmost edge of the spruce-fir zone in GRSM and being more southwest-facing and less sheltered by surrounding landforms, may never have supported as much spruce-fir vegetation as other large spruce-fir-containing watersheds. For lack of better record, 809 hectares was taken as the total spruce-fir area encountered by loggers.

A final word on methods concerns the separate tallying of selectively cut areas. In most cases, selectively cut areas correspond to small areas designated "light cut" by Miller on the wilderness overlay he made in 1942 for his type map. However, in Forney Creek, Straight Fork, and Cataloochee Creek, small areas designated virgin by Miller were treated by the author as selectively cut, based on field observation and corroborating evidence from air photos.

RESULTS

Of the 28 major watersheds in GRSM, 17 have spruce-fir vegetation. In three of the watersheds, there were major logging slash fires which resulted in a loss of one-fourth of the spruce-fir area believed to have been found in the Great Smoky Mountains prior to logging. Prior to logging, it was estimated there were 17,910 hectares of spruce-fir type. This is equal to 8.7 percent of the total area of the park. The area of spruce-fir extant following logging in the park was 13,370 hectares, or 6.5 percent of the total park area. Of the extant area, 90 percent (12,100 hectares) was not logged. It should be pointed out that these 12,100 hectares of unlogged forest represent only 68 percent of the area occupied by spruce-fir prior to logging and logging slash fires. Table 1 shows tabulations by watershed of spruce-fir type area. The "cut and burned" or "burned/no cut" area within certain watersheds is based on estimates outlined under "Methods" and represents areas believed to have been covered with spruce-fir prior to logging activities in GRSM. The tabulations in Table 2 deal only with extant spruce-fir.

Prior to logging in the park, spruce-fir was most important in the West Prong, Middle Prong, Big Creek, Cataloochee Creek, and Raven Fork watersheds. Fire following logging decimated the spruce-fir in Big Creek and Cataloochee Creek, removing 78 percent and 85 percent, respectively, of the spruce-fir vegetation. Slash fires were also important in Forney Creek, where the spruce-fir was reduced to 20 percent of its original area. In general, if a watershed was logged extensively, it burned. An exception was Bunches Creek, which, as far as the records show, did not have fire in its 280 hectares of extant but heavily cut spruce-fir.

Today, over 45 percent of the extant spruce-fir in the park is in two watersheds. Raven Fork and the Middle Prong. Addition of the West Prong makes three of the 17 spruce-fir-containing watersheds in GRSM account for nearly 60 percent of the spruce-fir.

Table 1. Tabulated areas of spruce-fir (S-F) vegetation type.

MAJOR WATERSHED		AREA 8Y WATERSHED				AREA WITHIN WATERSHED (Spruce-fir type only)								
Name	No.	Total S-F Type* (hectares)	Total all types (hectares)	% S-F	Uncut/ burned (hectares)	%	Heavy Cut (hectares)	%	Light Cut (hectares)	%	Cut and burned (hectares)	%	Burned/ no cut (hectares)	%
Forney Creek	18	809	12,696	6			83	10	79	10	647	80		
Noland Creek	19	378	7,046	5	378	100								
Deep Creek	20	874	8,735	10	874	100								
Oconaluftee River	22	436	8,045	5	15	3	303	69	63	14	55	13	23	2
Bradley Fork	23	968	5,233	18	945	98								
Raven Fork	24	3,252	5,482	59	3,252	100								
Straight Fork	25	929	5,332	17	799	86	75	8	55	6				
Bunches Creek	26	280	3,415	8			280	100			2,222	85		
Cataloochee Creek	27	2,626	15,417	17	374	14	28	1	2	--				
Big Creek	28	1,963	9,321	21	296**	15	130**	7			1,537	78		
Cosby Creek	1	165	5,540	3	165	100							55	2
Indian Camp Creek	2	228	1,374	17	228	100								
Webb Creek	3	28	4,580	0.6	28	100								
Middle Prong	4	2,587	12,078	21	2,532	98								
Roaring Fork	5	197	4,842	4	197	100								
West Prong	6	1,402	8,327	17	1,402	100								
East Prong of the Little River	7	792	15,866	5	614	78	142	18	32	4	4	--		
GRAND TOTALS***		17,910	133,330	13%	12,100	68%	1,040	6%	230	1%	4,460	25%	80	

*Includes total burned areas estimated to have been covered by spruce-fir vegetation prior to logging.

**Number taken from Miller's tabulation.

***Rounded to tens.

Table 2. Classification of disturbance type within areas of extant spruce-fir vegetation.

Major Watershed Name	No.	Total Area (hectares)	Uncut/Unburned (hectares)	Percent	Heavy Cut (hectares)	Percent	Light Cut (hectares)	Percent
Forney Creek	18	162			83	51	79	49
Noland Creek	19	378	378	100				
Deep Creek	20	874	874	100				
Oconaluftee River	22	381	15	4	303	80	63	17
Bradley Fork	23	945	945	100				
Raven Fork	24	3252	3252	100				
Straight Fork	25	929	799	86	75	8	55	6
Bunches Creek	26	280			280	100		
Cataloochee Creek	27	404	374	93	28	7	2	---
Big Creek	28	426	296	69	130	31		
Cosby Creek	1	165	165	100				
Indian Camp Creek	2	228	228	100				
Webb Creek	3	28	28	100				
Middle Prong	4	2352	2352	100				
Roaring Fork	5	197	197	100				
West Prong	6	1402	1402	100				
East Prong of the Little River	7	788	614	78	142	18	32	4
GRAND TOTALS*		13,370	12,100	90%	1,040	8%	230	2%

*Rounded to tens.

DISCUSSION

Both prelogging and postlogging area estimates of spruce-fir vegetation in the Southern Appalachians have produced widely differing sets of numbers as a result of widely differing sets of assumptions. A major source of variation is in the definition of "spruce-fir." For purposes of this paper, "spruce-fir" includes pure fir, spruce and fir mixed, pure spruce, spruce and hardwoods and/or hemlock, and spruce and rhododendron. Because spruce was a tree of commercial importance, there are more historical records of distribution of spruce forests than of the spruce-fir vegetation type itself.

Barring competitive interactions, the best forest site for spruce is the sandy loams found on moist but well-drained slopes and benches (Korstian 1937). These rich moist upper cove positions are generally dominated by northern hardwoods vegetation in the Great Smoky Mountains. Holmes (1911) described the spruce forests in Western North Carolina as chiefly spruce and balsam with a small percentage of yellow birch and other hardwoods. While Holmes agreed that spruce individuals reach their best development on richer sites, he said that red spruce "is confined almost entirely to the spruce forest of higher mountains, though a few straggling trees descend into the hardwood forest below." In contrast, with respect to the distribution of spruce, Miller (Brief narrative descriptions of the vegetative types in Great Smoky Mountains National Park, 1938, unpublished) as well as Schofield (1960) described the transition in the spruce-fir zone between pure conifers and pure hardwoods as gradual in undisturbed forests.

It appears that Holmes' impression of spruce forest was one based on looking from a great distance at the patterns in the landscape. From such a viewpoint, the boundary between broad bands of coniferous versus hardwood forest appears well defined, and the "few straggling trees" descending into the hardwood belt are those trees on ridgetops, where the elevational boundary of the spruce type may drop 500 feet below that of the general boundary.

To the observer standing in the forests of GRSM, "a few straggling trees" describes the pattern of individual spruce trees as the spruce type gives way gradually to the northern hardwood type. Given that, from a closeup point of view, the transition between spruce-fir and hardwoods is gradual (except, as Schofield (1960) points out, where there was logging followed by fire), in order to map spruce-fir vegetation one needs a definition that addresses allowable extent of species other than spruce or fir. The Society of American Foresters (SAF) defines cover types by the following rules: (1) names are given according to which species (of the dominant and codominant stems only) are numerically predominant in a forest, and (2) the species which appear in the type name should form 50 percent or more of the forest composition, with the most numerically important species listed first (SAF 1954). Spruce-fir SAF forest cover types applicable in the Southern Appalachians are red spruce-yellow birch (which can be associated with Fraser fir, yellow buckeye, beech, sugar maple, and mountain-ash); red spruce (in which red spruce can be pure or predominant and associated with yellow birch, sugar maple, red maple, hemlock, white ash, mountain-ash, Fraser fir, and yellow buckeye); and red spruce-Fraser fir (in which red spruce and Fraser fir can be in pure association or predominant and associated at the lower altitudinal portions of the type with hemlock, yellow birch, beech, sugar maple, yellow buckeye, mountain-ash, and hawthorn).

Spruce types such as those defined by SAF allow one to type a forest stand in which one has counted the trees. It says nothing about general patterns on the landscape. However, most areal estimates of extent of widespread forest cover types have been based on perception of some pattern in the landscape rather than on field plots. In general, for spruce-fir in the Southern Appalachians, the pattern has been defined via the lower elevational limit of spruce, due to the fact that spruce-fir is the uppermost vegetational belt in the region, with spruce having lower elevational limits than fir.

Elevational placement of the lower limit of spruce-fir depends on the definition of spruce-fir vegetation and the latitude of the observer. Frothingham (1931) generalized the spruce forest as "found at altitudes of over 4500 feet in the mountains of North Carolina, Tennessee, and Virginia, and at altitudes of over 3500 feet in West Virginia." Because early records of spruce-fir were often written from a forester's point of view, many of them address the lower elevational boundary, not of spruce and fir but of "spruce lands" (meaning forest valued for its large spruce trees which often grew, on good sites especially, along with hardwoods in varying unrecorded proportions). Furthermore, some early literature on elevational boundaries of spruce actually addressed the lower limit of observed individual spruce trees rather than the limit of spruce forest or "spruce lands."

These differences in latitude and attitude of early writers led to a wide variation in conceptualized boundaries of the spruce-fir vegetation type. Such differences in boundaries led to difference in area estimates of extant spruce-fir vegetation.

When one attempts to estimate the area spruce-fir occupied before disturbance of white people, a further source of variation is introduced. Because spruce-fir does not regenerate well (if at all) in burned cut-over areas and because logging followed by fire was the typical pattern of disturbance (Korstian 1937, Minckler 1940) in the Southern Appalachians, there are vast areas which may or may not have had spruce-fir vegetation prior to logging. Locations, as well as elevational boundaries of these areas, are open to debate. Hopkins (1899) was of the opinion that a large area of West Virginia, not then forested in spruce, once supported spruce forests in the elevational belt from 2400 to 4000 feet elevation. Hopkins came to this conclusion based on his observations of trees in stands of a few acres at elevations between 2400 and 4000 feet coupled with his belief that, prior to settlement by the white people, the area was covered by an unbroken forest in which:

"the more abundant moisture in the soil and atmosphere attending this forest covered condition made it possible for spruce to occupy, as the principal growth all of these higher elevations which at present are covered with other kinds of timber. The area of the belt in which spruce was then found, probably covered all of the higher elevations of the Appalachian range that rise above 2400 feet, which would be an area of about 2,000,000 acres, on which one-half the timber was probably spruce. If so, there were about 1,500,000 acres of spruce forest here (in West Virginia, present author's note) when the first white settler occupied the territory."

Minckler (1940) apparently intuitively mistrusted Hopkins' total spruce acreage as he made reference to Hopkins (1899) for the estimate of 1,500,000 acres of spruce forest prior to logging in West Virginia, Virginia, Tennessee, and North Carolina (whereas Hopkins' topic and discussion was on West Virginia alone).

Clark (1954), in discussing the original spruce forests of West Virginia, used the number "500,000 acres." This corresponds to Hopkins (1899) if one leaves out Hopkins' 2,000,000 acres "on which one-half the timber was probably spruce." Ostensibly, this would set Clark's lower spruce forest boundary at 4000 feet. This is higher than Frothingham's (1931) estimate for West Virginia but not unreasonable, especially allowing for variation in definition of what constitutes spruce forest.

Saunders (1979) took spruce and spruce-fir forests as those above the spruce-fir hardwood ecotone. Without documentation of his source of information, he cited 1670 meters as the "generally recognized" lower limit of spruce-fir forest (Saunders 1979). He then settled upon "approximately 1670 meters" (Saunders 1979) as the elevation of the spruce-fir/hardwood ecotone. This elevation (≈ 5480 feet), which Saunders (1979) equated to 5500 feet, is close to the 5600 feet (≈ 1707 meters) Whittaker (1956) used as the lower boundary of spruce and fir forests based on field transects on the Tennessee side of GRSM. Whittaker went on to describe a spruce forest (which could be up to 30 percent hardwoods or up to 84 percent rhododendron) at elevations from 4500 to 5500 feet (≈ 1372 to 1676 meters) in GRSM. Similarly, Schofield (1960) intimated that the hardwood/spruce ecotone is a gradual transition occurring from 4500 to 5000 feet (≈ 1372 to 1524 meters) elevation in GRSM. In taking the lower boundary of spruce-fir as 1670 meters ("=5500 feet"), it appears that Saunders was thinking in terms of what would have been the average Southern Appalachian boundary of more or less pure spruce and fir rather than an intermediate point (i.e., ecotone) between spruce-fir and hardwoods. In fact, 5500 feet (≈ 1676 meters) was cited by Davis (1930) as the lower elevation of spruce and fir forests above the spruce fir/hardwood ecotone on Black Mountain, North Carolina. Thus Saunders' (1979) use of 1670 meters to define the lower boundary of spruce-fir corresponds to a narrow definition of what may be included in "spruce-fir" which led to a conservative estimate of pre- and postlogging spruce-fir area.

Miller (1938) agreed with Schofield (1960) and Whittaker (1956) in recognizing nonspruce or nonfir members of the spruce forest (e.g., spruce-hardwoods, spruce-rhododendron). The use of Miller's map in order to estimate spruce-fir forest area results in numbers based on local field observations rather than on theory meant to cover a widespread geographic area. Miller's boundaries were based on field plots and ocular field mapping of vegetation extant in 1935-1938. Taking a closeup view through Miller's map of the Great Smoky Mountains, several patterns emerge: (1) truncated boundaries in burned areas, (2) the unusual Raven Fork watershed with its high average elevation and abundance of spruce-covered slopes, and (3) the general topographically influenced position of spruce forests. For example, the mean draw position elevation of spruce in the Bradley Fork watershed was 5350 feet in contrast to 4500 feet on ridges. The detailed pattern of spruce-fir distribution shown on Miller's map precludes taking a single map contour as the lower elevational boundary of past or present spruce-fir vegetation.

Given the preceding discussion, the variability in spruce-fir areal estimates shown in Table 3 should not be unexpected.

As can be seen in Table 3, there is great disagreement as to both the prelogging and postlogging extent of spruce-fir vegetation in the Southern Appalachians. However, most pre-balsam woolly aphid authors (Clark 1954,

Table 3. Areal estimates of spruce-fir vegetation.

Source	Location	Vegetation Type*	Prelogging**	Postlogging**
Frothingham 1931	GRSM	Spruce		18,211
Saunders 1979	GRSM	Spruce-fir	6,013	3,665
Pyle 1984	GRSM	Spruce-fir	17,910	13,370***
Cruikshank 1941	Southern Appalachians apparently exclusive of GRSM	Spruce	60,704	9,308
Saunders 1979	Southern Appalachians exclusive of GRSM	Spruce, spruce-fir	8,264	3,216
Korstian	Southern Appalachians plus West Virginia	Spruce	404,694	40,469

*Terminology according to individual source.

**All area estimates were converted to hectares.

***Based on "spruce" type shown on Frank Miller's (1935-1938) vegetative type map.

Cruikshank 1941, Holmes 1911, Minckler 1940, and Schofield 1960) are in agreement with Korstian (1937) that "the depletion of the Southern Appalachian spruce forest is due chiefly to fire following destructive logging." The naturally moist conditions of spruce-fir forests resulted in a low incidence of natural fire. Logging removed trees that previously had helped create the cool damp microclimate of this forest type. Dry conditions following logging were further promoted by exposure of the thick layer of soil surface organic matter to sunlight (Korstian 1937). Unnaturally dry conditions coupled with high fuel loading from natural organic matter on the ground (plus addition of logging slash) made logged-over spruce-fir exceedingly susceptible to fire (Holmes 1911, Korstian 1937, Minckler 1940). Ignition was readily accomplished by sparks from coal-burning logging equipment, escaped campfires, or lightning. Fire following logging was so common that, according to Korstian (1937), "Practically all cut-over spruce lands have been burned one or more times."

One reason spruce-fir logging was destructive, especially in the early 1900s, was that most areas were then being logged for pulp by mechanized equipment. Trees of smaller diameter than sawtimber were acceptable for pulp, so more trees were removed and more low quality sites were logged. The mechanized logging equipment destroyed both the soil and advance reproduction. Such logging practices made the area prone to erosion as well as fire (Korstian 1937).

Not all logging in spruce-fir forests resulted in creation of sites unsuitable for spruce or fir regeneration. In fact, regeneration could be very good where fire was excluded (Holmes 1911, Minckler 1940). However, where spruce was removed from mixed hardwood/spruce forests, reproduction of spruce was not good due to thick hardwood litter (Korstian 1937, Schofield 1960).

Overall, the logging-induced loss of spruce-fir in the Southern Appalachians was due both to destruction of soil organic matter by logging slash fires (and, to some extent, erosion) and encroachment of logged sites by hardwoods.

In GRSM, spruce-fir logging operations were frequently followed by fire. Reasons for prevalence of fire have been discussed above. Fire may have been avoided in areas where high-grading took place. For example, in the East Prong of the Little River, areas such as Goshen Ridge were high-graded for spruce. Also, in the Cataloochee watershed, the area north and south of Poll's Gap was high-graded for valuable trees, including spruce. Though logged prior to the drought year of 1925, neither of these areas burned immediately following logging nor during 1925 when nearby areas burned.

The method used for this paper in determining extent of spruce-fir prior to logging did not address loss of spruce due to lack of regeneration in unburned spruce-hardwood or spruce-hemlock stands. This loss was probably not significant in the East Prong of the Little River nor in the upper reaches of Noland Creek, where a truncated spruce vegetation boundary on a minor ridges suggests removal of some outlying spruce. Loss of spruce may have been important in Straight Fork and possibly Bunches Creek and Cataloochee as well.

The ridge area (typed as northern hardwoods by Miller) near Poll's Gap between Cataloochee and Bunches Creeks is relatively low in elevation and somewhat far removed from the main crest of the Great Smoky Mountains. Whittaker (1956), in discussing the southwestern boundary of spruce distribution in GRSM, postulated that the climatic warming period some 4000 years ago drove the lower spruce boundary up to elevations of 5700 feet. This resulted in spruce having to reinvade lower areas from peaks of over 5700 feet. South of Poll's Gap there are no such peaks in GRSM. However, spruce stumps seen by the author indicate spruce was definitely present south of Poll's Gap. To determine if spruce was once important enough to have made the forest a spruce type by SAF standards would require field work that was beyond the scope of this report.

In the Straight Fork watershed there is record of "a good deal of spruce" taken from Dan's Branch in 1918-1919 (Lambert 1958). This area was shown as spruce on Miller's map. There is also record of logging (species not documented) in Balsam Corner Creek. Very little of this area was typed as spruce by Miller. I concluded that if a good deal of spruce removed from Dan's Branch did not change the vegetation type, it would not have done so in the adjacent unburned Balsam Corner Creek.

There is a weakness to this rationale in that Straight Fork is topographically different from the adjacent major watersheds which are covered or believed to have been previously forested in spruce. Both Dan's Branch and Balsam Corner Creek are quite concave in comparison to the adjacent headwaters of Cataloochee Creek. They are also lower in average elevation than Raven Fork watershed to the west. Further, Balsam Corner Creek is not nestled up to the mountain mass of the Smoky Mountains which supported well-developed spruce and fir. These topographic characteristics combined in Balsam Creek may have resulted in the presence of spruce, not as a dominant species but rather as large individuals in mixed stands with hardwoods or hemlock. If large amounts of spruce were selectively removed from such mixed hardwood or hemlock stands in Balsam Corner Branch, then the present pattern of hardwood and hemlock cover would indicate a loss of spruce. By this interpretation, Dan's Branch supports well-developed spruce because it is geographically closer to the main mountain mass than Balsam Corner Creek.

Because hardwood overstory encroachment resulting in conversion of cut-over mixed spruce-hardwood stands to hardwood types was not considered in the present author's estimates of spruce-fir loss in GRSM, the totals given for original spruce-fir area may be conservative in logged but unburned areas. Possibly significant logged but unburned areas in GRSM are Straight Fork and, to some extent, the Caldwell Fork portion of Cataloochee and the higher elevations of the southeastern corner of Bunches Creek.

In the Cataloochee watershed, E. J. Rosser (a logging engineer hired to cruise timber for the North Carolina Park Commission (NCPC)) gave a total of 1662 acres ($\approx$ 673 hectares) of "spruce soil" (Box 111-6, Suncrest Lumber Company Papers, GRSM Archives). This total included 422 acres ($\approx$ 171 hectares) of cut-over spruce in the Caldwell Fork drainage (i.e., in the area of aforementioned spruce and hardwood forest north and south of Poll's Gap). Four hundred twenty-two acres of spruce was a generous estimate for this area, considering its low elevation and the fact that the unlogged area to the south supports no spruce at all.

The 1240 acres ($\approx$ 502 hectares) remaining of Rosser's 1662 acres were located in the upper elevations of Big Cataloochee Creek. Based on Miller's map (which had no spruce in Caldwell Fork), the author estimated there were 404 hectares ($\approx$ 998 acres) of spruce fir extant in Cataloochee. It seems likely that Rosser included these 998 acres in his 1240, plus another 242 acres ($\approx$ 98 hectares) in burned or unburned areas that he had reason to believe could still support spruce.

A line of reasoning such as outlined above would have been likely for someone attempting to place a value on the land NCPC was acquiring. It does not help one working 50 years later in determination of the original extent of spruce-fir forest. The reconstruction of spruce-fir forest boundaries in Cataloochee Creek was based on the best historic evidence available (i.e., old maps and correspondence). The reconstructed boundaries represent, to a great extent, spruce boundaries defined by an anonymous mapmaker's unrecorded assumptions as to what constitutes spruce forest.

Estimation of loss of original spruce-fir forest cover in Big and Forney Creeks was based on estimation of prelogging-era spruce acreage. Again, the assumptions concerning what constitutes spruce forest, on which these estimates were made, are not known. Given that the estimates of spruce for these three watersheds

(Cataloochee, Big, and Forney Creeks) were made by people interested in exploitation of spruce, it is likely their estimates of spruce lands reflected the fact that, in some areas, spruce was the only tree worth cutting, even if it was not the dominant forest canopy cover. Consequently, the numbers derived from these estimates and given in Table I under "cut and burned" spruce-fir type may be overestimations for Cataloochee, Big, and Forney Creeks.

CONCLUSION

The halting of loggers in GRSM by the move to acquire timber company lands for the impending national park left extant 75 percent (13,370 hectares) of the estimated original 17,910 hectares of spruce-fir forest. This continuous spruce-fir cover, extending 56 kilometers along the crest of the Great Smoky Mountains, is the largest remaining block of the 404,694 hectares of spruce forest estimated by Korstian (1937) to have once covered the mountains of West Virginia, Virginia, Tennessee, and North Carolina. Most (12,100 hectares) of the spruce-fir left in GRSM was untouched by loggers and presents the ideal opportunity in which to study spruce-fir. Prior to recent disturbance of Fraser fir by the balsam woolly aphid, the Middle Prong watershed (in Tennessee) plus the adjacent Raven Fork and (in part) Straight Fork watersheds (in North Carolina) contained a large unbroken expanse of well-developed spruce-fir forest extending the full elevational range of the type in GRSM from below 4000 feet ($\approx$ 1220 meters) to over 6500 feet ($\approx$ 1980 meters). Even following balsam woolly aphid infestation, Raven Fork, with its high percentage of unlogged spruce-fir forest, remains overall the least disturbed watershed in GRSM.

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A STATUS REPORT ON BRYOPHYTES OF THE SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS

David K. Smith¹

Abstract. Bryophytes of the spruce-fir forests of the southern Appalachians are discussed in terms of historical, floristic, phytogeographic, and ecological knowledge. Rare and critical species commonly associated on fir will require careful monitoring to formulate management strategies for their preservation given the rapid decline of Fraser fir from balsam wooly aphid destruction of the forests.

Any discussion of the bryoflora of the spruce fir forests of the southern Appalachians is handicapped by the lack of information for many of the stands of spruce and fir isolated along the mountain crests of the region. The most complete knowledge available is that of the Great Smoky Mountains. While this discussion draws heavily upon the investigations of bryophytes in the spruce-fir of the Smokies, it is reasonable to assume that other areas will show a high degree of similarity when they become investigated.

The area described within the boundaries of the Great Smoky Mountains National Park represents a significant subset of the natural biological resources of the greater southern Appalachian region. This region has long been acclaimed for its high diversity of species reflecting a long, rather stable history, that has been periodically enriched by floral and faunal elements from adjacent regions. Sharp (1941) and others have attempted to account for the peculiar mixture of floristic elements in the Smokies by drawing attention to the influences of "prehistoric phenomena" (e.g. glaciation, oceanic transgression, and orogenic activity) that have variously affected earth history in eastern North America.

Focus has come to bear on the high elevation forests of the southern Appalachians because of accelerating destruction of Fraser fir by the balsam wooly aphid and general threats to this forest ecosystem resulting from concentrated loads of atmospheric pollutants. Spruce and fir forests are the dominant structural unit of the high montane portions of the southern Appalachians. The significance of this irreplaceable forest ecosystem is succinctly described by Sharp (1941) as "... the largest stands of relatively homogeneous nature are those of the Fraser fir on the high tops and of red spruce just below. These are the largest virgin areas of these species in the eastern United States."

¹ David K. Smith, Department of Botany, The University of Tennessee, Knoxville, Tennessee, 37916, U.S.A.

BRYOPHYTES OF THE SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS

Floristic and Phytogeographic Discussions

A total of 1690 species of bryophytes (plus nearly 400 subspecific taxa) are currently ascribed to North America (including the conterminous United States, Canada, Alaska, and the Aleutian Islands). Mosses comprise the majority with 1170 species (Crum, Steere, Anderson 1973) and the remaining 526 species are liverworts (Stotler and Stotler, 1977).

Sharp (1939) listed 426 species of bryophytes in eastern Tennessee alone, roughly equivalent to 25% of the total North American complement. Of these, more than 325 species including over 100 liverworts inhabit the Smokies (Sharp, 1941). Ecological investigations of bryophyte communities in the spruce-fir zone by Cain & Sharp (1938) treated 81 species, at that time, thought to represent approximately one-third of the total spruce-fir bryoflora. A more detailed study of the spruce-fir of the Smokies by Norris (1964) documented 203 species as present. A reasonable total estimate of the bryophytes of the spruce-fir might increase the number by no more than 15% to approximately 235 species.

The rich diversity of bryophytes in the spruce-fir is a distinctive feature of the forest. Furthermore, in abundance, they form a conspicuous part of the terrestrial and epiphytic flora. Species richness and abundance is a result of the cool moist climate and floristic enrichment by northern, southern and rare disjunctive elements.

Elements of boreal, coastal plain, and subtropical bryofloras have merged and persisted in numerous, narrowly defined habitats within the spruce-fir forest. By far the majority of species are allied to the north temperate or subarctic-alpine zones, especially the circumboreal belt of the northern coniferous forest.

Common and abundant species such as Dicranum spp., Polytrichum spp., Sphagnum spp., Hylocomium splendens (Hedw.) B.S.G., and Rhytidiadelphus triquetrus (Hedw.) Warnst. form extensive clumps and mats as is typical in the circumboreal forest. Less conspicuous and less abundant members of the northern forest and subarctic alliances of bryophytes include mosses such as Arctoa fulvella (Dicks.) B.S.G. [= Dicranum fulvellum, Sharp 1936b, unverified by Crum and Anderson 1981], Blindia acuta (Hedw.) B.S.G., Dichodontium pellucidum (Hedw.) Schimp. [= Oreoweisia serrulata, Sharp 1939b], Hygrohypnum spp., Hylocomium umbratum (Hedw.) B.S.G., Oncophorus wahlenbergii Brid., Paraleucobryum longifolium (Hedw.) Loeske, Pohlia cruda (Hedw.) Lindb., Pohlia elongata Hedw., Racomitrium aciculare (Hedw.) Brid., Racomitrium heterostichum (Hedw.) Brid., and Rhytidiadelphus squarrosus (Hedw.) Warnst. Liverworts such as Anastrophyllum minutum (Schreb.) Schust., Anastrophyllum michauxii (Web.) Buch ex Evans [= Sphenolobus michauxii, Norris 1964], Bazzania spp., Blepharostoma trichophyllum (L.) Dum., Cephalozia spp., Gymnocolea inflata (Huds.) Dum., Jungermannia atrovirens Dum. [= Jungermannia lanceolata, Norris 1964], Lophozia spp., Marsupella emarginata (Ehrh.) Dum., Tritomaria spp., and others are additional evidence of a northern influence.

Less extensive, although more critical, components of the spruce-fir bryoflora are associated with specific substrates. While many species form neat, predicable

associations, others are quite sporadic in their occurrences. In particular, rock outcrops and live Fraser fir are the most critical habitats.

Some of the more "precious" species exhibit wide-ranging, disjunctive world distributions. Others are rather narrow endemics of eastern montane North America or strictly of the southern Appalachians. Whereas, only a few species of eastern or all of North America, are restricted to the spruce-fir zone, a more substantial list of endemics and/or disjuncts can be constructed by including species predominantly of mid- and low elevations that also occur in the spruce-fir.

Only a few mosses fit patterns of major disjunction or endemism, although the number of examples of such among liverworts is more impressive. This, in part, reflects differences in the modern taxonomy of both groups as well as an especially rich biotypic liverwort flora within the southern Appalachian mountain system (including the eastern escarpment of the Blue Ridge gorge system).

Leptodontium excelsum (Sull.) Britt. and Pterigynandrum sharpii Crum et Anders. [= Hylocomium splendens var. tenuis, Sharp 1933] are the only two mosses that fit a strict pattern of spruce-fir endemism. Leptodontium is nearly restricted to the bark and twigs of Abies and Pterigynandrum appears exclusively on very moist, shaded rocks between 4000 and 5500 ft. elevations. Both species are regarded as rare within their total ranges.

Fissidens appalachensis Zand., Oncophorus ravii (Aust.) Grout, and Brachydontium trichodes (Web.) Milde are outstanding examples of unusual endemic and disjunct mosses in the spruce-fir forests. Fissidens, a southern Appalachian endemic, is an aquatic species originally described from and regarded as a mid-elevation Blue Ridge gorge species. It has been reported once from Roan Mountain, Tennessee above 5000 ft. elevation. Oncophorus is an Appalachian endemic, occurring in Pennsylvania and skipping south to the mid- and upper elevations of Georgia, North Carolina, South Carolina, and Tennessee. Brachydontium exhibits a sporadic and disjunctive distribution (the peaks of North Carolina and Tennessee, New Hampshire, Washington, northern and central Europe, British Isles, and Caucasus) that may be explained as a Tertiary relict.

A more peculiar pattern of distribution is shown by Isothecium stoloniferum Brid. (sensu Crum & Anderson 1981, reported as Pseudisothecium myosuroides Gott., Sharp 1936b). This moss is common and widely distributed in western North America, becoming less frequent in the eastern portion of its range, there occurring in eastern Canada, upper New England, and jumping south to the spruce-fir of Tennessee and North Carolina. Closely related if not identical, Isothecium myosuroides Brid. occurs in similar habitats of northern, central, and western Europe (Crum & Anderson, 1981).

A number of liverworts exhibit somewhat parallel patterns of distribution similar to the moss endemics and disjuncts.

Bazzania nudicaulis Evans is the only example of a strict spruce-fir endemic, occurring only on the highest peaks mostly above 5500 ft. elevation in the southern Appalachians.

Several other southern Appalachian endemics are more generally distributed among hardwood forests of the mid- and lower elevations, but range upwards in

elevation to the lower fringes or well into the spruce-fir zone. As examples of this distributional pattern one may cite Drepanolejeunea appalachiana Schust., Lejeunea ruthii (Evans) Schust., Plagiochila caduciloba Blomq., P. sharpii Blomq., and P. sullivanii Gott. ex Evans.

Three additional species exhibit even wider patterns of endemism. Lejeunea lamacerina subsp. gemminata Schust. and Plagiochila austinii Evans are confined to the Appalachian region, extending from Nova Scotia in the north (infrequent) south through New England, the central Appalachians and into Georgia, North Carolina, and Tennessee. Leucolejeunea clypeata (Schwein.) Evans fits into a pattern of eastern North American distribution. Schuster (1980) considered this species as Appalachian with a post-Pleistocene radiation west to Oklahoma, east throughout the Piedmont and Coastal Plain, and south into Florida.

Several species of North American or wider patterns of disjunct distribution further enrich the spruce-fir bryoflora. Marsupella funckii (Web. et Mohr) Dum. occurs in the southern Appalachians and again in the Great Lakes Region. Sphenolobopsis pearsonii (Spr.) Schust. & Kitag. and Plagiochila corniculata (Dum.) Dum. occur at high elevations in the southern Appalachians and in western Europe; the former species also occurring in the Pacific Northwest and Japan. Acrobolbus ciliatus (Mitt.) Schiffn. [= Acrobolbus rhizophyllus Sharp 1936a] is considered an ancient species of Tertiary age, widely disjunct and occurring in Himalaya, Japan, Aleutian Islands, and the southern Appalachians.

Rock outcrops, although a fractional component of available substrate in the spruce-fir zone, contain one of the most unique communities of bryophytes. Schuster (1974) stressed the critical importance of liverwort associations found on the highly exposed crevices and surfaces of rocks at high elevations in the southern Appalachians. Gymnomitrium laceratum (Steph.) Horik., Marsupella funckii, Marsupella paroica Schust., Cephaloziella massalongi (Spruce) K. Muell., Microlepidozia sylvatica (Evans) Joerg., Mylia taylori (Hook.) S.F. Gray, and Nardia scalaris (Schrad.) S.F. Gray form an important association of species with endemic, disjunctive, widespread, predominantly northern and Coastal Plain distributions.

Gymnomitrium laceratum is extremely rare with a North American distribution that is restricted to four localities in Tennessee (Mt. LeConte and Mt. Kephart) (Schuster 1974). It is an extreme disjunct, occurring elsewhere in mountainous regions of Japan, tropical east and south Africa, South America, and Mexico. Nearly parallel patterns of distribution are shared in this association by Marsupella funckii, Cephaloziella massalongi, and Nardia scalaris, but all three lacking in the Southern Hemisphere (Schuster 1974). Marsupella paroica is an eastern North American endemic centered in the southern Appalachians where it occurs from the mid-elevational deciduous (cool and moist) to the upper limits of spruce-fir forests and jumping to a few locations in the Great Lakes Region. Mylia taylori and Nardia scalaris illustrate circumboreal patterns of distribution with sporadic occurrences in all continents of the Northern Hemisphere. In North America they follow "oceanic tendencies" indicated by occurrences in the Pacific Northwest (including Alaska) and Atlantic Coastal upper East and Canada. Their occurrence in the southern Appalachian spruce-fir is regarded by Schuster (1969) as relict. Microlepidozia sylvatica and Cephaloziella massalongi are more limited in their distributions. Both exhibit trans-Atlantic distributions, the former more abundant in eastern North America where it is common in the Coastal Plain and penetrating to the high ridges

of the Appalachian Plateau; the latter most common in Europe and reported in North America only from Vermont and Tennessee.

Live Fraser fir must be regarded as the most critical habitat of the spruce-fir forest. Not only is fir the dominant canopy species (Cain 1935) above 6000 ft. elevation, the bole, branch and twig flora of bryophytes and lichens is extremely rich, distinctive, and often a restrictive substrate.

Table I lists 36 species of mosses and liverworts that frequently occur growing on the bark of fir. Of these, two mosses, Leptodontium excelsum and Zygodon viridissimus (Dicks.) Brid., and four liverworts Bazzania nudicaulis, Leptoscyphus cuneifolius (Hook.) Mitt., Plagiochila corniculata, and Sphenolobopsis pearsonii are nearly restricted to fir. Of these species not previously discussed, Leptoscyphus is considered by Schuster (1980) to be an ancient oceanic species confined in North America to the high elevation southern Appalachians, elsewhere with a north and south (antipodal) oceanic and montane tropical distribution. Zygodon is an equally widely disjunct species occurring in Michigan, Nova Scotia, Quebec, northern and central Europe, Japan, Himalaya, and Venezuela (Crum & Anderson, 1981).

Table I. Bryophytes reported on Fraser Fir (compiled from Cain & Sharp 1938, Norris 1964, Schuster 1969, 1974, 1980).

HEPATICAЕ	MUSCI
<u>Anastropyllum michauxii</u> (Web.) Buch ex Evans	<u>Brotherella recurvans</u> (Michx.) Fleisch.
<u>Bazzania denudata</u> (Tor. ex Gott. et. al.) Trev.	<u>Dicranum fuscescens</u> Turn.
<u>Bazzania nudicaulis</u> Evans	<u>Hylocomium splendens</u> (Hedw.) B.S.G.
<u>Bazzania trilobata</u> (L.) S. Gray	<u>Hylocomium umbratum</u> (Hedw.) B.S.G.
<u>Blepharostoma trichophyllum</u> (L.) Dum.	<u>Hypnum pallescens</u> (Hedw.) P.- Beauv.
<u>Cephalozia lunulifolia</u> (Dum.) Dum.	<u>Leptodontium excelsum</u> (Sull.) Britt.
<u>Frullania asagrayana</u> Mont.	<u>Paraleucobryum longifolium</u> (Hedw.) Loeske
<u>Frullania oakesiana</u> Aust.	<u>Plagiothecium laetum</u> B.S.G.
<u>Geocalyx graveolens</u> (Schrad.) Nees	<u>Polytrichum ohioense</u> Ren. & Card.
<u>Harpalejeunea ovata</u> (Hook.) Schiffn.	<u>Ptilium crista-castrensis</u> (Hedw.) De Not.
<u>Herberta tenuis</u> Evans	<u>Rhytidiadelphus triquetrus</u> (Hedw.) Warnst.
<u>Jamesoniella autumnalis</u> (D.C.) Steph.	<u>Tetraphis pellucida</u> Hedw.
<u>Lejeunea ruthii</u> (Evans) Schust.	<u>Thuidium delicatulum</u> (Hedw.) B.S.G.
<u>Lejeunea ulicina</u> (Tayl.) Gott.	<u>Ulota crispa</u> (Hedw.) Brid.
<u>Lepidozia reptans</u> (L.) Dum.	<u>Zygodon viridissimus</u> (Dicks.) Brid.
<u>Leptoscyphus cuneifolius</u> (Hook.) Mitt.	
<u>Lophozia incisa</u> (Schrad.) Dum.	
<u>Metzgeria temperata</u> Kuwah.	
<u>Plagiochila corniculata</u> (Dum.) Dum.	
<u>Plagiochila sharpii</u> Blomq.	
<u>Sphenolobopsis pearsonii</u> (Spruce) Schust.	
<u>Tritomaria exsecta</u> (Schrad.) Loeske	

Ecology and Community Structure

Two studies stand as major investigations of bryophytes in the spruce-fir forests. Cain and Sharp (1938) described bryophytic unions of the Great Smokies based upon quadrat and map samples. Their descriptions of spruce-fir communities were amplified considerably by Norris (1964) who devoted his investigation exclusively to the spruce-fir zone.

The study by Cain and Sharp (1938) delineated bryophyte unions among three principal forest associations of the spruce-fir zone. They sampled Fraser fir forest on Mt. Leconte, red spruce forest on Mt. Mingus, and American beech forest on Trillium Gap. Fourteen unions and several subordinate facies and unstructured associules were distributed among the three forest types: eight unions within the Abietum fraseri Association, four unions within the Piceetum rubentis Association, and two unions within the Fagetum grandifloriae subalpinum Association.

A total of 81 species sampled in their investigation were distributed among the three forest associations. Forty-seven species occurred in the Fraser fir forest, 27 species (only two not found under fir) in spruce forest, and 28 species (22 exclusive to beech forest) in beech forest. These figures suggest that nearly half of the bryophytes occurring in fir forest might be severely impacted by altering the canopy structure. The high number of species exclusive to beech forests reflects the northern and cove hardwoods bryofloristic influence.

The significance of fir as an important substrate is attested to by the fact that five of the eight unions of this association occurred on either live, standing dead, or fallen trees. Standing dead or fallen fir had the highest diversity of species (26) distributed among four unions; but these values reflect compositional changes during stages of decay and ecesis. Living fir supported two unions and one facie along with 22 associated species.

Norris' study (1964) is more detailed than that of Cain and Sharp. His study increased the species list to 203 species and delineated 22 unions for the spruce-fir forest. While this study attempted to classify bryophytes objectively on the basis of species associations, one must refer to descriptions of each union to determine substrate identities. Unstated by Norris is the fact that 31 species were restricted to one or two unions or substrates; giving notice to the rather narrow ecological limits for those species.

Impacts From Fraser Fir Deforestation

The depletion of Fraser fir in the southern Appalachians poses a major threat to the rich diversity and abundance of bryophytes of high elevation forests. Species diversity and abundance is a direct reflection of microclimatic and substrate diversity. Live, standing dead, and fallen fir are important substrates that cycle through a healthy enduring forest. A continuum of combinations of both moisture and illumination is created as natural death and replacement occurs in fir forest. Small windows form in the canopy as trees die and defoliate. The dimensions of openings increase when trees fall, allowing greater penetration of light and further shifts in moisture at the forest floor and along the edges of openings. Decortication and humification of fir logs represent the final stages of substrate cycling.

Death of large tracts of mature fir will undoubtedly shift the equilibrium of abiotic factors in the primeval forest. Illumination values will increase and superficial drying of the forest floor will ensue. Initially, standing dead trees will dominate. Finally, as limbs prune and boles fall, the forest floor will be smothered by the skeletons of the original forest. Processes of decay and bryophyte succession on logs will dominate if conditions of moisture and light are not too extreme. The canopy will be replaced by a more heterogeneous mixture of northern hardwoods and spruce, ultimately favoring bryophytes of those forest types.

It is this writer's opinion that rapid and large scale death of mature fir forest will severely impact the distinctive bryoflora of fir. The abundance of rare species will decline and some extirpations are probable.

Research priorities

The investigations of Cain and Sharp (1938) and Norris (1964) have provided an excellent working knowledge of the bryoflora and its community structure within the spruce-fir that predate the infestations by the balsam woolly aphid. There still remains room for more detailed studies of bryophytes in pure fir stands to more carefully assess total diversity, abundance, and ecosystem role.

Epiphytic, terrestrial, and epilithic habitats of fir forest should be restudied in intact forest and compared to parallel studies of lightly and heavily disturbed forest. A most important consideration should be the determination of rates and degrees of bryophyte depletion on live fir. Secondary considerations should be given to evaluating alternate hosting of rare epiphytic species and changes in the abundance of terricolous and epilithic species.

Virtually nothing is known concerning nutrient partitioning, cycling, water relations, or the bryophyte microcosm in the spruce-fir. It has been speculated that epiphytic species act as wicks or nets to entrap moisture in fog belts. This undoubtedly benefits the bryophytes by maintaining compensation levels of hydration, but may also act as a drip system for irrigating the forest floor. Thick mats of mosses on the forest floor may function as sponges to retard moisture and nutrient loss. Bryophyte-microfaunal-microfloral associations are well known to bryophyte taxonomists. Only a few studies have actually been conducted to investigate these microscopic communities, none of which treat habitats in spruce-fir.

Although the effects of atmospheric pollution on the vigor of bryophytes has not been documented for the spruce-fir forest, this subject should be examined along with well-documented effects known to adversely affect lichens. It has been clearly demonstrated that terrestrial bryophytes concentrate heavy metal pollutants and such a role for spruce-fir bryophytes should be examined.

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LICHENS OF THE SOUTHERN APPALACHIAN MOUNTAIN SPRUCE-FIR ZONE
AND SOME UNANSWERED ECOLOGICAL QUESTIONS

Jonathan P. Dey¹

Abstract.--Species composition, general substrate affinities, floristic relationships, and uniqueness of the macrolichen flora of the high-mountain areas of the southern Appalachian Mountains are known. Attention needs to be given to the microlichen flora of the region and to obtaining quantitative data on the structure of lichen communities and their importance in local ecosystems. The consequences of the balsam woolly aphids' continuing destruction of Fraser fir trees on the composition and structure of lichen communities in the spruce-fir forest need to be ascertained. Lichens should be utilized as biomonitors of air pollution in the spruce-fir zone.

Additional keywords: Abies fraseri, Adelges piceae, lichens as biomonitors, air pollution and lichens, island biogeography

At various sites within the southern Appalachian spruce-fir zone, lichenized ascomycete fungi form a very conspicuous part of the local vegetation as epiphytes on coniferous and deciduous trees, as ground cover organisms, or as rock cover organisms. Any consideration of the status of lichens or the current role of lichens in the southern Appalachian spruce-fir ecosystem must include an analysis of what is known about the lichens locally and what still needs to be determined about them. With the conspicuous, ongoing destruction of Fraser fir [Abies fraseri (Pursh) Poir.] by the balsam woolly aphid (Adelges piceae Ratz.) and the subtle effects of air pollution both threatening to irreversibly alter the southern Appalachian spruce-fir ecosystem, it is timely to evaluate the lichens and their role in the ecosystem.

LICHENS OF THE SOUTHERN APPALACHIAN SPRUCE-FIR ZONE

Our knowledge of the fruticose and foliose macrolichen flora of the southern Appalachian spruce-fir zone is excellent. The studies by Degelius (1941), Moore (1963), Perry and Moore (1969), and Dey (1978) are the most comprehensive ones of the region. In the only study specifically of the lichen flora of the high-mountain areas of the southern Appalachians above 1676 m (5500 ft.), Dey reported 178 macrolichen species. Subsequent refinement of taxonomic concepts brings the total to at least 181 macrolichens in the high-mountain areas with the addition of Cetrelia monochorum (Zahlbr.) Culb. & Culb., Hypogymnia appalachensis Pike, and Hypotrachyna showmanii Hale to the list. Most remaining taxonomic problems are restricted to the genus Usnea.

In contrast, our knowledge of the crustose microlichen flora of the spruce-fir zone is very uneven. The preliminary annotated list of crustose

¹Associate Professor of Biology, Department of Biology, Illinois Wesleyan University, Bloomington, Illinois, 61701, U.S.A.

species in the Great Smoky Mountains National Park prepared by Degelius (1941) is particularly valuable. Many lichenologists have made general collecting trips in the southern Appalachians including the spruce-fir zone and have identified crustose specimens. However, their collections have been used primarily as regional reference specimens in herbaria or as research specimens for monographic studies rather than as the basis of a comprehensive investigation of the southern Appalachian crustose lichen flora.

Species-substrate and species-plant community relationships

Although collections of southern Appalachian macrolichens have never been made using a statistically valid sampling method to provide sound quantitative data of the lichen vegetation, examination of label data of macrolichen specimens housed in the Duke University herbarium provide considerable information about species-substrate relationships and species-vascular plant community relationships of the macrolichens in the southern Appalachian spruce-fir zone. The following observations will supplement and complement those made previously by Dey (1978).

In a consideration of the spruce-fir ecosystem, epiphytic macrolichens which occur on Fraser fir, red spruce (Picea rubens Sarg.), mountain ash (Sorbus americana Marsh.), and yellow birch (Betula lutea Michx.) are probably of greatest interest and importance. Fraser fir and red spruce, the only conifer trees, dominate the forest and its canopy while mountain ash and yellow birch, the most important deciduous trees, are only of minor significance in the forest canopy. Of these four trees in the spruce-fir forest, only the yellow birch is an important tree species in the deciduous forest beneath the spruce-fir forest and the various fire cherry communities (see Ramseur, 1960) successional to the spruce-fir forest. Consequently, examination of occurrence records of macrolichens on these four tree species will provide useful information about the corticolous macrolichen flora of the spruce-fir forest. That the diversity and frequency of lichens on Fraser fir are much greater than on red spruce is illustrated in Table 1. Evidently physical characteristics, such as flakiness, and chemical characteristics of

Table 1. Numbers of macrolichen species epiphytic on Fraser fir, red spruce, mountain ash, and yellow birch trees in the southern Appalachian high-mountain areas

Substrate tree species	Number of lichen species collected				
	Total	Twice of more	Once only	Not on fir	Not on fir & other 2 trees
Fraser fir	66	59	7	--	--
Red spruce	52	31	21	3	1
Mountain ash	63	44	19	27	3
Yellow birch	74	61	13	30	6
Four trees combined	100	--	--	--	--

the bark greatly reduce the ability of lichens both to colonize and to persist on red spruce as compared to their ability to live on the bark of Fraser fir (Dey, 1978). Virtually all non-rare macrolichens which occur on spruce also occur with equal or greater frequency on fir with the exception of Parmeliopsis aleurites (Ach.) Nyl. and Pseudevernia consocians (Vain.) Hale & Culb., two species also common at lower elevations in the southern Appalachians on pine (Pinus spp.) trees. Some of the 67 macrolichen species occurring on spruce and fir trees are found more frequently growing on deciduous trees such as mountain ash and yellow birch. Of the 100 corticolous macrolichens epiphytic on the four tree species, 33 species occur only on the mountain ash and/or yellow birch trees. Therefore, a significant portion of the epiphytic macrolichen lichens in the southern Appalachian spruce-fir forest grow chiefly on the scattered deciduous trees in the forest.

In contrast to numbers of macrolichens per tree species, examination of Tables 2 and 3 show that only 12 of the 100 corticolous species are strongly restricted (over 90% of collected specimens) to spruce-fir forest communities and an additional 11 species are mainly restricted (over 90% of collected specimens) to spruce-fir forest and successional fire cherry communities.

Table 2. Macrolichen species in which 90% or more of the specimens collected in the southern Appalachian high-mountain areas were collected in the spruce-fir forest

<u>Alectoria fallacina</u> Mot.	<u>Hypotrachyna croceopustulata</u>
<u>Bryoria nadvornikiana</u> (Gyeln.) Brodo & Hawksw.	(Kurok.) Hale
<u>B. tenuis</u> (Dahl.) Brodo & Hawksw.	<u>H. densirhizinata</u> (Kurok.) Hale
<u>B. trichodes</u> var. <u>americana</u> (Mot.) Brodo & Hawksw.	<u>H. imbricatula</u> (Zahlbr.) Hale
<u>Hypogymnia vittata</u> (Ach.) Gas.	<u>H. laevigata</u> (Sm.) Hale
	<u>H. oostingii</u> (Dey) Hale
	<u>H. producta</u> Hale
	<u>H. prolongata</u> (Kurok.) Hale

Table 3. Macrolichen species in which 90% or more of the specimens collected in the southern Appalachian high-mountain areas were collected in the spruce-fir forest and fire cherry communities (when taken together, not either by itself)

<u>Bryoria bicolor</u> (Ehrh.) Brodo & Hawksw.	<u>Parmelia saxatilis</u> (L.) Ach.
<u>Hypotrachyna gondylophora</u> (Hale) Hale	<u>Parmelina dissecta</u> (Nyl.) Hale
<u>H. thysanota</u> (Kurok.) Hale	<u>Platismatia glauca</u> (L.) Culb. & Culb.
<u>H. virginica</u> (Hale) Hale	<u>Pseudevernia cladonia</u> (Tuck.) Hale & Culb.
<u>Menegazzia terebrata</u> (Hoffm.) Mass.	<u>Usnea confusa</u> Asah.
	<u>U. trichodea</u> Ach.

Most of these species are found predominantly on the coniferous spruce and fir trees, but some are not infrequently also collected off deciduous trees and rock. Ramseur (1960) has estimated that together the spruce-fir forest and fire cherry communities occupy 90% of the total area of the southern Appalachian high-mountain areas. See Dey (1978) for a discussion of other lichen-vascular plant community relationships in the high-mountain areas.

Table 4 summarizes the substrate relationships of the macrolichens in the southern Appalachian high-mountain areas. Having already discussed the corticolous species with emphasis on species occurring in the spruce-fir forest, it is interesting to note that of the terricolous and lignicolous species only Cladonia gracilis (L.) Willd. and C. digitata (L.) Hoffm. are restricted to the spruce-fir forest. Similarly, of the saxicolous species

Table 4. Numbers of macrolichen species on various substrates in the high-mountain areas above 1676 m in the southern Appalachians

Substrate	Number of species ^a
Coniferous trees	62
Conifer trees only	5
Conifer and deciduous trees	15
Conifer and deciduous trees and rock (± wood ± soil)	37
Conifer trees and rock (± wood and soil)	5
Deciduous trees	109
Deciduous trees only	40
Deciduous and conifer trees	15
Deciduous and conifer trees and rock (± wood ± soil)	37
Deciduous trees and rock (± soil ± wood)	17
All trees	119
Rock	99
Rock only	27
Rock and trees (± soil ± wood)	37
Rock and soil	8
Rock and wood (± soil)	7
Soil	39
Soil only	10
Soil and rock (± wood)	14
Soil, rock and trees (± wood)	12
Soil and wood	3
Wood (rotting logs and stumps primarily)	35
Wood only	4
Wood and rock or soil	4
Wood, rock and trees (± soil)	21
Wood, rock and soil	6
All substrates	178

^aRecognized by Dey (1978) and collected off substrate(s) at least twice (or once if less than ten total collections of the species were taken from all substrates in southern Appalachian high-mountain areas)

Baeomyces rufus (Huds.) Rebert. is the only species characteristically growing on small shady rocks within the spruce-fir forest proper while the other common saxicolous species -- Umbilicaria spp., Lasallia spp., Xanthoparmelia spp., Stereocaulon spp., and Parmelia stygia (L.) Ach.--are found on rock outcrops within a variety of vascular plant communities.

Macrolichen species diversity within high-mountain areas

Specimens cited in Dey (1975) provide information concerning macrolichen species diversity within the various southern Appalachian high-mountain areas above 1676 m (Table 5). Except for the smallest high-mountain areas, the decrease in macrolichen species diversity is positively correlated with the decreasing size of the various high-mountain areas. For the seven largest areas, the species-area curve, when both are plotted on log scales, is a straight line with a slope (Z) of 0.14 ($r = 0.98$). If data for all ten high-mountain areas are plotted, the regression line has a lower slope ($Z = 0.12$ with $r = 0.86$). The decrease in macrolichen species diversity also reflects decreasing habitat diversity within the individual high-mountain areas as measured by the number of vascular plant communities recognized by Ramseur (1960) for each high-mountain area (Table 5). Grandfather Mt. and Mt. Pisgah are the two exceptions. These two high-mountain areas have greater macrolichen species diversities than either Mt. Rogers or White Top Mt., two areas with equal or greater numbers of vascular plant communities than the former. Perhaps the greater areas of exposed rock and rock outcrops available for saxicolous lichens on Grandfather Mt. and Mt. Pisgah account for their high species diversities.

Table 5. Macrolichen species diversity within the high-mountain areas above 1676 m in the southern Appalachians

High-mountain area	Size of area (km ²) above 1676 m	Vascular plants (Ramseur, 1960)		Macrolichens (Dey, 1978)
		No. spp.	No. community types	No. spp.
Great Smoky Mts.	49.0	194	8	149
Balsam Mts.	29.4	244	8	139
Black Mts.	24.8	130	8	129
Roan Mt.	8.8	105	6	119
Plott Balsams	5.7	100	6	99
Great Craggies	2.0	98	5	91
Grandfather Mt.	1.1	58	3	87
Mt. Rogers	0.4	43	3	48
Mt. Pisgah	0.05	114	2	78
White Top Mt.	0.03	76	4	60
Totals	121.1	366	8	178

For macrolichens the southern Appalachian high-mountain areas above 1676 m, which includes most of the spruce-fir forest stands of the region, can not be considered continental habitat islands which are effectively isolated from one another. Many of the macrolichen species found in high-mountain areas have continuous distributions at lower elevations in the mountains. Besides many terricolous and saxicolous species, this includes many corticolous species which grow on a combination of deciduous tree species whose overlapping elevational ranges extend upward from low-elevation deciduous forests up into the high-elevation spruce-fir and deciduous tree forests. Thus, it is not surprising that the Z values of the macrolichen species-area curves given above fall within the normal range of Z values of 0.12 to 0.17 reported for areas of continental mainland (Gorman, 1979). This is in sharp contrast to the relationship between the numbers of vascular plant species in the various high-mountain areas reported by Ramseur in 1960 (Table 5) and the sizes of the high-mountain areas. The Z values of the species-area curves using data from the seven largest areas is 0.30 ($r = 0.89$) and using data from the eight largest areas is 0.31 ($r = 0.94$). Both of these Z values fall within the reported range of Z values (0.24 to 0.34) for real islands and continental habitat islands (Gorman, 1979). Therefore, the eight largest areas of the southern Appalachian high-mountain areas can be considered to be continental habitat islands for vascular plants but not for macrolichens. Interestingly, the numbers of species of both macrolichens and vascular plants in the three smallest high-mountain areas--Mt. Rogers, Mt. Pisgah and White Top Mt.--are negatively correlated with the sizes of the areas with regression lines of slope (Z) -0.12 ($r = -0.70$) and of slope -0.27 ($r = -0.78$) respectively.

Geographic relationships

Seven of the 178 macrolichen species recognized by Dey in 1978 are narrowly endemic to the Appalachian Mountains. Five other species found in the high-mountain areas are essentially Appalachian in distribution but range into the adjacent Great Lakes region. Of these endemics only Alectoria fallacina Mot. and Hypotrachyna virginica (Hale) Hale are among the corticolous species collected over 90% of the time from spruce-fir forest only or from spruce-fir forests and fire cherry communities. Another 18 species are known in North America north of Mexico only in the Appalachians, but have disjunctive representatives in other countries or continents (Dey, 1978). Since the montane southern Appalachian spruce-fir forests have geographic affinities with the northern boreal coniferous forests, it is not surprising that the northern floristic element is well represented in the lichen flora. It should be noted, moreover, that many of the northern species are not restricted in their southern Appalachian distributions to the spruce-fir forests and often occur with equal frequency in other community types both at higher and lower elevations in the mountains. While many of the species with southern or tropical affinities also have broad distributions at both lower and higher elevations in the mountains and in surrounding low lands, there is a group of Hypotrachyna species--H. croceopustulata, H. densirhizinata, H. gondylophora, H. imbricatula, H. oostingii, H. producta, H. prolongata, H. rockii (Zahlbr.) Hale, and H. thysanota--which are particularly interesting and restricted locally to the

spruce-fir forest and successional fire cherry communities at high elevations. These nine Hypotrachyna species are known in North America north of Mexico only in the southern Appalachian high-mountain areas, and they have disjunctive representatives in tropical America or in South America and/or Africa (Dey, 1979). Other interesting disjuncts in the high-mountain areas, but not necessarily organisms of the spruce-fir forest or restricted to the high-mountain areas in the southern Appalachians, include Anzia americana Yosh. & Sharp, Hypotrachyna sinuosa (Sm.) Hale, Pseudevernia cladonia (Tuck.) Hale & Culb., Stereocaulon microcarpum Mull. Arg. [= S. ramulosum (Sw.) Rausch. in Dey, 1979], S. tennesseense Magn., Sticta limbata (Sm.) Ach., Umbilicaria caroliniana Tuck., and Xanthoparmelia incurva (Pers.) Hale. See Dey (1976 & 1979) for the distribution patterns of these and other interesting southern Appalachian macrolichens.

THREATS TO THE LICHENS OF THE SPRUCE-FIR ECOSYSTEM

Balsam woolly aphid

The balsam woolly aphid has replaced fire and logging as the most destructive force threatening the southern Appalachian spruce-fir forest. The ongoing destruction of the Fraser fir trees by the aphid may have serious affects on the corticolous lichen flora of the southern Appalachian spruce-fir forest and particularly some of the noteworthy disjunctive Hypotrachyna species listed previously. All of these species are most readily collected off Fraser fir (except H. producta collected locally only once and then off a spruce tree), usually infrequently to rarely off spruce, and for some species rarely or apparently not at all off either deciduous trees or rocks. Some of these species may be vulnerable for local extinction as the balsam woolly aphid destroys their most preferred substrate tree (Dey, 1974). Besides the destruction of the substrate fir trees, the microclimatic changes resulting from the opening up of the canopy as the fir trees die may have deleterious effects on a lichen's growth rate, reproductive rate, thallus persistence, and ability to colonize substrates. Such microclimatic changes may thus affect the ability of various lichen species to effectively utilize the remaining spruce trees as a substrate and possibly may even affect the future of the remaining spruce trees in some areas by affecting spruce reproduction and/or disease resistance. There are numerous questions which might be asked about how the balsam woolly aphid will indirectly affect the ecology of the local lichens of the spruce-fir forest.

Air pollution

Species of lichens are well known to be differentially sensitive to various air pollutants such as oxidants, sulfur dioxide, hydrogen flouride and trace elements, with a few species being very tolerant and others being at least as sensitive (if not more sensitive) to air pollution as the most sensitive higher plants (Nash, 1976; Nash and Sigal, 1980). Contrasting some of the results of Degelius (1941) with those of Dey (1978), it appears likely that air pollution may be responsible for some changes in the macrolichen flora of the spruce-fir forest during the past 35 years. For example, Degelius indicates small, sterile specimens of Erioderma mollissimum (Samp.) DuRietz were found on mountain ash and Fraser fir trees in the spruce-fir

forest, but I did not find any during my collecting in the spruce-fir forest (the species is still rarely collected at lower elevations in the Great Smoky Mountains). More striking was the remarkable decrease in thallus size and fertility seen in my collections of the lichen Sticta fuliginosa (Dicks.) Ach. in the early 1970's compared to Degelius' collections in 1939 (Dey, unpublished). Reduction in luxuriance (i.e., cover and size of specimens) and fertility (i.e., frequency of production of ascocarps) are common symptoms in macrolichens and microlichens sensitive to air pollutants before the specimens are eliminated altogether from a polluted area (Hawksworth, Rose and Coppins, 1973). Studies on the interactions of lichens and air pollutants are currently an area of intense investigation worldwide (Ferry, Baddeley and Hawksworth, 1973; Nash and Sigal, 1980).

AREAS WHERE MORE INFORMATION IS NEEDED

Although the composition and geographic relationships of the macrolichen flora of the southern Appalachian spruce-fir forests are known, there are many areas where further information is needed to allow us to better understand the total lichen flora and its local ecology as follows:

1) Microlichen flora

A comprehensive floristic study of the crustose lichens of the southern Appalachian spruce-fir forest and other community types in the high-mountain areas is needed. The catalog of lichens from the State of Tennessee prepared by Skorepa (1972) and the initial study of Degelius (1941) will be helpful to anyone beginning a study of these crustose lichens.

2) Quantitative sampling and analysis of the lichen vegetation

In order to make empirical statements about the lichen vegetation, lichen communities, and ecological processes involving lichens within the spruce-fir ecosystem, quantitative studies must be undertaken and analyzed. Except for the corticolous lichens in the tree canopy, the lichen vegetation is sparse in most closed canopied spruce-fir forest stands growing on broad rounded mountain tops and gentle slopes, the sites best suited for the development of the forest. Therefore, to obtain a true appreciation of the importance of the lichens in the spruce-fir forest, it is also necessary to sample the forest on poorer sites such as along narrow ridge tops and steep slopes. Here the forest is poorly developed; the canopy is more open, but the lichen vegetation is more luxuriant. In any case, lichen biomass and primary productivity are likely to be very small or insignificant compared to that of higher plants, but the lichens may not be insignificant.

3) Role of lichens in local mineral cycling

In some ecosystems lichens are important in mineral cycling. Not only do they have the ability to alter precipitation chemistry (Lang, Reiners and Heier, 1976), but those lichens containing blue-green algae also have the ability to fix atmospheric nitrogen (Nash and Sigal, 1980). For example, Pike (1978) studied three ecosystems, comparing Douglas fir [Pseudotsuga menziesii (Mirb.) Franco], balsam fir [Abies balsamea (L.) Mill.] and Oregon

Oak (*Quercus garryana* Dougl.) woodland ecosystems, and found that epiphytic lichens seldom accounted for more than 10% of the annual, above-ground turnover of minerals. According to him, lichens were relatively more important in the cycling of N than of P and K and of least importance in the cycling of Ca and Mg. The only study of mineral cycling by lichens in the southern Appalachian forests was conducted by Becker (1980) who studied nitrogen fixation by lichens. In his sampling of two southern Appalachian spruce forests, the few nitrogen-fixing lichens he encountered grew only on the relatively few deciduous trees in these forests and not on the conifers. He concluded that nitrogen fixation by lichens in the spruce forests of the southern Appalachians was very insignificant. Systems ecologists will have to decide whether or not further analysis of mineral cycling would be worthwhile.

4) Effects of air pollution and the utilization of lichens as biomonitors of air pollution

The need for studies to determine the effects of air pollution on the lichen flora of the southern Appalachians has already been mentioned.

Lichens are useful as biomonitors of air pollution, and they should be used to document the magnitude of the air pollution problems in the southern Appalachians. Recognition of the fact that lichens could be useful as biomonitors comes from field observations of the differential sensitivity of species of lichens to various air pollutants, from laboratory studies in which a similar degree of differential sensitivity of the species to specific pollutants was confirmed, and from field studies documenting lichen recovery in areas following pollution abatement (Nash and Sigal, 1980). Examples of lichen recovery include the fairly rapid reinvasion of *Lecanora muralis* (Schreb.) Rabenh. into an urban area in southern England following a reduction of atmospheric sulfur dioxide (Seaward, 1976) and recolonization by *Pseudoparmelia caperata* (L.) Hale into areas around a coal-fired generating power plant in Ohio within four years of the installation of tall emission stacks allowing a more rapid dispersal of sulfur dioxide from the plant site (Showman, 1981). Baseline studies to determine which sensitive lichens should be used as biomonitoring organisms in the southern Appalachians should be undertaken now.

While lichens have been shown to be too effective at accumulating lead to be useful in monitoring lead deposition from vehicular exhaust along highways (Laaksovirta, Olkkonen and Alakuijala, 1976), Lawrey and Hale (1981) in a retrospective study of lichen lead accumulation in the northeastern United States concluded that lichens may be useful in monitoring long term increases in background Pb levels due to large-scale atmospheric transport. Perhaps a similar study in the southern Appalachians would provide useful information complementary to the ongoing study of lead levels in the vegetation litter and soils of the spruce-fir forest in the Great Smoky Mountain National Park being conducted by R. Turner and M. Bogle of the Oak Ridge National Laboratories, Oak Ridge, Tennessee.

5) Effects of the balsam woolly aphid

The need to monitor responses of the lichens to the environmental changes induced directly or indirectly by the death of Fraser fir trees infested with balsam woolly aphids is clear and timely. Such a study could complement ecological studies of vascular plant succession due to aphid damage.

6) Lichen-invertebrate associations

When one collects fruticose and foliose lichens, one readily becomes impressed with the abundance and diversity of insects and other invertebrates that one uncovers or inadvertently collects with the specimens. Lichens serve as a protective environment for invertebrates as places for concealment, as sources of camouflage, and as objects to be mimicked. For example, Skorepa and Sharp (1971) report that the larvae of the lacewing Nodita pavida (Chrysopidae) in the southern Appalachians construct and carry trash packets consisting solely of lichens presumably as camouflage for themselves. The movement of these larvae may be a method of dispersal for the lichens. Invertebrate feeding on lichens, the resistance of some lichens to invertebrate feeding, and the recognition of invertebrate-lichen communities in the southern Appalachian spruce-fir ecosystem are also worthy of study. Gerson and Seaward (1977) have reviewed much of the worldwide work on lichen-invertebrate associations. Since such studies would require specialists to identify the insects and other invertebrates and would be very time consuming, it may be unrealistic to expect that a high priority will be given to these studies by entomologists and other specialists.

While more information in all of these areas would enable us to obtain a better understanding of the lichens in the southern Appalachian spruce-fir ecosystem, it is suggested that the following studies should be given priority: 1) quantitative studies of the lichen vegetation, 2) studies of the ramifying effects of the balsam woolly aphid on the lichen flora and vegetation, 3) studies of air pollution effects in the southern Appalachians utilizing lichens as biomonitors of the magnitude of local pollution problems in conjunction with other ongoing studies of air pollution in the region, and 4) further study to inventory the crustose lichens of the area.

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COMMENTS ON THE FUNGI OF THE SPRUCE-FIR FOREST OF THE SOUTHERN APPALACHIAN MOUNTAINS

Ronald H. Petersen¹

Abstract - The identities and distribution patterns of fungi occurring in the spruce-fir forest are imperfectly known, for research has not emphasized this ecological niche. Potential major research projects are identified.

It may be safely stated that no concerted research effort presently is underway on the fungi of the spruce-fir forest of the Great Smoky Mountains National Park. Two pre-doctoral projects are progressing, one at Virginia Polytechnic Institute (Mr. Gerald Bills) on the mushrooms (Agaricales) of selected spruce-fir forest sites in West Virginia, the other at the University of Tennessee (Mr. Hack Sung-Jung) on the taxonomy of the Basidiomycetes decaying spruce and fir wood in the Park. Other research efforts on the fungi of this forest type, while perhaps applicable to conditions within the range in question, are not being carried out nearby, and will be mentioned below.

Traditionally, the amount of research has been directly proportional to the number of researchers in the area. In this case, the University of Tennessee has had a mycologist in residence for nearly 70 years, but while those individuals have produced significant monographs of various fungal groups over the years, they have not concentrated on a particular ecological niche. Of the surrounding institutions, few have had a mycologist, and when such people were present, their research took them in other directions.

As most research on fungi of an ecotype, efforts on the spruce-fir forest may be divided into two categories: 1). Inventory and taxonomy, and 2). Ecology.

INVENTORY AND TAXONOMY:

Any effort to compile floristic profiles of the fungi of this forest type is bound to be hampered by the inaccessibility of all stands of spruce and fir. Even within the Park, several such stands are almost a full day's hike from the nearest road, making collecting difficult. In the many years of mycologizing in the Smokies by Hesler, he did not visit most of the spruce-fir sites, considering them remote and relatively unprofitable. Only the areas on Clingman's Dome and adjacent to Newfound Gap saw frequent visits, and even on those occasions only mushrooms were gathered.

Until the two dissertation projects mentioned above were undertaken, no floristic treatment of fungi of this forest type has been undertaken. The best information has resided in scattered monographic treatments of various groups of fungi, or floristic treatments of wider areas. A prime example is the "Checklist of Fungi for the Great Smoky Mountains National Park" originally compiled by L.R. Hesler,

¹ Botany Department, University of Tennessee, Knoxville, TN 37916

and lately revised and edited by R.H. Petersen. In that document, about 1700 species of fungi were listed, of which about 1150 were mushrooms, an incredibly rich flora for an area of this size. Nonetheless, no break-down of forest type, elevation or other subunits was attempted, and it is necessary to check individual herbarium specimens to ascertain their collection sites. Likewise, monographs of various agaric (mushroom) genera, though written or co-authored from the University of Tennessee, and based on many collections from the Smokies, have little or no disributional data explicitly stated, and again individual collections must be traced for more accurate information. Such a task is so formidable as to be prohibitive. Instead, it may be more efficacious to start over again in the spruce-fir forests, exactly the concept which has prompted the two dissertations cited above.

This does not mean that no statement can be made concerning these fungi, but merely that accurate, inclusive information is lacking. The fungi found in this forest type may be divided into three categories, much as any fungus flora: 1) parasites; 2) decay orgnaisms; and 3) mycorrhizal associates.

Parasites: To my knowledge, no catastrophic or serious fungus parasites have been identified on these trees. There is no reason to suppose that a counterpart to the Pine Blister Rust or Chestnut Blight is about to befall the spruce-fir forest, although the Balsam Wooly Aphid is catastrophic enough. When found, parasites seem centered in the Loculoascomycetes, as might be expected from research in northern Europe.

Decay Organisms: It must be emphasized that virtually all of the taxonomy of decay organisms of spruce and fir biomass has been based on fruitbodies of those fungi. Thus, while a number of taxa could be identified as occurring on these substrates, many other fungi may grow there, but may be inhibited for fruiting for a variety of reasons, and therefore may escape the inventories thus far compiled. While no profile for such organisms has been drawn up for the spruce-fir forest, certain conclusions can be drawn. First; there are a few conspicuous fungi which fruit in such profusion as to be obvious to anyone walking through the forest. The brilliant yellow cups of Helotium citrinum fit this category, for example, as do the similar structures of Dasyscypha agasizzii. In the late summer, the bright rusty red mushroom Pholiota kauffmanii stands out on rotting logs. Second; the number of such decay fungi is surely much higher than ever predicted, with the unreported taxa to come largely from small or inconspicuously fruiting types. The jelly fungi, for example, have never been inventoried, but will yield several taxa, among which will be some new to science. Third; of those already identified, there is a definite, significant "northern" element not found at lower altitudes. Whether these fungi are limited to spruce and fir wood is open to question, but they fruit only at the tops of the mountains. Thus, as in other organismal groups, one can identify a circum-boreal flora which extends down the Appalachian chain to the mountaintops in the Park.

Mycorrhizal Associations: Aside from general conclusions on mycorrhizal symbionts based on observations of tree species found in the vicinity of fungus collections, little has been done to systematically identify the fungi associated with spruce and fir. Currently, as part of the VPI project, such pure-culture syntheses are being established, but in many cases, the fungal component does not culture well, and is difficult, therefore, to grow in a condition from which to make the aseptic synthesis.

Field observations would seem to indicate that the genera Russula, Lactarius, Amanita, and Cortinarius are among the most common mycorrhizal symbionts. Of these, the first three genera have been treated in alpha taxonomic monographic works. The latter is by far the largest (perhaps a thousand species in North America), and will be the most difficult to bring to order. Several other genera are represented in putative mycorrhizal associations, but the lack of emphatic collecting in these high-altitude forests has resulted in only superficial knowledge of the fungus flora as a whole.

ECOLOGY

As might be inferred from the paragraph above on mycorrhizal fungi, rather little can be said about the ecology of these fungi if their identities remain unknown or confused. Experiments with reproducible results are based on correct identification of the organisms involved. Nonetheless, the following studies seem to hold high potential for the future.

Inventory and experimentation within the spruce-fir forest: The first order of business in the concerted inventorying of this same time, modern techniques can be applied to synthesize axenic mycorrhizal associations under laboratory conditions. In such a way, at least the dominant associations may be identified.

Interface between spruce-fir forest and Beech Gaps: In the Smoky Mountains (at least), many of the saddles along the ridge and associated peaks show a markedly different forest type, dominated by Fagus sometimes mixed with Betula. While the causes of this abrupt change in forest type may be largely edaphic, it has been proposed that the change in forest type may be accompanied by, or caused by, a concomitant change in mycorrhizal symbionts. A study of the fungi fruiting in the Beech Gaps (following the inventory of fungi of the spruce-fir forest) would give an inventory of those areas. This may lead to isolations from soil samples across transects traversing both forests in an attempt to sample the change in fungal components.

Equally interesting would be similar studies on the grassy balds and their interface with the spruce-fir forest. The grassy balds do not appear to be stable, however, so the same barriers to colonization by the spruce and fir apparently do not exist as they do in the Beech Gap situation.

Decay of spruce and fir biomass: The Balsam Woolly Aphid is about to cause the demise of fir in these forests. The natural sequence of events will be the defoliation of the trees, followed by pruning of the boughs, and finally the fall of the trunk. Each step will add significantly more biomass to the forest floor than has been the case for the recorded past. At the same time, a fungus "bloom" can be anticipated at each step of the way, although perhaps not visible to the casual observer. The catastrophe presents an ideal opportunity to chronicle this sequence of fungal invasions, and on the longer term, to sample downed fir logs over a period of years in order to elucidate the sequence of fungal fruiting and permeation of the wood.

Acid rain: In the past decade or two, serious decline in growth of high-elevation coniferous trees has been noted. While acid rain is suspected as the cause, or at

least as a significant factor, it is not known whether such conditions operate directly on the tree, or whether the tree is affected because of a decline in its mycorrhizal symbionts. Work at the University of Vermont and elsewhere is attempting to clarify this situation, but research is still very young. Because the Smoky Mountains are exposed to significant amounts of acid rain, they make an ideal laboratory in which to study the phenomenon and its ramifications. Because of their mycorrhizal role, the fungi will become pivotal in such studies.

HERPETOFAUNA OF THE SPRUCE-FIR ECOSYSTEM IN THE SOUTHERN
APPALACHIAN MOUNTAIN REGIONS, WITH EMPHASIS ON THE GREAT
SMOKY MOUNTAINS NATIONAL PARK

Raymond C. Mathews, Jr.¹ and Arthur C. Echternacht²

Abstract. The diversity of amphibians and reptiles in the topographically complex region of the Southern Appalachian Mountains is high, especially with respect to salamanders. The salamander fauna is unmatched anywhere else in the world and the region has a long history of herpetofaunal study. Surprisingly, however, relatively little research has been centered in the spruce-fir ecosystem. The herpetofaunal diversity in the spruce-fir ecosystem of the Great Smoky Mountains National Park is less diverse than lower elevation ecosystems of the Park, but still includes 3 species of frogs, 13 of salamanders and 8 snakes. Only two species, both salamanders, may be said to be characteristic of the spruce-fir ecosystem. These are the imitator salamander, Desmognathus imitator and the pygmy salamander, Desmognathus wrighti. The remainder of the species of amphibians and reptiles which occur in the spruce-fir ecosystem occur relatively widely in ecosystems at lower elevations. Resource management problems associated with herpetofauna in the spruce-fir forest include roadcuts through Anakeesta formations, acid precipitation effects, Balsam Woolly Aphid parasitism of Fraser Fir and subsequent loss of habitat, and European wild boar rooting.

Additional Keywords: Salamanders, Frogs, Snakes, Anakeesta Formations, Acid Precipitation.

INTRODUCTION

Spruce-fir forest occur as isolated ecological islands in the southern Appalachian mountains of southwestern Virginia, western North Carolina, and east Tennessee. The diversity of amphibians and reptiles in the topographically complex region which includes spruce-fir islands is high, especially with respect to salamanders. The salamander fauna is unmatched anywhere else in the world and the region has a long history of herpetofaunal study. Surprisingly, however, relatively little research has been centered in the spruce-fir ecosystem. It is the purpose of this paper to introduce the herpetofauna of the spruce-fir

¹Graduate Student, Graduate Program in Ecology, University of Tennessee, Knoxville, Tenn. 37996. Present address: Vice-President, Geo-Marine Inc., Engineering and Environmental Services, 1316 Fourteenth Street, Plano, Texas 75074.

²Associate Professor, Department of Zoology and Graduate Program in Ecology, University of Tennessee, Knoxville, Tenn. 37996.

ecosystem, to comment on selected species, and to identify factors which threaten the herpetofaunal community.

The Great Smoky Mountains National Park, with an area of only 2,072 square kilometers, is home to 72 species of amphibians and reptiles. Of these, 35 are amphibians (12 frogs, 25 salamanders) and 35 are reptiles (6 turtles, 8 lizards, and 21 snakes). The magnitude of this diversity is evident when one considers that the State of Tennessee, with an area of 109,417 square kilometers, has a herpetofauna of 115 species, only 40 percent more than are found in the Park. The herpetofaunal diversity in the spruce-fir ecosystem is less diverse, but still includes 3 species of frogs, 13 of salamanders and 8 snakes (Table 1). The herpetofaunal diversity of the spruce-fir ecosystem above 1650 m is further reduced to 3 frog species, 10 salamanders and 4 snakes (Table 1). As advanced techniques of biochemical systematics are employed, additional species will no doubt be identified. Three species of salamanders which occur in the spruce-fir ecosystem have only recently been recognized as distinct on the basis of such techniques: Desmognathus imitator (Tilley et al. 1978), D. santeetlah (Tilley 1981), and Plethodon serratus (Highton and Webster 1976).

SPRUCE-FIR HERPETOFAUNAL ENDEMICIS

Only two species, both salamanders, may be said to be characteristic of the spruce-fir ecosystem. These are the imitator salamander, Desmognathus imitator and the pygmy salamander, Desmognathus wrighti. The red-cheeked salamander, a unique color morph of the Appalachian woodland salamander, Plethodon jordani, is also characteristic of spruce-fir, but its limited distribution does not encompass the entire series of spruce-fir islands.

Desmognathus imitator, many individuals of which have cheek patches which contrast in color to the generally dark coloration of the salamander, has been considered a Batesian mimic of the red-cheeked salamander with which it is sympatric (Huheey 1966, Orr 1968, Brodie and Howard 1973). The species is found in moist situations and is commonly encountered under rocks and under or in rotting logs. Its congener, D. wrighti, is one of the smallest of salamanders, reaching a maximum length of just over 2 inches. Desmognathus wrighti is the most terrestrial of its genus, having done away with the larval stage of its life cycle; eggs hatch directly into miniature adult-like salamanders. Like D. imitator, the pygmy salamander favors moist areas but may be found relatively far from free-flowing or standing water. Both desmognathines are most active on cool, damp nights. On especially damp nights, following rains or when fog is present, D. wrighti may be found on leaves some distance from the ground, and D. imitator has been found several feet off the ground having climbed the rough bark of trees. Tilley and Harrison (1969) emphasized that, although D. wrighti is characteristic of the spruce-fir ecosystem, it is not restricted to ranges which presently support spruce-fir. They suggest that populations of the pygmy salamander found on mountains which lack

Table 1. Species of amphibians and reptiles known to range above 1305 m in the Great Smoky Mountains National Park. Species which range to above 1650 m are indicated with an asterisk (*).

			Habitat Type	
			<u>Aquatic</u>	<u>Terrestrial</u>
ANURA (Frogs)				
* <u>Bufo</u>	<u>americanus</u>	American Toad		X
* <u>Hyla</u>	<u>crucifer</u>	Spring Peeper		X
* <u>Hyla</u>	<u>versicolor</u>	Gray Treefrog		X
CAUDATA (Salamanders)				
* <u>Desmognathus</u>	<u>imitator</u>	Imitator Salamander		X
	<u>Desmognathus</u>	Seal Salamander	X	
* <u>Desmognathus</u>	<u>ochrophaeus</u>	Mountain Dusky Salamander	X	
* <u>Desmognathus</u>	<u>quadramaculatus</u>	Black-Bellied Salamander	X	
* <u>Desmognathus</u>	<u>santeetlah</u>	Santeetlah Salamander		X
* <u>Desmognathus</u>	<u>wrighti</u>	Pygmy Salamander		X
* <u>Leurognathus</u>	<u>marmoratus</u>	Shovel-Nosed Salamander	X	
	<u>Plethodon</u>	Slimy Salamander		X
* <u>Plethodon</u>	<u>jordani</u>	Appalachian Woodland Salamander		X
* <u>Plethodon</u>	<u>serratus</u>	Southern Red-Backed Salamander		X
* <u>Gyrinophilus</u>	<u>porphyriticus</u>	Spring Salamander	X	
	<u>Pseudotriton</u>	Red Salamander		X
* <u>Eurycea</u>	<u>bislineata</u>	Two-Lined Salamander	X	
SERPENTES (Snakes)				
	<u>Nerodia</u>	Northern Watersnake	X	
* <u>Storeria</u>	<u>occipitomaculata</u>	Red-Bellied Snake		X
* <u>Thamnophis</u>	<u>sirtalis</u>	Eastern Garter Snake		X
* <u>Diadophis</u>	<u>punctatus</u>	Ringneck Snake		X
	<u>Coluber</u>	Black Racer		X
	<u>Elaphe</u>	Black Rat Snake		X
	<u>Lampropeltis</u>	Milk Snake		X
* <u>Crotalus</u>	<u>horridus</u>	Timber Rattlesnake		X

spruce-fir are relicts of a time when spruce-fir occurred more widely in the southern Appalachians.

Delcourt and Delcourt (this volume) have documented the withdrawal of spruce-fir forests over the period since the full- and late-glacial interval 18,000 YR BP to 12,500 YR BP. With gradual climatic amelioration, spruce-fir forests became disjunct and, at the period of peak warmth 8,000 YR to 4,000 YR BP, were finally restricted to high elevations in the southern Appalachians. It is by this mechanism that ancestral populations of Desmognathus wrighti became disjunct. The present extent of spruce-fir forest in the southern Appalachians is only about 120 km², and the range of D. wrighti is correspondingly small. No detailed analyses of geographic variation in morphology or genetics of the pygmy salamander has been published, but as it becomes possible with increasing accuracy to determine the age of spruce-fir islands, the species should be valuable in studies aimed at assessing rates of evolutionary change. All populations are presently considered conspecific and no geographic variants (described subspecies or local morphs) have been identified.

With the exceptions noted above, the remainder of the species of amphibians and reptiles which occur in the spruce-fir ecosystem occur relatively widely in ecosystems at lower elevations. Among these is the eastern garter snake, Thamnophis sirtalis. High-elevation populations of this species in the Great Smoky Mountains National Park tend toward melanism, adults having only faint dorsal stripes and dark brown overall coloration. This seems to be the only instance of a high elevation morph associated with any of the amphibians and reptiles of the spruce-fir ecosystem with the exception of that of Plethodon jordani already mentioned.

HIGH ELEVATION STREAM ASSOCIATED SALAMANDERS

Due to the unique diversity of salamanders in the Southern Appalachian Mountain region, a great deal more research has been conducted on that element of the herpetofauna. High elevation (> 1200 m) stream associated salamanders (those that live in the stream and/or on the stream side) in the Great Smoky Mountains National Park occupying the virgin spruce-fir forest account for only about 17% of the overall abundance (Mathews 1984). The greatest abundance (63%) of such salamanders occur in the mesic type hemlock-hardwood cove forest. Other forest types produced lesser abundances of salamanders associated with stream environs: 14% in virgin mesic type mixed cove hardwoods, 3% in mature northern hardwoods (Gray Beech gap), 2% in second growth mesic type hemlock-hardwood cove forest, and 1% in virgin mesic type hardwood flats. Species commonly associated with streams in the spruce-fir forest are indicated in Table 1. The density of stream associated salamanders is less in high elevation areas of the Great Smoky Mountains National Park as indicated in Tables 2 and 3 (Mathews 1984). An explanation for this distribution is lacking at the present time, though the environmental extremes in temperature and precipitation encountered

Table 2. Number of sites with the indicated density of stream associated salamanders at different elevations in the Great Smoky Mountains National Park.

		<u>Elevation</u>			
NO./HECTARE		<600m	≥600m	≥1200m	ROW TOTAL FREQ.(%)
<	50	32	31	4	67 (3.9)
>	50	66	188	20	274 (15.9)
>	100	66	220	13	299 (17.4)
>	200	73	150	14	237 (13.8)
>	300	70	201	11	282 (16.4)
>	500	50	138	23	211 (12.3)
>	1000	34	179	39	252 (14.7)
>	2000	32	34	11	97 (5.6)
COLUMN TOTAL FREQ. (%)		423 (24.6)	1141 (66.4)	155 (9.0)	1719 (100)

Table 3. Number of sites with the indicated biomass of stream associated salamanders at different elevations in the Great Smoky Mountains National Park.

		<u>Elevation</u>			
GRAM WT./HECTARE		<600m	≥600m	≥1200m	ROW TOTAL FREQ.(%)
<	50	71	106	8	185 (10.8)
>	50	100	229	15	344 (20.0)
>	200	80	293	53	426 (24.8)
>	500	81	222	31	334 (19.4)
>	1000	55	183	8	246 (14.3)
>	3000	36	108	40	184 (10.7)
COLUMN TOTAL FREQ. (%)		423 (24.6)	1141 (66.4)	155 (9.0)	1719 (100)

TABLE 4. Partial correlation and statistical significance of stream associated salamander density in the Great Smoky Mountains National Park as associated with environmental parameters while adjusting for the effects of other variables. Degrees of Freedom = 1719.

Environmental Parameter Controlling for: Elevation												
Salamander Density Variable	Forest Type	Air Temp.	Water Temp.	Stream Flow	Watershed	Logging History	Substrate Type	Stream pH	Stream Order	Terrain Slope	Season	Elevation
No. Species	-.0750 P=.001	.1395 P<.001	.1199 P<.001	.0132 P=.293	.0777 P=.001	.0560 P=.010	.0227 P=.173	-.0411 P=.044	.1173 P<.001	-.0471 P=.025	.1280 P<.001	
No./Hectare	-.0965 P=.001	.0064 P=.395	.0137 P=.285	-.0782 P=.001	-.1523 P<.001	.1701 P<.001	.0305 P=.103	.1326 P<.001	-.1161 P<.001	.1045 P<.001	.0353 P=.072	
Wt./Hectare	.0157 P=.258	.0028 P=.453	.0119 P=.311	-.0868 P<.001	-.0627 P=.005	.0356 P=.070	.0496 P=.020	.0057 P=.406	-.1414 P<.001	.1081 P<.001	.0784 P=.001	
Wet Weight	.1191 P<.001	.0292 P=.113	.0389 P=.053	-.0285 P=.119	.0456 P=.029	-.0852 P<.001	-.0133 P=.290	-.0489 P=.021	.0065 P<.393	.0158 P=.256	.0626 P=.005	
Controlling for: Watershed												
No. Species	.0130 P=.297						.0087 P=.361	.0033 P=.447				-.1506 P<.001
No./Hectare	-.2296 P<.001						.0440 P=.036	.0531 P=.015				.3017 P<.001
Wt./Hectare	-.0288 P=.119						.0579 P=.009	-.0141 P=.281				.0906 P<.001
Controlling for: Air Temperature												
No. Species	.0308 P=.104						.0140 P=.283	.0252 P=.151				-.1445 P<.001
No./Hectare	-.2348 P<.001						.0532 P=.015	-.0078 P=.374				.2700 P<.001
Wt./Hectare	-.0318 P=.096						.0341 P=.082	.0694 P=.002				.0781 P=.001
Controlling for: Water Temperature												
No. Species	.0269 P=.135						.0109 P=.327	.0268 P=.137				-.1359 P<.001
No./Hectare	-.2352 P<.001						.0336 P=.084	.0693 P=.002				.0785 P=.001
Wt./Hectare	-.0316 P=.098						.0529 P=.015	-.0067 P=.392				.2710 P<.001

by salamanders at high elevations is presumed to account for much of this profile.

Partial correlation analyses (Nie 1983) were used as a measure of association between stream salamander density and environmental parameters simultaneously examined while adjusting for the effects of one or more additional variables. The results of these analyses are given in Table 4. It is evident that no one environmental variable among those examined accounts for the density patterns of stream associated salamanders in the Park. The most important relationships influencing the number of species are air and water temperature, stream order, season, forest type, and elevation. Similarly for number per hectare it is watershed, logging history, stream pH, stream order, terrain slope, forest type, and elevation. Weight per hectare is most influenced by stream order, and terrain slope. The wet weight of salamanders is most influenced by forest type. Other partial correlations of importance which are not presented in Table 4 are the following: number per hectare with forest type controlling for stream nitrate (NO_3) concentration = $-.2249$ ($P < .001$), number per hectare with elevation controlling for NO_3 = $.2603$ ($P < .001$), number per hectare with forest type controlling for turbidity = $-.2102$ ($P < .001$), and number per hectare with elevation controlling for turbidity = $.2485$ ($P < .001$). Although we cannot explain by these analyses the reason for the influence on stream associated salamander density of these environmental variables, it is evident that the spruce-fir forest type has an effect on the observed pattern.

RESOURCE MANAGEMENT PERSPECTIVE

From a resource management perspective, the impacts on the herpetofauna of the spruce-fir zone in the Great Smoky Mountains National Park of greatest importance are as follows:

- (1) Roadcuts through Anakeesta Formations
- (2) Acid precipitation effects
- (3) Balsam Wooly Aphid parasitism of Frasier Fir
- (4) European wild boar rooting

To these we add a fifth factor--a past research project which may have continuing effects on park distribution patterns:

- (5) Unauthorized collecting and associated habitat disturbance

Road construction through Anakeesta Formations in the Park have had a serious effect on salamanders. The problem first became apparent when Huckabee et al. (1975) discovered that mortalities of native brook trout (Salvelinus fontinalis) had occurred during the construction of U.S. Highway 441 in 1963 near Newfound Gap on the outer edge of the spruce-fir zone. Fish were reportedly eliminated for approximately 8 km below roadfill areas, and attempts to reestablish a fishery by stocking failed. Salamander mortality in Beech Flats stream below the roadcut

was attributed to acidic heavy metal leachate formed through redox processes associated with pyritic content of the Anakeesta roadfill bedrock (Mathews and Morgan 1982). Soluble aluminum in high concentrations is believed to be a major factor in the intoxication process. Observations of gill hyperplasia in the aquatic shovel-nosed salamander (Leurognathus marmoratus) were made in Beech Flat Creek as specimens intrained by the flow passed through the culvert under Highway 441, from which they were exposed to Anakeesta leachate where death eventually ensued. An isolated population of stream dwelling salamanders thus appears to have resulted as a consequence of this barrier to stream migration. Although some possible forms of reclamation have been described through sodium hydroxide neutralization (Mathews et al. 1976), nothing has been done to alleviate this problem. The best advice appears to be to avoid roadcuts through Anakeesta Formations so that other streams may not be so impacted.

Acid precipitation has been documented in Great Smoky Mountains National Park through the monitoring of pH levels as part of the National Atmospheric Deposition Program (Mathews et al. 1979, Mathews and Larson 1980), and remote monitoring of depressed stream pH levels in experimental streams of the Park (Mathews 1980). Bioassay studies of pH depression effects on the shovel-nosed salamander (Leurognathus marmoratus), suggest that some pH depressions presently occurring in Park streams are near acutely toxic levels for larval and subadult forms (Mathews and Larson 1980). The shallow acidic soils of the spruce-fir forest offer little buffering to acid rain, making that area a potentially high impact zone. Additionally, the coniferous forest is a poor scavenger of hydrogen ions in throughfall precipitation and the conifer needles breakdown more acidic than broadleaf deciduous leaves, compounding the acidic exposure to this type environ (Abrahamsen and Horntvedt 1976; Knabe and Gunther 1976; Scholz and Reck 1976). The potential effect of acidic deposition to the spruce-fir forest community should be an area of extensive investigation.

The loss of the Fraser Fir forest in the Southern Appalachians through the attack of the Balsam Woolly Aphid is a threat which parallels the loss of the American Chestnut forest. Although the spruce-fir forest community has few endemic amphibians or reptiles, the few species already mentioned may also be lost as the Fraser-Fir forest community deteriorates. Resistance and/or susceptibility to biotic pathogens and parasites may be affected by acid precipitation and long term effects may be presently expected (Tamm and Cowling 1976), which may be related to the infestation of the Balsam Woolly Aphid on Fraser Fir in the Park. Since research has not been focused on the relationships of the herpetofauna to the spruce-fir zone, we will not comment further on this subject, except to emphasize the need to fill that gap in our knowledge.

Since the European wild boar (Sus scrofa) was accidentally introduced into the Great Smoky Mountains National Park, its population has expanded and presently occupies about three-quarters of the Park (Howe and Bratton 1976, Howe et al. 1981). The hogs' rooting activity have severely

damaged the herbaceous understories of several types of forest, including the spruce-fir. Rooting occurs in the spruce-fir forest in the Park to a lesser extent than other forest types and usually occurs there during the hottest months of the year, likely associated with thermoregulatory response of the European wild hog to move into higher elevations (Belden and Pelton 1975). Scott and Pelton (1975) reported rooting in shallow stream beds as a possible attempt to obtain aquatic invertebrates. Where rooting in such streams has occurred, we have observed extensive disruption of substrate, sediments, and natural debris dams, with consequent high turbidity levels. Direct predation of some species is also attributable to the wild boar. They eat large quantities of invertebrates, including snails and crayfish, and a variety of amphibians, including the Appalachian woodland salamander (Plethodon jordani) of which the red-cheeked morph is endemic to the Park (Singer and Ackerman 1981). Since P. jordani exists in very dense but patchy populations in the spruce-fir and cove hardwood forests of the Park the effect of rooting on their habitat and direct foraging effects could pose a severe impact. Singer et al. (1982), however, reported no significant difference in salamander numbers between pristine and rooted stands ($P > 0.95$), and only pygmy salamanders (Desmognathus wrighti) significantly declined. Only surface ground dwelling salamanders were studied, however, so as to minimize collecting effects. Thus, the overall effect of rooting activity on the salamanders may not have been assessed. Salamanders may find adequate alternate habitats in rooted areas such as on vegetation (Hairston 1949), in soil refugia (Taub 1961) and inside or under the larger logs that are not disturbed by wild boar. The disturbance by rooting appears to be long lasting, however, as we have observed rooted areas that remain disturbed for several years. Huff (1977) reported damaged areas in the Gray Beech forest of the Park had a substantial reduction in total plant cover, including both herbaceous and woody species. We suggest that similar disturbance appears in the spruce-fir forest, and in particular in the grassy balds surrounded by spruce-fir.

The collecting of herpetofauna in the Park for research purposes is of unquestioned value to the scientific understanding and management of Park resources, though little collecting ethic is administered by Park staff and some studies have caused impacts. Sometimes the value of the derived data warrants temporal impacts, and this is a value judgement only the Park staff can evaluate. However, we have noticed with increasing frequency the presence of collecting activity (e.g., overturned rocks, moved logs, broken open tree trunks). The Park staff should continue to exercise tight but judicious control in issuing permits to collect amphibians and reptiles in the Park, and in approval of research programs to be carried out there. Aside from the obvious concerns about over-collecting and habitat disturbance, care should be taken to guarantee the genetic integrity of populations is maintained. Translocation experiments should receive especially thorough review. In general, it may be appropriate to request what would amount to a biological environmental impact assessment prior to approving collecting and/or research in the Park.

FUTURE RESEARCH

There is too little information available on geographic variation in life history characteristics of wide ranging species. The southern Appalachians offer an ideal research area for studies aimed at comparing life history strategies of species which range from low elevation to high. Many of the species indicated by an asterisk in Table 1 would be suitable for such study (e.g., Bufo americanus, Hyla crucifer, Desmognathus quadramaculatus, Eurycea bislineata, Diadophis punctuatus, Nerodia sipedon). These studies might be coupled with investigations of thermal ecology to better understand adaptation of these species to high elevation environments. In particular, it would be valuable to know to what extent any observed differences between low and high elevation populations in critical thermal maximum and critical thermal minimum are based on acclimation and how much to genetic differentiation. Thermal considerations may be implicated in the evolution of melanism in high elevation populations of Thamnophis sirtalis. The extent of melanism, both in terms of the proportion of the population exhibiting it and its geographic and elevational limits needs documentation.

Data is lacking on population densities for those species of amphibians and reptiles as they occur in spruce-fir forest. Without such data, biomass estimates are impossible and it is not possible to evaluate the importance of the species in terms of energy flow. In this regard, Table 1 is misleading in according each species equal weight. Whereas salamanders like Plethodon jordani and Desmognathus ochrophaeus are very abundant at high elevations within their range, certain other species (e.g., the spring peeper, Hyla crucifer) are reported in spruce-fir forest, but very infrequently.

Resource management oriented research should concentrate on the effects of acid precipitation and European wild boar rooting as well as on the relationships between salamander communities and the spruce-fir forest which have not previously been investigated in the Southern Appalachians.

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BIRDS OF APPALACHIAN SPRUCE-FIR FORESTS:
DYNAMICS OF HABITAT-ISLAND COMMUNITIES

Kerry N. Rabenold¹

Abstract.--The birds inhabiting the patchy high-elevation forests of Spruce and Fir in the southern Appalachians are both distinctively boreal compared to the lowland forests and unique in their species composition. These communities contain characteristically southern Appalachian endemic forms among a reduced number of species compared to similar northern forests. These characteristics are consistent with an island model for the dynamics of these communities but a strict application of the analogy with oceanic islands is not tenable. Both sedentary and highly migratory northern birds are strikingly few in these forests and in their absence short-distance altitudinal migrants are numerically dominant. These local populations probably compete very effectively with tropical migrants that may be better adapted to the more concentrated flush of productivity and lower densities of residents characteristic of northern Spruce-fir. Explanations for the depauperate status of the avifauna that appeal to the history of glaciation in the region have limited explanatory power.

Carolina Juncos in Great Smoky Mountains National Park migrate short distances altitudinally and show patterns of sex-specific migratory effort that parallel those shown by latitudinally migrating juncos. Patterns of segregation on wintering grounds between Carolina and Northern Juncos and between the sexes of Carolinas are variable, depending on climatic conditions. A few male Carolinas are year-round residents in the breeding habitat while recapture information shows that others migrate to nearly the limits of the winter range. Site tenacity of Carolina Juncos is high on several time scales, making more thorough study of demography feasible. Differential and partial migration among these birds is best explained by competitive effects both for winter food and for breeding opportunities.

Research priorities should focus on the island-like dynamics of these bird communities and explore the functional limits of their populations, particularly the altitudinal migrants. Management problems are urgent; the most remediable is the incursion of feral swine. The demise of Fraser's Fir will probably bring considerable change to the avifauna, diluting the boreal character of this unique ecosystem.

Additional Keywords: montane bird communities, Spruce-fir, island biogeography, species diversity, altitudinal migration, Junco hyemalis, Great Smoky Mountains.

¹Assistant Professor, Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907.

INTRODUCTION

The avian communities of Spruce-fir forests of the southern Appalachian Mountains are a unique subset of the family of communities extending into New England and southern Canada, united and defined by the dominance of Red Spruce (Picea rubens). These avifaunas of the highest ridges of the unglaciated Appalachians are definitely boreal in character and strikingly distinct from those of lower-elevation deciduous forests. Like the coniferous flora, the avian assemblies that inhabit the high altitudes are simpler in taxonomic composition than their higher-latitude counterparts. Migrants from the tropics are conspicuously few in the breeding season and, instead, altitudinal and short-distance migrants dominate. Endemic forms characterize the avifauna as they do the flora; the Carolina Junco (Junco hyemalis carolinensis) is as emblematic of the birds as Fraser's Fir (Abies fraseri) is of the plants.

The uniquely southern Appalachian relict Spruce-fir ecosystem ties these mountains biologically to the alpine systems of the Rockies and to the boreal Canadian biome. It covers a far smaller area than a century ago (Korstian 1937) and is now further threatened by a concentrated dose of the airborne pollutants weakening all eastern forests and by invasions of destructive insects and feral swine. This symposium is a timely opportunity to take stock of the biological character of the birds of this system, our understanding of its history and interdependence with others, and prospects for continued study and conservation.

THE STRUCTURE AND DYNAMICS OF THE AVIFAUNA

The distribution of Spruce-fir forests on southern Appalachian mountaintops resembles an archipelago; it is therefore tempting to ask whether their fauna is island-like. In fact, in one major attribute these bird communities do resemble those of oceanic islands: their species richness is depauperate compared to the extensive coniferous forests of New England, Quebec and New Brunswick (Rabenold 1978). Breeding-season censuses in old-growth Spruce-fir of the Great Smoky Mountains compared to northwestern Maine show twice as many species in the northern forests (e.g., Table 1). In spite of the lower number of species, the southern Spruce-fir can contain higher densities of individual birds and greater avian biomass.

Other species could be added to the list provided in Table 1. Uncommon but characteristic species that can be difficult to census include Saw-whet Owls (Aegolius acadicus), Ruffed Grouse (Bonasa umbellus) and Olive-sided Flycatchers (Nuttallornis borealis). Species mostly confined to special sub-habitats include Black-throated Blue Warblers (Dendroica caerulescens) in Rhododendron thickets and Chestnut-sided Warblers (Dendroica pennsylvanica) in clearings and disturbed areas. The families of birds represented in Appalachian Spruce-fir are identical north and south, and the genera nearly so. Northern Spruce-fir holds a larger number of species that are congeneric -- high northern species diversity results from increased coexistence of many species that are very similar morphologically and ecologically. Conversely, bird species in the southern Spruce-fir tend to be the sole representatives of families and are more ecologically distinct from each other.

TABLE 1. List of breeding birds in spruce-fir forests of 2 study sites: Mount Collins, North Carolina (NC) and Shepherd Brook Mountain, Maine (ME). Species are arranged by family and singing male densities per 20 ha are shown in parentheses. Densities could not be estimated for some species (from Rabenold, 1978)

Shepherd Brook Mountain, Maine		Mount Collins, North Carolina	
Parulidae		Parulidae	
<i>Dendroica virens</i> (Black-throated Green Warbler)	(13)	<i>Dendroica virens</i> (Black-throated Green Warbler)	(06)
<i>D. fusca</i> (Blackburnian Warbler)	(11)	<i>D. fusca</i> (Blackburnian Warbler)	(++)
<i>D. castanea</i> (Bay-breasted Warbler)	(19)	<i>D. pennsylvanica</i> (Chestnut-sided Warbler)	(++)
<i>D. coronata</i> (Yellow-rumped Warbler)	(08)		
<i>D. magnolia</i> (Magnolia Warbler)	(02)		
<i>D. tigrina</i> (Cape May Warbler)	(++)		
<i>Parula americana</i> (Parula Warbler)	(06)		
<i>Seiurus aurocapillus</i> (Ovenbird)	(11)		
Paridae		Paridae	
<i>Parus atricapillus</i> (Black-capped Chickadee)	(04)	<i>Parus atricapillus</i> (Black-capped Chickadee)	(25)
<i>P. hudsonicus</i> (Boreal Chickadee)	(02)		
Sylviidae		Sylviidae	
<i>Regulus satrapa</i> (Golden-crowned Kinglet)	(15)	<i>Regulus satrapa</i> (Golden-crowned Kinglet)	(25)
<i>R. calendula</i> (Ruby-crowned Kinglet)	(02)		
Fringillidae		Fringillidae	
<i>Junco hyemalis</i> (Dark-eyed Junco)	(11)	<i>Junco hyemalis</i> (Dark-eyed Junco)	(52)
<i>Carpodacus purpureus</i> (Purple Finch)	(04)	<i>Loxia curvirostra</i> (Red Crossbill)	(++)
<i>Zonotrichia albicollis</i> (White-throated Sparrow)	(02)		
<i>Pinicola enucleator</i> (Pine Grosbeak)	(02)		
<i>Hesperiphona vespertina</i> (Evening Grosbeak)	(++)		
<i>Spinus pinus</i> (Pine Siskin)	(++)		
<i>Loxia curvirostra</i> (Red Crossbill)	(++)		
Turdidae		Turdidae	
<i>Turdus migratorius</i> (American Robin)	(++)	<i>Turdus migratorius</i> (American Robin)	(04)
<i>Catharus ustulata</i> (Olive-backed Thrush)	(13)	<i>Catharus fuscescens</i> (Veery)	(08)
<i>C. guttata</i> (Hermit Thrush)	(++)		
Sittidae		Sittidae	
<i>Sitta canadensis</i> (Red-breasted Nuthatch)	(06)	<i>Sitta canadensis</i> (Red-breasted Nuthatch)	(20)
Vireonidae		Vireonidae	
<i>Vireo solitarius</i> (Solitary Vireo)	(06)	<i>Vireo solitarius</i> (Solitary Vireo)	(25)
Troglodytidae		Troglodytidae	
<i>Troglodytes troglodytes</i> (Winter Wren)	(11)	<i>Troglodytes troglodytes</i> (Winter Wren)	(34)
Certhiidae		Certhiidae	
<i>Certhia familiaris</i> (Brown Creeper)	(08)	<i>Certhia familiaris</i> (Brown Creeper)	(13)
Apodidae		Apodidae	
<i>Choetura pelagica</i> (Chimney Swift)		<i>Choetura pelagica</i> (Chimney Swift)	
Tyrannidae			
<i>Nuttallornis borealis</i> (Olive-sided Flycatcher)	(++)		
<i>Empidonax flaviventris</i> (Yellow-bellied Flycatcher)	(++)		
Corvidae		Corvidae	
<i>Cyanocitta cristata</i> (Blue Jay)		<i>Cyanocitta cristata</i> (Blue Jay)	
<i>Perisoreus canadensis</i> (Canada Jay)			
<i>Corvus corax</i> (Raven)		<i>Corvus corax</i> (Raven)	
Buteonidae		Buteonidae	
<i>Buteo jamaicensis</i> (Red-tailed Hawk)		<i>Buteo platypterus</i> (Broad-winged Hawk)	
<i>B. platypterus</i> (Broad-winged Hawk)			
Picidae		Picidae	
<i>Dendrocopos villosus</i> (Hairy Woodpecker)		<i>Dendrocopos villosus</i> (Hairy Woodpecker)	
<i>D. pubescens</i> (Downy Woodpecker)			
<i>Picoides arcticus</i> (Arctic Three-toed Woodpecker)			
<i>Sphyrapicus varius</i> (Yellow-bellied Sapsucker)			
<i>Hylatomus pileatus</i> (Pileated Woodpecker)			
Species richness: $S = 38$		18	
Species diversity: $H = 2.79$		2.15	

++ < 1 singing ♂ per 20 ha (possibly transient).

The pattern of diversification of the avifauna at higher latitudes in Appalachian Spruce-fir is a gradual one; West Virginia spruce forests support intermediate species diversities (Figure 1).

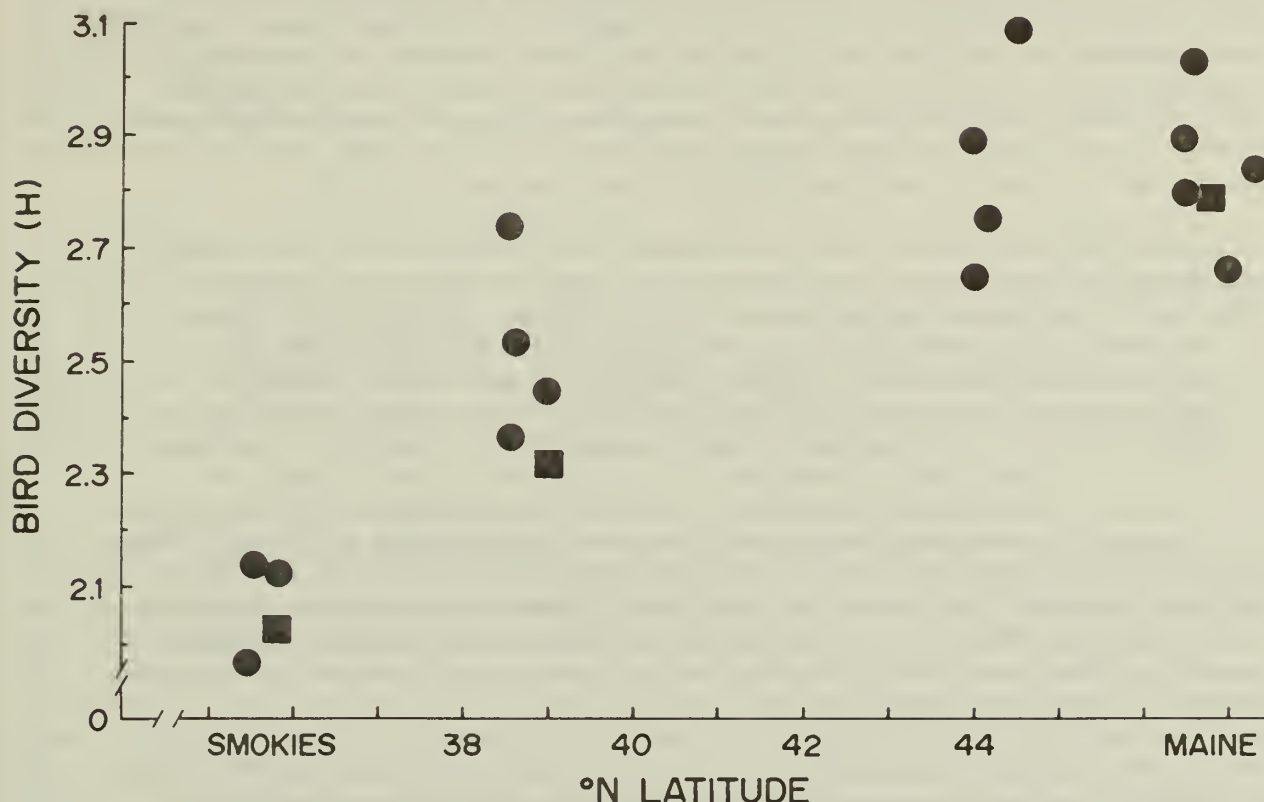


Figure 1.--Species diversity of breeding bird communities of Spruce-fir forests along a latitudinal cline in eastern North America from North Carolina to New Brunswick. Only passerines (Order Passeriformes) are considered, so that hawks, owls, and woodpeckers are excluded. Diversity is expressed using the Shannon-Weaver information theory index (Peet 1974):

$$H = - \sum_{i=1}^n (p_i \ln p_i)$$

This index weights both number of species and evenness of representation. In North Carolina, the mean number of all bird species is 17, in West Virginia 23, and in Maine the mean number is 35, doubling in 10° of latitude. All censuses are in nearly pure, mature upland stands dominated by Spruce (*Picea*) and Fir (*Abies*) of at least 10 ha. Data are from Stewart and Aldrich (1949), Stewart and Webster (1951), Cruickshank and Cadbury (1954), Adams (1959; Mt. Mitchell), Nichols (1968), Alsop (1969; Smokies), Erskine (1969a, b), Bush *et al.* (1973), Metcalf (1977), Rabenold (1978; including Smokies), Christie and Dalzell (1980), Kendeigh and Fawver (1981; Smokies), Crowell (1983), Ball *et al.* (1984), and Berdine *et al.* (1984). Square data points indicate censuses by the author.

In addition, the pattern of increased coexistence of congeneric and confamilial species with increasing latitude is also a general and gradual one (Rabenold 1978). Hubbard (1971) points out that many of the Spruce-fir species that are absent in the southern Appalachians are sedentary like the Spruce Grouse (Canachites canadensis), Canada Jay (Perisoreus canadensis) and Arctic Three-toed Woodpecker (Picoides arcticus). However, most conspicuously absent in southern Spruce-fir are the many species and large numbers of New-World Warblers (Parulidae) so characteristic of northern forests (Brewster 1886). Nearly half of the individual passerines in northern Spruce-fir during summer are warblers, especially the genus Dendroica (e.g. Table 1 = 45% warblers), that migrate long distances latitudinally, often from the tropics.

Very few warblers breed in southern Appalachian Spruce-fir (3% in Table 1) and the numerical dominants are instead residents or short-distance migrants like Carolina Juncos, Winter Wrens (Troglodytes troglodytes), Black-capped chickadees (Parus atricapillus), Golden-crowned Kinglets (Regulus satrapa), Red-breasted Nuthatches (Sitta canadensis) and Brown Creepers (Certhia familiaris). These species comprise 80% of individual birds in the breeding season, and all of them have winter ranges in the foothills of the mountains. Most of these populations are likely migrating only short distances altitudinally in autumn and spring. Juncos, chickadees, nuthatches and creepers, along with occasional Hairy Woodpeckers (Dendrocopus villosus), Blue Jays (Cyanocitta cristata) and Ravens (Corvus corax) can all be found in at least the lower reaches of Spruce-fir in winter although very few individuals of any species winter there. The numerical dominants among southern Appalachian Spruce-fir birds are likely altitudinal migrants that are at least partly residential in the breeding habitat.

Birds of the southern Spruce-fir forests are in general species that are more characteristic of northern coniferous forest than of lower elevation deciduous forest. With the exception of the Veery (Catharus fuscescens), all the passerines of the southern forests are common in northern Spruce-fir. Of the passerines in Table 1, only the warblers and thrushes are very common in low-elevation deciduous forests (Stupka 1963, Kendeigh and Fawver 1981). Spruce-fir bird communities in the southern Appalachians are, then, island-like in their distinctness from the surrounding lowland communities and their greater similarity to distant boreal forest communities.

This summary so far has been somewhat oversimplified in dealing typologically with nearly pure Spruce-fir forest mixed only with some Yellow Birch (Betula lutea) and occasional Mountain Ash (Sorbus americana) and American Beech (Fagus grandifolia). In the altitudinal transition between northern hardwoods and spruce-dominated forest, many other bird species occur. For instance, the following species, more characteristic of deciduous and mixed forests, were observed at Newfound Gap (1538m elevation), Great Smoky Mountains, in July 1984: Song Sparrow (Melospiza melodia), Indigo Bunting (Passerina cyanea), Catbird (Dumetella carolinensis), Rufous-sided Towhee (Pipilo erythrophthalmus), Red-eyed Vireo (Vireo olivaceus), Canada Warbler (Wilsonia canadensis), Black-and-white Warbler (Mniotilta varia) and Ruby-throated Hummingbird (Archilochus colubris). Some mixing of Spruce-fir and deciduous avifaunas also occurs, at elevations down to 1000m, in Hemlock (Tsuga canadensis) stands in creek valleys, and in successional stands following fire or windthrow at higher elevations. Of course, during vernal and

autumnal migrations many species of birds uncharacteristic of the breeding fauna pass through the high elevations. In late summer, lowland species like the Black-and-white Warbler disperse widely and wander into Spruce-fir forests (Burleigh 1948; Stupka 1963; R. Wauer, pers. comm.). Less regular "invasions" can have greater impact as in years when transients like Red Crossbills (Loxia curvirostra), Evening Grosbeaks (Hesperiphona vespertina), and Pine Siskins (Spinus pinus) arrive; the last species can occur in very large numbers in winters when the Spruce seed production is high, as in 1982 in the Great Smoky Mountains. Mountaintop "islands" of Spruce-fir forests do not have sharp boundaries, nor are they isolated from the larger montane fauna.

Theory of island biogeography makes predictions about the behavioral characteristics of species present on oceanic islands or in habitat islands. In general, species with good colonizing ability have proven to be behaviorally flexible and often inhabit second growth areas on the "mainland" (MacArthur and Wilson 1967; MacArthur 1972). Once part of a depauperate island fauna, populations of birds often show ecological release: an expansion of feeding behavior, habitat use and/or numbers that presumably results from reduced competition from ecologically similar species (Diamond 1975; MacArthur 1972).

Species representing their families in southern Appalachian Spruce-fir are generally not the representatives one might expect on a true island. For instance, the Black-throated Green Warbler, the Golden-crowned Kinglet, and the Black-capped Chickadee are more characteristic of climax old-growth forest than their congeners that are sympatric in the north. The Black-throated Green Warbler has proven to be a poor colonizer of offshore islands and less flexible in its foraging than other warblers (Morse 1971). Of course the sheer distance separating southern Spruce-fir islands from each other or from the larger Canadian coniferous forest cannot by itself be a significant barrier to colonization to birds that return each summer from the tropics. In a study comparing foraging behavior of Spruce-fir birds in the Great Smoky Mountains with that shown in northwestern Maine, I found that six species of arboreal insectivores were more generalized in their foraging in the southern forests, as expected. However, the degree of change was not correlated with the degree of expected release from exclusively northern species, suggesting that a more general condition was affecting the foraging behavior of these populations and causing some of the island-like characteristics (Rabenold 1978). The ecological characteristics of southern Spruce-fir birds do not support a strict analogy with oceanic island avifaunas.

True islands are thought to be depauperate because distance from a mainland species pool depresses likelihood of colonization and because small physical area supports small populations with greater probability of local extinction. A dynamic equilibrium between colonization and extinction is expected on islands (MacArthur and Wilson 1967; Diamond 1969; MacArthur 1972), yet no such species turnover can be detected in the near-century since Brewster's studies in 1886. Contributing to a species-area relationship can also be a limited sample of habitat types on small islands or producer populations that themselves show little variety. No strong effect of island area can be detected in southern Appalachian Spruce-fir avifaunas with current information. Smaller areas like the Black Mountains of North Carolina have supported the same avifauna as areas twice as large like the Great Smoky Mountains. However, more careful censusing must be done, especially in the

smaller areas outside the Great Smoky Mountains, before a firm conclusion can be drawn concerning the species-area relationship.

The pattern of increasing bird species diversity and increasing similarity of coexisting species with increasing latitude that has been shown for Appalachian Spruce-fir also applies to eastern deciduous forests (Rabenold 1979). This generality has led me to look for an explanation of species diversity in Spruce-fir that is not tied to its similarity to an archipelago, since eastern deciduous forest does not share this characteristic. Even on the highest ridges of the southern Appalachians, the climate is more equable than that of far northern Spruce-fir. The productive season is less compressed into a short summer in the south than in the north and winters are not so harsh. Long-distance migrants, especially the warblers, vireos and thrushes, undoubtedly can capitalize so effectively on the short burst of summer productivity in boreal forests partly because resident temperate species cannot effectively track the strong resource oscillations. Food levels in the breeding season in northern Spruce-fir could be high enough to ease competition and promote coexistence between similar species. Densities of food for insectivores did reach much higher levels in Maine than in the Great Smoky Mountains in my 1978 study. Relative food abundance in the north can be due not only to an intense burst of productivity in summer, but also to the fact that in winter all bird populations must either migrate long distances or endure a boreal winter and therefore suffer greater overwinter mortality. In the southern Spruce-fir forests, winters are milder but, more importantly, downslope refugia exist to which essentially resident populations can easily retreat. The widespread altitudinal migrations performed by the numerically dominant species may be effective enough that overwinter mortality is reduced and arrival time hastened, crowding out the later-arriving long-distance migrants.

In summary, the bird communities of southern Appalachian Spruce-fir forest, and of the peaks of the Great Smoky Mountains in particular, do in many respects resemble islands of Canadian biome. In spite of their distinctiveness from downslope communities, the boreal distribution of most of the species and their low species diversity, they do not seem to function strictly as true islands. Most importantly, they are dominated by altitudinally migrating populations so that the dynamics of their populations are likely very different from those of northern Spruce-fir, where latitudinally migrating warblers dominate. The next section will present further evidence of the distinctiveness of this avifauna and possible application of the island paradigm over evolutionary time.

HISTORICAL DISTINCTNESS OF THE MONTANE ISLAND RELICTS

Endemism is an indicator of the degree of isolation of a fauna over evolutionary time and of the independence of development from other systems. Levels of endemism have been used to recreate the history of speciation in studies of other montane systems where unique evolutionary pathways are expected because of the patchy distribution of high-elevation habitat types (B. Vuilleumier 1971; F. Vuilleumier 1981). Seven species of birds characteristic of Spruce-fir forests have developed recognized subspecies that are unique to the southern Appalachians (south of Pennsylvania) (Table 2). This level of taxonomic divergence, although it has not reached recognized speciation, establishes that the southern Appalachian Spruce-fir avifauna is distinctive

Table 2.--Avian species breeding in Spruce-fir forests that show recognized subspecies endemic to the southern Appalachians. (AOU checklist, 5th ed.)

Species	Endemic form	Common Name
<u>Junco hyemalis</u>	<u>J.h. carolinensis</u>	Carolina Dark-eyed Junco
<u>Parus atricapillus</u>	<u>P.a. praticus</u>	Appalachian Black-capped Chickadee
<u>Troglodytes troglodytes</u>	<u>T.t. pullus</u>	Southern Winter Wren
<u>Certhia familiaris</u>	<u>C.f. nigrescens</u>	Southern Brown Creeper
<u>Vireo solitarius</u>	<u>V.s. alticola</u>	Mountain Solitary Vireo
<u>Dendroica caerulescens</u>	<u>D.c. cairnsi</u>	Cairns's Black-throated Blue Warbler
<u>Sphyrapicus varius</u>	<u>S.v. appalachiensis</u>	Appalachian Yellow-bellied sapsucker

more than just for its paucity of species; this relict fauna has diverged evolutionarily from the northern fauna to form a unique assembly.

The island model of community dynamics is probably more applicable to this montane system on an evolutionary time scale than in ecological time. The southern Appalachians served as the colonizing source for emerging northern Spruce-fir habitats following the last glaciation in North America. As the retreating glaciers allowed expansion of northern Spruce-fir, coniferous forests in the Southeast began to shrink toward the mountains (Watts 1970; Hubbard 1971; Delcourt and Delcourt, this volume). Groups like the warblers (Parulidae) that had adapted to boreal forest and speciated during successive glaciations moved northward (Mengel 1964; Cook 1969). Selective pressures must have been very different in the shrinking forests of the southern Appalachians than in the north. The flexibility of colonists was likely at a premium in the north, while persistence in small populations through competitive superiority would have been favored in the south. Species that have proven to be good colonizers and flexible in foraging and habitat use, like Yellow-rumped Warblers (Dendroica coronata), have since lost their southern Appalachian breeding ranges. In contrast, species that are now numerical and social dominants in their genera in the north persisted in the southern Appalachians (e.g. Black-throated Green Warblers, Golden-crowned Kinglets, Black-capped Chickadees).

Post-glacial southern Appalachian Spruce-fir forest can be likened to a shrinking land-bridge island gradually cut off from the mainland by rising seas (of deciduous forest). The avifauna of this system seems to fit the "persistent relict" pattern (MacArthur et al. 1972; Wilcox 1978). In particular, the Black-throated Green Warbler has been characterized as a competitive and social dominant in Maine, and is a poorer colonizer of offshore islands

than exclusively northern species like the Yellow-rumped Warbler (Morse 1971). The Black-throated Green consistently dominates in mature forests in the north, while exclusively northern warblers tend more to occur in second-growth and edge habitats. The Black-capped Chickadee and Golden-crowned Kinglet, representatives of their families in the south, are numerical dominants in mature northern forests. The exclusively northern Boreal Chickadee (Parus hudsonicus) and Ruby-crowned Kinglet (Regulus calendula) occur more commonly in edaphic subclimax communities like bogs and poor upland sites (Dixon 1961; Bent 1964; Erskine 1971). In addition, species occurring in both the north and southern Appalachians in these families are more specialized in their foraging than their exclusively northern congeners (Rabenold 1978). The southern Spruce-fir avifauna appears to be a nonrandom subset of the larger northern fauna in that selection for persistence in an island-like depauperate fauna has probably favored competitively dominant species. The northern avifauna, by comparison, consists more of very similar, generalized species. This "stacking" of generalists in the north is probably allowed by seasonally compressed productivity and winter limitation of consumers, as outlined earlier. The historical selection for dominant specialists in the south is probably currently reinforced by poorer resource conditions during the breeding season and the greater success of locally resident, altitudinally migrating species.

Alternative historical perspectives paint a different picture of the origins of the characteristically depauperate southern Spruce-fir avifauna. Kendeigh and Fawver (1981) suggest that the avifauna of the Great Smoky Mountains Spruce-fir is depauperate because of insufficient time (2000-4000 yr) for recolonization of these forests by species driven north by the mid-Holocene post-glacial xerothermic period (the hypsithermal interval of Deevey and Flint 1957; see also Hubbard 1971). During this warmer and drier epoch, southern Appalachian Spruce-fir was likely of much lesser extent than in the recent century (Whittaker 1956; Delcourt and Delcourt, this volume). This shrinkage would certainly have exacerbated island effects, but evidence that it actually caused local extinction is lacking. Of course, such reconstructions of biogeographic processes over evolutionary time are very difficult to test, and they are not logically incompatible with the kind of ecological explanation I proposed earlier. That 3000 yr is insufficient time for recolonization of the southeastern Spruce-fir by tropical migrants passing through each spring may seem implausible in view of the rapid range expansions of eastern bird species in the 20th century. Furthermore, several species that are characteristic of Spruce-fir in New England occur at the lower elevations in the Great Smoky Mountains but generally not in the high-elevation Spruce-fir. Ovenbirds (Seiurus aurocapillus), Parula Warblers (Parula americana) and Blackburnian Warblers (Dendroica fusca) are common in northern Spruce-fir but in the Smokies are restricted to breeding at lower elevations. This suggests at least that some ecological factors limit the presence of these long-distance migrants in the southern Spruce-fir. In addition, many birds characteristic of Spruce-fir in New England are common winter residents in the Smokies: for example, Yellow-rumped Warblers, Ruby-crowned Kinglets, White-throated Sparrows (Zonotrichia albicollis) and Purple Finches (Carpodacus purpureus). The challenge in this field is to devise tests of these alternative explanatory schemes, and the Spruce-fir avifauna, because of the clear patterns it presents, should continue to be a fruitful subject.

FUNCTIONAL BOUNDS OF SPRUCE-FIR POPULATIONS:
ALTITUDINAL MIGRATION OF CAROLINA JUNCOS

Altitudinal migration is probably a key to the structure of southern Appalachian Spruce-fir avian communities. The ability of the numerically dominant populations to escape the boreal winter of the high elevations just by moving a few kilometers downslope may help explain the relative absence of latitudinal migrants. This seasonal movement among habitat types also demonstrates the importance of ecological conditions in other ecosystems for population dynamics and community structure in Spruce-fir.

Since 1979, Patricia Parker Rabenold and I have studied the altitudinal migration of the most abundant breeding bird species in the Spruce-fir system of the Great Smoky Mountains: the Carolina Junco (Rabenold and Rabenold, in press). Our basic empirical questions have been: (1) Over what distance does this migration occur? (2) Is there differential migration between the sexes similar to that found for latitudinally migrating juncos (Ketterson and Nolan 1976)? (3) How commonly does year-round residency in the breeding habitat occur? (4) Does the winter range of the latitudinally migrating northern Dark-eyed Junco (*J.h. hyemalis*) overlap that of the Carolina Junco? and (5) How likely are juncos to remain at the same site within winters and between years? Our conceptual goal has been to ask whether the workings of this short-distance migration system can be understood using ideas developed in studies of latitudinal migrants concerning the ecological determinants of variation in migratory effort.

Carolina juncos cover a range of climates and habitats during their annual cycle that is comparable to that encountered by the northern subspecies in more than a thousand kilometers of latitudinal travel. Over 4 years we have captured and individually marked 1832 juncos of both subspecies in the drainage of the Oconaluftee River from Indian Gap, in Spruce-fir breeding habitat within Great Smoky Mountains National Park, to Whittier, NC, 21 km distant. Over this 1000m elevational gradient, mean January temperatures differ by more than 7°C and snow cover is much more common in winter at the high elevations. We have studied juncos at 22 different sites in this valley but for this discussion I will refer simply to distant sites near Whittier (610m altitude, 21 km from Indian Gap), low elevation sites near Oconaluftee Ranger Station (640m, 16 km), middle elevation sites near Smokemont (730m, 13 km) and high-elevation sites in the vicinity of Indian Gap (1610m) in breeding habitat. Juncos do not generally breed below 1200m elevation in this drainage, except in hemlock stands along streams.

In the Oconaluftee drainage, most juncos spend the winter outside the breeding habitat (below 1200m). Using mark-recapture calculations, we estimate that more than 150 individuals use a feeding site at Smokemont or Oconaluftee, but fewer than 20 use sites at Indian Gap. Because the breeding habitat is a very small area compared to the winter range, this indicates that only a small proportion of the population spends the winter on the Spruce-fir breeding ground. Most Carolina Juncos in the Oconaluftee drainage winter more than 10 km from breeding habitat at elevations from 600-800m in deciduous forests and clearings. Great Smoky Mountains National Park is large enough to encompass most, but not all of the winter population of Carolina Juncos.

Winter flocks of juncos within Park boundaries in the study drainage are composed mostly of Carolina Juncos, and most of these Carolinas are males (Figure 2). Of 1654 individuals captured in January, February and March 1980-1984 in the Oconaluftee valley 76% were Carolinas and 77% of the Carolinas were male (mostly near Oconaluftee and Smokemont). Outside Park boundaries,

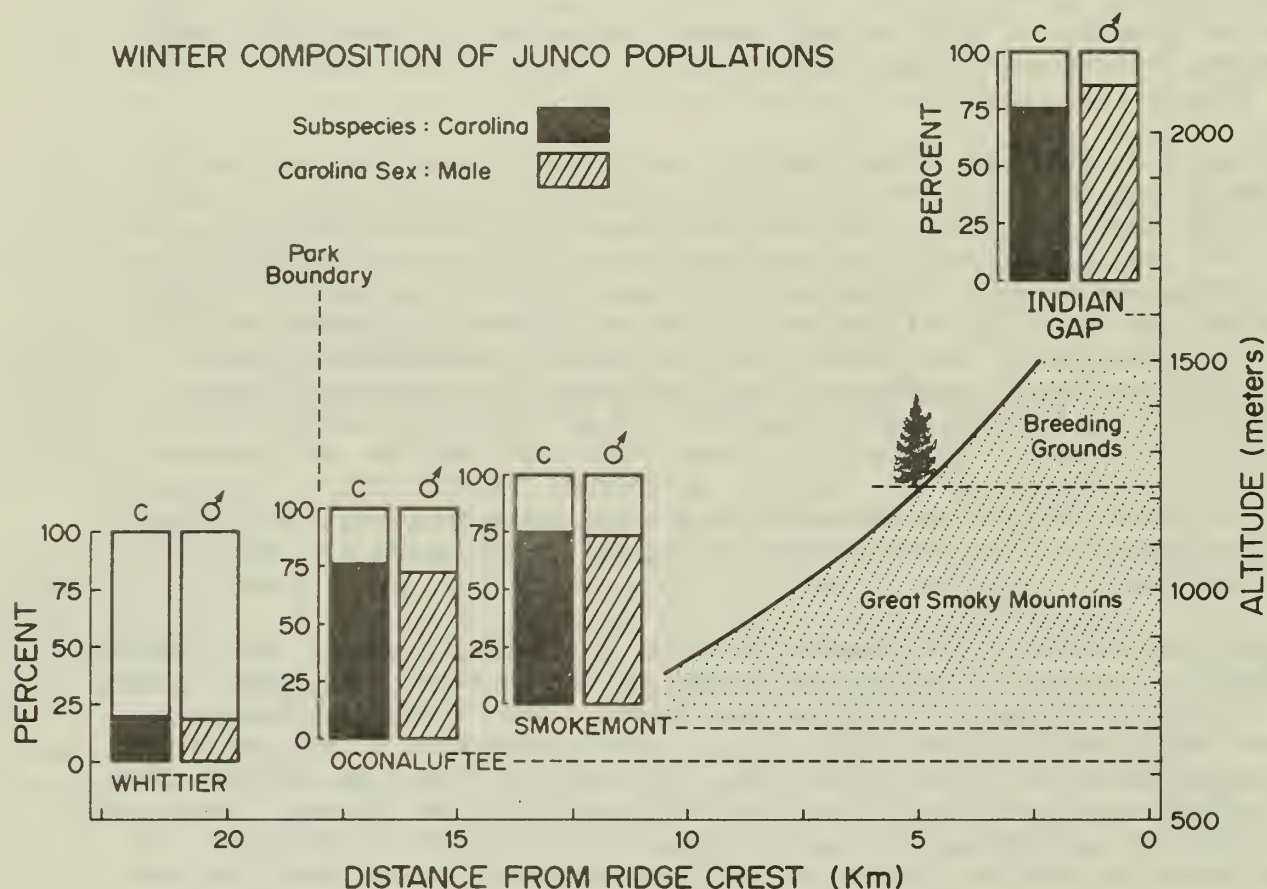


Figure 2.--Composition by subspecies and sex of winter flocks of Dark-eyed Juncos (Carolinas - *J.h. carolinensis*, and Northerns - *J.h. hyemalis*) in the Oconaluftee drainage 1980-1984. Sample sizes are: Whittier - 101 individuals of both subspecies; Oconaluftee - 495; Smokemont - 339; Indian Gap - 108. Subspecies and sex determinations are made by size and plumage characteristics. Data are from January/February 1981, 1982 and 1984 and from March 1980. Results from March 1981 and 1982 are omitted because spring migration was underway (1981) or complete (1982).

farther than 20 km from breeding habitat, 83% have been Northerns in January (N = 97) and 80% of the Carolinas have been female (N = 20) (Figure 2). In the breeding habitat of Spruce-fir around Indian Gap, few wintering juncos are Northerns (25%; N = 108) and very few Carolinas are females (15%; N = 66). The subspecies of juncos segregate in winter: Carolinas remain at the feet of mountains bearing Spruce-fir while Northerns winter mostly farther from the peaks and throughout the Piedmont. Differential migration between the sexes of

Carolina Juncos is striking since males more commonly remain close to breeding habitat than females. Partial migration among male Carolinas results in some year-round residency in the breeding habitat. Recapture information from marked birds shows that some males remain on the same small home range year-round for several years in Spruce-fir forest, while other males migrate from the crest of the Smokies to winter up to 20 km away in lowland deciduous forest.

Patterns of subspecies segregation in winter, and of differential migration of the sexes in Carolina Juncos, are variable from year to year. The winter of 1980-1981 was colder than that of 1981-1982. For 7 weather stations within 30 km of Oconaluftee, temperatures were 2.7°C colder in January and 4.2°C colder in February of 1981 compared to 1982, and these months were 4-7°C colder than average in 1981. In January 1981, 87% (N = 203) of juncos were Carolinas in the Oconaluftee drainage, compared to 66% (N = 319) in 1982 ($p < .001$; χ^2 test). Females were better represented in the study area in the warm January of 1982 (37%) than the colder January of 1981 (17%) ($p < .001$; χ^2). Because Carolinas are larger than Northernns and males are larger than females, the pattern of Carolina males dominating at middle and high altitudes means that average body size of wintering juncos is higher at higher altitudes. Even within the class of Carolina males, the cold winter of 1981 produced a gradient of body size in the Oconaluftee drainage that did not appear in 1982. In general, smaller juncos (Northernns, Carolina females and small Carolina males) were better represented at middle and high elevations during a milder winter. Timing of spring migration is also variable. In the warm winter of 1982, juncos had left the winter grounds near Smokemont and Oconaluftee by the first week in March. In the two previous colder years, juncos had either just begun migratory movement (1981) or were still in a stable winter distribution (1980) at the same calendar dates. The altitudinal migrations of Carolina Juncos are flexible and apparently responsive to changing environmental conditions.

In spite of some variation in timing, the Carolina Junco population usually recolonizes Spruce-fir by late March each spring. Males arrive before females, but not much before. In March 1981, the first-arriving migrants at Indian Gap were 91% male (N = 35), but in March 1982, when the low-elevation winter grounds had been vacated, the sex ratio was near 1:1 (54% male; N = 39). This arrival by females in the first week of March is fully 6 weeks before the earliest recorded egg-laying of Carolina Juncos and 2-6 weeks before the earliest recorded arrivals of long-distance migrants like Black-throated Green Warblers, Solitary Vireos, Blackburnian Warblers, and Veerys (Stupka 1963). Exclusively northern warblers like the Baybreasted (*Dendroica castanea*) and Cape May (*D. tigrina*) do not pass through the park until mid to late April, when Juncos are already nesting. Altitudinal migrants like Carolina Juncos clearly get a head-start on territory formation and breeding over the late-arriving tropical migrants.

We have used recapture data to analyze site tenacity in Dark-eyed Juncos over several time scales: (1) Carolina Juncos show greater probabilities of recapture than Northernns both between and within winter months, but no greater tendency to visit capture sites separated by 200-400 m, probably indicating higher survival by Carolinas; (2) male and female Carolinas show no difference in probability of recapture in winter but females seem to have larger ranges;

(3) Carolina Juncos are more site-tenacious in winter at high altitudes than low; (4) Carolinas return faithfully both to winter and summer ranges after migratory absences. To illustrate the last result, 79% of birds captured in successive winters had returned to the site where originally banded ($N = 66$) and 97% ($N = 29$) of marked birds censused in successive summers were found on the same breeding territories as the previous year. All of the 21 birds banded in winter in Spruce-fir that have been recaptured in a later winter were found at the same sites as before. Furthermore, we have banded 164 Carolinas in breeding habitat in January or March and resighted 57 of these in the following breeding season. All resightings have been within 200m of the original capture. Within their system of altitudinal migration, Carolina Juncos are surprisingly sedentary--they tend not to stray from relatively small ranges except for the brief bouts of migratory movement in spring and fall and they tend to return to sites after a migratory absence. Further study is needed of winter ranges and natal dispersal before an accurate picture of the demography of this population will be possible, and these patterns of site tenacity make such study feasible.

Three hypotheses developed in the study of long-distance migrants to explain differential and partial migration lend some insight into this system of altitudinal migration. Migratory effort and choice of wintering ground by Carolina Juncos appears to be a flexible response adjustable to pressures created by behavioral interactions with other birds. In reviewing evidence for adaptive adjustment of migratory effort in latitudinal migrants, especially Northern Juncos, Ketterson and Nolan (1983) point out that (1) physiological tolerances that vary systematically between classes of individuals could produce differential migration and winter segregation, (2) behavioral differences among individuals in dominance interactions and competition for food in winter could produce similar patterns, and (3) competition in the breeding season for territories and mates could contribute to the advantage of residency in, or wintering near, the breeding habitat. Patterns of survival and ranging revealed by mark-recapture calculations are consistent with the hypothesis that small competitively subordinate classes of juncos - Northerns and female Carolinas - either suffer greater mortality or are forced to range more widely in search of food in winter.

The basic patterns of assortment on the winter grounds in this study are consistent with all 3 hypotheses considered. Carolina males have been socially dominant over females and Northerns in our preliminary aviary experiments. This dominance can produce a marked effect on diet when a range of food types is available - subordinates in flocks shift their diets considerably away from foods preferred in isolation (see also Fretwell 1969; Balph 1977; Baker et al. 1981 on dominance in Northern Juncos). Female Carolinas might be forced to migrate farther to avoid competition with males and to range more widely on the winter grounds as well. The warm winter of 1982 may have ameliorated such competitive effects and allowed females and Northerns to winter in greater numbers in the study area. The larger body size of Carolina males compared to females and Northerns should also confer greater physiological tolerance of cold and fasting at high altitudes. In addition, territory establishment in spring by males may exert selective pressure on them to remain as near as possible to places where they are likely to breed to reap the benefits, described in other studies, of dominance determined by prior occupancy. While consistent with the major pattern of male-biased sex ratio at high altitudes in winter, these last two considerations are of limited application to Carolina Juncos.

The balance of selective forces determining migratory effort in Carolina Juncos are likely different from those affecting long-distance migrants. Physiological and distributional studies suggest that size-related tolerance of cold and fasting may not be a plausible explanation of differential migration even in Northern Juncos (reviewed in Ketterson and Nolan 1983). The short distances separating male and female Carolinas in winter make it likely that energetic costs of migratory travel and effects of wintering ground on time of return to Spruce-fir will be relatively less important, and competitive effects more important, than for long-distance migrants. Year-round residency by males in Spruce-fir is best explained by the "home court" advantage - a head-start on breeding on an already-established territory. Differential migration of the sexes of Carolinas is best explained by competitive effects in winter, but more study is needed of the relationships among competitive interactions, movement patterns, survival and reproductive success. The altitudinal migrations of Carolina Juncos could prove to be a model for similar movement patterns of other numerically dominant species of the Spruce-fir breeding bird community.

FUTURE AVIAN RESEARCH AND CONSERVATION PRIORITIES

Our understanding of the determinants of community structure in the southern Appalachian Spruce-fir avifauna is imperfect and this unique, peculiarly southern Appalachian assembly continues to be enigmatic. In the next decade this small and probably fragile ecosystem will undoubtedly be changed by the environmental stresses now besetting it. Some of these issues can only be addressed at the national level but some are local management matters. The future of this relict ecosystem depends mainly on the degree to which it functions as a biological island, and much research will be needed to properly address that question. To the extent that Spruce-fir-clad mountaintops are islands, the expanse of this habitat in Great Smoky Mountains National Park may have already proven too small to support a complete boreal avifauna and the limits of the Park too narrow to fully protect even the remaining populations. Further inroads into this habitat and destruction of winter habitat within and outside the Park can only lead to further dilution or diminution of a fauna that is the most unique and vulnerable ward of the Park. Little of it is adequately protected elsewhere, and none in such a pristine state.

The application of the theory of island biogeography to conservation issues and the management of wildlife preserves has been hotly debated recently (May 1975, Terborgh 1976; Soulé and Wilcox 1980; Simberloff and Abele 1982). Some clear empirical lessons remain, however. Oceanic islands and habitat islands do have fewer species than large expanses of similar habitats - the existence of a positive relationship between area of habitat and number of species has long been clear. Furthermore, there are repeated patterns in depauperate faunas regarding which species are absent relative to the regional species pool. Southern Appalachian Spruce-fir supports a low diversity of bird species. Comparison with lower-elevation habitats is confused by the general trend for diversity to decline with altitude (Able and Noon 1976). More importantly, southern Spruce-fir is lacking the abundance of neotropical migrants common to northern Spruce-fir, and parallels can be found in studies of deciduous forest fragments. In a comprehensive study of remnant woodlots in the eastern U.S., Whitcomb and coworkers (1981) point out that neotropical migrant bird species, especially the warblers that are forest interior

specialists, are the most vulnerable to extirpation as woodlands are fragmented into smaller and more isolated patches. These authors attempt to explain the sensitivity of long-distance migrants to habitat fragmentation by the "unsuitability of several life history features common to forest interior neotropical migrants" (p. 190). The applicability of the parallel with southern Spruce-fir habitat islands can be judged only once better information concerning composition of Spruce-fir bird communities of the southern Appalachians is in hand.

Further study is needed of the composition of bird communities in Spruce-fir forests, particularly of the variability between sites within a large range like the Great Smoky Mountains, and differences in smaller ranges like the Plott Balsams and Black Mountains of North Carolina. If the island paradigm is applicable, there should be an appreciable species-area effect within the southern Appalachians. The absence of chickadees on Mt. Mitchell (Burleigh 1948; Adams 1959) suggests that such a pattern may exist. As a calibration for these comparisons, more must also be known about the year-to-year variation within a particular site.

To intelligently anticipate the fate of the southern Spruce-fir system, further study should be made of the effects of downslope systems on high-altitude population dynamics. Dispersal data would help reveal the degree to which Spruce-fir populations are replenished by the productivity of lower-elevation populations. It is also possible that the composition of downslope communities is altered by proximity to Spruce-fir. The possibly reciprocal effects at the ecotone of Spruce-fir could be explored with altitudinal transects of censusing and banding from Hemlock or northern hardwoods into Spruce-fir. Possibly most important is further study of altitudinal migration. The structure of Spruce-fir bird communities may be vulnerable to changes in the low-elevation wintering grounds of short-distance migrants. For instance, if cleared areas at low elevations within the Park are allowed to revert to forest, Carolina Junco populations could be forced outside the Park boundaries where they could suffer from effects of shrinking habitat. Before this effect could be reasonably predicted, however, surveys of habitat preferences of wintering altitudinal migrants would have to be undertaken. Our study of Carolina Juncos suggests that one sex is particularly affected by conditions outside the Park; studies of other altitudinal migrants could similarly explore the functional limits of Spruce-fir populations. More extensive censuses in both winter and summer would also document effects that changes in the densities of altitudinal migrants might have on the representation of long-distance migrants in the community, thereby testing some of the ecological hypotheses presented here for the determination of community structure.

The last half of this decade will bring tests of the stability and invasibility of the Spruce-fir avifauna, but as experiments these tests may confuse the causes of change. The wholesale death of Fraser's Fir, whether the causes are airborne pollutants or destructive insects, can probably no longer be prevented. The opening of the canopy has already begun to change the forest floor by encouraging growth of Rubus thickets. Productivity will become more concentrated near the ground, adversely affecting canopy-foraging and canopy-nesting birds like the warblers and kinglets. The climate and cover near the ground will also change, perhaps interfering with near-ground foragers and nesters like the juncos and wrens. These trends will be exacerbated by

increased wind-throw of spruce following the death of fir. As broad-leaved vegetation invades, deciduous-forest bird species will probably expand their altitudinal ranges and diminish the boreal character of the avifauna. Catbirds, Towhees, Song Sparrows and others can be expected. Confusing these effects will be the increasingly destructive effects of feral swine. These animals have already turned over large areas of forest floor and are bound to have a detrimental effect on ground-nesting species. This situation is probably controllable, and the threat to the ecosystem is serious. If the mission of a National Park is partly to preserve working ecosystems, the Spruce-fir of the Great Smoky Mountains is probably the most unique the Park shelters and the one most threatened, in part because of its small size. Research and conservation energies should be focused there, and the avifauna holds great potential rewards for both.

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MAMMALS OF THE SPRUCE-FIR FOREST IN
GREAT SMOKY MOUNTAINS NATIONAL PARK

Michael R. Pelton¹

At the present time there are 60 species of mammals listed as likely occurring in Great Smoky Mountains National Park (Linzey and Linzey 1968). The distributional range of 31 (52%) (16 of 17 possible families) is believed to encompass the spruce-fir vegetation zone of the Park (Table 1). However 22 (71%) have been reported from a wide range of elevations with only 9 species (29%) restricted to higher elevations and none totally restricted to the spruce-fir forest. Other species, particularly bats may occasionally occur in the spruce-fir but have not been reported to date.

Mammals of the spruce-fir include 5 of 8 shrew species (Soricidae), 2 of 3 moles (Talpidae), 1 of 8 bats (Vespertilionidae) 2 of 2 rabbits (Leporidae), 5 of 7 squirrels (Sciuridae), 6 of 20 other rodents represented by native rats and mice (Cricetidae), old world rats and mice (Muridae), and jumping mice (Zapodidae). All of the members of the order Carnivora (n = 9) with the exception of the skunks (Spilogale putorius and Mephitis mephitis) are represented in the spruce-fir; this includes the families Canidae, Ursidae, Procyonidae, Mustelidae, and Felidae.

The relatively large home range and/or movement patterns of the larger mammals such as white-tailed deer (Odocoileus virginianus), European wild hog (Sus scrofa), and the Carnivora in general results in their occasional presence and/or use of the spruce-fir forest. However food or cover resources for many of these larger mammals often are limited in this vegetation type. For example there is little available or palatable food in the spruce-fir for white-tailed deer or European wild hogs. In the pure spruce-fir stands bears find few berries and no acorns. In addition the limited area of the spruce-fir and the occurrence of most of the smaller prey species (i.e. Cricetidae) in other, more extensive vegetation types in the Park, results in more limited use of the spruce-fir than other vegetation types by carnivores. Consequently, the overall use of the spruce-fir zone by the larger mammals is oftentimes incidental compared to their use of other vegetation types.

At the present time no definitive population data are available for any mammalian species in the spruce-fir forest. Although population studies have been conducted on a number of Park mammals including black bears (Ursus americanus) (Pelton and Marcum 1975), white-tailed deer (Kinningham 1980), raccoons (Procyon lotor) (Keeler 1978, Rabinowitz 1981), woodchucks (Marmota monax) (Taylor 1979), striped skunks (Goldsmith 1981), and golden mice (Linzey 1966), all such studies have been conducted in vegetation types other than the

1. Professor, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, Knoxville, 1984.

spruce-fir. Data accumulated to date predominantly consist of general distributional records accumulated by various workers since the 1930's (Komarek and Komarek 1938 and Linzey and Linzey 1968).

Even though the southern extension of the spruce-fir forest terminates in the Park, it appears that no single species is totally dependent on this vegetation type.

Because so little is known about the population status of mammals residing or using the spruce-fir forest, the impacts of any significant vegetation change on mammal populations is unknown. Obviously, those species whose ranges are more closely associated with spruce-fir [i.e. masked shrew (Sorex cinereus), long-tailed shrew (Sorex dispar), Pigmy shrew (Microsorex hoyi), Northern flying squirrel (Glaucomys sabrinus) and Rock vole (Microtus chrotorrhinus)] are the ones that would be most significantly affected. Major disruptions of this area could have significant impacts on these species since most are at or near the southern extremity of their range in North America. Wind, fire, or insect damage in the spruce-fir create openings in the canopy and consequently new microhabitats; these new habitats may then be beneficial or detrimental to certain mammals. Such openings and their new successional plant species may allow new mammal species to invade and/or cause a decline in resident animals, or result in an increase in some resident species. Successional vegetation may illicit a more resident species. Successional vegetation may illicit a more positive response from larger mammalian species whose presence had only been incidental in the past. Food plants in the form of berry crops or succulent browse attract bears, hogs, deer and raccoon. In addition a positive response of some small mammal populations to the altered conditions could result in more use of the spruce-fir habitat by mammalian predators.

Future research efforts should concentrate on the status of the 9 mammalian species restricted to higher elevations and specifically the 5 species reportedly found only in the northern hardwood/spruce-fir forests of the Park. The status of the above 5 species should be evaluated on disturbed and undisturbed spruce-fir sites to assess the impacts of vegetation changes occurring. In addition the relative use or lack thereof by larger, more mobile mammals also should be assessed on these contrasting spruce-fir sites.

The spruce-fir forest is a logical selection for initiating future small mammal studies in the Park. It is a relatively restricted and well defined vegetation type, its southern terminus in North America occurs in the Park, and it is undergoing significant change at the present time.

For more detailed information the readers are referred to Komarek and Komarek (1938), Kellogg (1939), and Linzey and Linzey (1968). The Park Library also contains the journal of Arthur Stupka, former naturalist and biologist for the Park (his journal covers the years 1935-1963) and a series of theses, dissertations and technical papers produced in the Department of Forestry, Wildlife, and Fisheries and Graduate Program in Ecology, The University of Tennessee, Knoxville from 1971 to present.

Table 1. Mammals occurring in the Spruce-fir forest of Great Smoky Mountains National Park.¹

Family and Scientific Name	Common Name	General Range
Didelphidae		
<u>Didelphis virginiana</u>	Virginia opossum	All elevations
Soricidae		
<u>Sorex cinereus</u>	Masked shrew	Northern hardwoods and spruce-fir
<u>Sorex fumeus</u>	Smoky shrew	Mid. to higher elevations
<u>Sorex dispar</u>	Long-tailed shrew	Northern hardwoods and spruce-fir
<u>Microsorex hoyi</u>	Pygmy shrew	Northern hardwoods and spruce-fir
<u>Blarina brevicauda</u>	Short-tailed shrew	All elevations
Talpidae		
<u>Parascalops breweri</u>	Hairy-tailed mole	All elevations
<u>Condylura cristata</u>	Star-nosed mole	All elevations
Vespertilionidae		
<u>Eptesicus fuscus</u>	Big brown bat	All elevations
Leporidae		
<u>Sylvilagus floridanus</u>	Eastern cottontail	All elevations
<u>Sylvilagus transitionalis</u>	New England cottontail	All elevations
Sciuridae		
<u>Sciurus carolinensis</u>	Gray squirrel	All elevations
<u>Marmota monax</u>	Woodchuck	All elevations
<u>Tamias striatus</u>	Eastern chipmunk	All elevations
<u>Tamiasciurus hudsonicus</u>	Red Squirrel	All elevations

Table 1. (Continued - page 2)

Family and Scientific Name	Common Name	General Range
Cricetidae		
<u>Peromyscus maniculatus</u>	Deer mouse	All elevations
<u>Clethrionomys gapperi</u>	Gapper's red-backed mouse	Mid to higher elevations
<u>Microtus chrotorrhinus</u>	Rock vole	Northern hardwood and spruce fir
Muridae (Old World Rats and Mice)		
<u>Rattus norvegicus</u>	Norway rat	All elevations
<u>Rattus rattus</u>	Black rat	All elevations
Zapodidae (Jumping mice)		
<u>Napaeozapus insignis</u>	Woodland jumping mouse	All elevations
Canidae		
<u>Vulpes vulpes</u>	Red fox	All elevations
<u>Urocyon cinereoargenteus</u>	Gray fox	All elevations
Ursidae		
<u>Ursus americanus</u>	Black bear	All elevations
Procyonidae		
<u>Procyon lotor</u>	Raccoon	All elevations
Mustelidae		
<u>Mustela frenata</u>	Long-tailed weasel	All elevations
<u>Mustela vison</u>	Mink	All elevations

Table 1. (Continued - page 3)

Family and Scientific Name	Common Name	General Range
Felidae		
<u>Lynx rufus</u>	Bobcat	All elevations
Suidae		
<u>Sus scrofa</u>	European wild hog	All elevations
Cervidae		
<u>Odocoileus virginianus</u>	White-tailed deer	All elevations

¹Summarized from Linzey and Linzey (1971).

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DISTRIBUTION AND STATUS OF THE NORTHERN FLYING
SQUIRREL AND THE NORTHERN WATER SHREW
IN THE SOUTHERN APPALACHIANS

Donald W. Linzey

Abstract.--The northern flying squirrel and northern water shrew exist in disjunct, relict populations in the southern Appalachians. Only 27 specimens of the northern flying squirrel from 8 localities in the southern Appalachians exist in collections. A recently completed two year study involved the placement of 490 nest boxes in high elevation habitat throughout a five state study area. The study resulted in this species being rediscovered on Mt. Mitchell after not having been recorded there for 31 years. No specimens have been recorded in the Great Smoky Mountains National Park since 1958 (24 years) nor from Whitetop Mountain in Virginia since 1966 (17 years). Habitat destruction, interspecific competition with the smaller, more aggressive southern flying squirrel, and infection by a parasitic nematode have been proposed as possible causes of the decline of this species. A survey to determine the status and distribution of this species is recommended.

Only 50 specimens of the northern water shrew from 10 localities exist in collections. These shrews have been taken from two new areas in the Great Smoky Mountains National Park. These specimens represent a new watershed record and a low elevation record. One population in existence in 1950 and 1965 was apparently gone in 1980. This species is currently known to inhabit only two localities in the Park. Additional population studies are recommended.

Additional keywords: Endangered species, Sorex palustris, Glaucomys sabrinus.

INTRODUCTION

The mammalian fauna of the southern Appalachians is diverse, ranging in size from the pygmy shrew to the black bear. Some species are widespread in distribution, whereas others inhabit only specific portions of the region. Those species with restricted ranges are, in many cases, the species which are increasingly being classified as rare, threatened, or endangered due in large part to modifications and/or elimination of their habitat.

Among the 60 or so species of mammals currently inhabiting the Great Smoky Mountains National Park, several have been recorded from only two or three localities. Some of these species reach the northernmost limit of their

1/ Consulting Biologist, 2101 Nellies Cave Road, Blacksburg, Virginia 24060

range in the Smokies (rice rat, cotton rat). Others prefer cultivated areas and fields which are becoming increasingly more scarce in the Park as succession proceeds. A few of these rare species reach the southernmost limit of their range in the Smokies. Such species are common in more northern states and in Canada, but in the southern Appalachians these species exist only in isolated, relict populations. Two species with restricted ranges which fall into this category are the northern flying squirrel (Glaucomys sabrinus) and the northern water shrew (Sorex palustris).

RANGE AND HABITAT OF FLYING SQUIRREL

The northern flying squirrel is represented in the southern Appalachians by two subspecies. Glaucomys sabrinus fuscus ranges from western Maryland south through West Virginia to southwestern Virginia. The range of Glaucomys sabrinus coloratus extends from southwestern Virginia south to the southern limit of the species' range in Tennessee and North Carolina. The subspecies fuscus has been recorded in West Virginia from Pocahontas and Randolph counties (Miller, 1936; Handley, 1953) and in Virginia from Smyth County (Handley, In: Linzey, 1979). The southern subspecies coloratus is known from only three localities. It has been taken in Yancey County, North Carolina (Handley, 1953) and in Sevier and Carter counties, Tennessee (Kellogg, 1939; Handley, 1953; Linzey and Linzey, 1971). Only 27 specimens and records of this species from 8 localities in the southern Appalachians exist in college, university, museum, and private collections. Seven are from West Virginia, one is from Virginia, four are from North Carolina (near Mt. Mitchell), and 15 are from Tennessee (13 from Roan Mountain, 2 from the Great Smoky Mountains National Park).

Both forms of flying squirrel are generally restricted to areas containing spruce and fir and to high elevation stands of hardwoods such as beech, birch, and maple. The hollows of large, old yellow birch trees in the ecotone between the spruce-fir forest and the northern hardwood forest provide many nesting cavities. Most records in the southern Appalachians are above 4000 feet elevation. The diet of these squirrels consists mostly of lichens, fungi, seeds, buds, fruit, and insects.

Glaucomys sabrinus fuscus may occur in the George Washington and Jefferson National Forests, while Glaucomys sabrinus coloratus may occur in the Jefferson, Pisgah, and Cherokee National Forests. The northern flying squirrel has been classified as Endangered in Virginia (Handley, In: Linzey, 1979), Threatened in North Carolina (Cooper, Robinson, and Funderburg, 1977), Deemed In Need of Management in Tennessee (Eagar and Hatcher, 1980), and Rare and Of Scientific Interest in West Virginia.

Only two specimens of the northern flying squirrel have ever been taken in the Park. One of these was taken in 1935 on Blanket Mountain southwest of Elkmont at an elevation of 4000 feet. In 1959, a nursing female was found dead on the road near Walker Prong. These squirrels have never been seen on Mt. LeConte or Clingman's Dome.

CURRENT STATUS OF FLYING SQUIRREL

A two year study of these species in the southern Appalachians has recently been completed. The study was jointly funded by the Office of Endangered Species of the U. S. Fish and Wildlife Service and Virginia Polytechnic Institute and State University. The study was a direct outgrowth of the Symposium on Endangered and Threatened Plants and Animals of Virginia which I organized in 1978 and for which I subsequently served as Editor of the Proceedings (Linzey, 1979). The study involved the distribution and status of these two mammals in parts of five states - Maryland, Virginia, West Virginia, North Carolina, and Tennessee.

To study the flying squirrel, we constructed nest boxes with sliding doors. A total of 490 nest boxes were erected in suitable high-elevation habitat throughout the study area. All boxes were checked periodically. We have boxes, for example, on Grandfather Mountain, Roan Mountain, Mt. Mitchell, and along the Blue Ridge Parkway. Here in the Smokies, I have 40 nest boxes in five areas from Newfound Gap to Clingman's Dome and in two areas on Balsam Mountain.

The nest boxes have been used primarily by southern flying squirrels (Glaucomys volans) and red squirrels (Tamiasciurus hudsonicus). Several litters of flying squirrels and red squirrels have been reared in the boxes.

Several northern flying squirrels have also been taken. One nest box on Mt. Mitchell yielded an adult male and an adult female northern flying squirrel - the first specimens of this species observed there since 1950, a period of 31 years. We have recorded other specimens in West Virginia. In the Smokies, however, I have been unsuccessful in finding any recent evidence of this species. Some nest boxes contain a few seeds or pieces of bark, but nothing in the way of nests as in most other localities. This does not necessarily mean that the northern flying squirrel has now been extirpated from the Park, but if they still do exist, their numbers must be minimal.

A similar situation exists in the Whitetop-Mt. Rogers-Pine Mountain area of southwestern Virginia. The only two specimens ever recorded from Virginia were taken on Whitetop in 1959 and 1966. Approximately 70 nest boxes have been erected in this area, but no northern flying squirrels have been taken.

Habitat destruction from clear cutting, certain forest management practices, and recreational development may have adversely affected some populations in the southern Appalachians. In addition, there is some evidence that interspecific competition between the northern and southern flying squirrel may be affecting the range of the former species. Although range maps show a broad zone of sympatry, in reality there is surprisingly little actual overlap in the ranges of these two species. Areas may be inhabited by one or the other of these marginally sympatric species at any given time, but not by both at the same time. The species' ranges in the overlap zone appear to be highly variable and often exclusive. Research has indicated that the larger northern flying squirrel may be displaced by the more aggressive, smaller southern flying squirrel in certain hardwood habitats where their ranges meet. In some areas, the southern flying squirrel has been taken near several sites where the northern flying squirrel had previously been recorded. There is also some evidence that the southern flying squirrel harbors a parasitic nematode of

the genus Strongyloides which may be transferred to the northern flying squirrel in areas where their ranges meet and overlap, and is lethal or debilitating (Weigl, 1977).

In Virginia, Handley (1979) noted: "Very likely, the numbers and range of the northern flying squirrel in the southern Appalachians have been shrinking as climate and habitat have changed ever since the Pleistocene. Even before the arrival of European settlers these processes probably had fragmented its range in the mountains of Virginia into relict segments. Logging and clearing for other land use and the consequent invasion of its habitat by the southern flying squirrel undoubtedly have accelerated the decline of the northern flying squirrel in the past two hundred years. It must now be on the verge of extinction in Virginia."

Handley (1979) further noted: "In Virginia, Glaucomys volans now occurs to the tops of the highest mountains and occupies the best remnants of habitat suitable for Glaucomys sabrinus.....The future looks bleak, indeed, for Glaucomys sabrinus in Virginia."

Speciation tends to occur most commonly near the periphery of a species' range as populations, for one reason or another, become isolated from each other. The relict populations of northern flying squirrels seem to be becoming increasingly isolated. This isolation can effectively prevent the free flow of genes among other members of the species. These geographical isolates eventually become recognized as distinct races or subspecies. This situation has already resulted in the naming of two subspecies of northern flying squirrel in the southern Appalachians. If viable populations continue to exist, further speciation may be expected.

MANAGEMENT RECOMMENDATIONS

Concerning Tennessee, Eagar and Hatcher (1980) stated: "A natural history survey is needed to establish the actual status of G. sabrinus in Tennessee and to provide information necessary in order to implement proper management measures. Lands with suitable habitat should not be disturbed, and more land acquisition should be urged by state and federal agencies."

For North Carolina, Weigl (1977) noted: "Additional research is needed on the Northern Flying Squirrel in the southern parts of its range before precise protective measures can be proposed. Preservation of high elevation forests and bogs, including both spruce-fir stands and adjacent zones of northern hardwood vegetation, is a necessity."

In Virginia, Handley (1979) stated: "Suitable habitats should be more thoroughly explored for Glaucomys sabrinus. If populations of this squirrel are found, an effort should be made to prevent further alteration of its habitat."

In order to determine the distribution and status of this species in the Park, an expansion of the existing network of nest boxes is recommended. Although considerable effort is required to construct, erect, and monitor these nest boxes on a regular basis, the cost of materials is minimal. A 24 month study should provide sufficient data to determine the status of this species in

the Park. Since the Blanket Mountain locality represents the southernmost locality for this species, every effort should be made to ascertain whether viable populations still remain within the protective confines of the Park.

RANGE AND HABITAT OF WATER SHREW

The northern water shrew is represented in the southern Appalachians by a single subspecies, Sorex palustris punctulatus. The range of this form extends from western Maryland south through West Virginia and western Virginia to Tennessee and North Carolina. Only 50 specimens and records of this species from 10 localities in the southern Appalachians exist in college, university, museum, and private collections. Nine are from West Virginia, one is from Virginia, five are from North Carolina, and 33 are from Tennessee (17 from the Cherokee National Forest and 16 from the Great Smoky Mountains National Park). It has been recorded in West Virginia from Preston, Randolph, Pendleton, and Tucker counties by Hooper (1942) and McKeever (1952). The only specimens ever recorded from Virginia were from Bath County (Pagels and Tate, 1976). Conaway and Pfitzer (1952) and Linzey and Linzey (1968; 1971) recorded this species in the Great Smoky Mountains National Park. Prior to 1980, the water shrew was known in North Carolina from only four specimens taken along Fires Creek in Clay County in 1973 (Whitaker, Jones, and Pascal, 1975).

In the southern Appalachians, Sorex palustris lives along the banks of swiftly flowing, rocky-bedded mountain streams, usually above 3000 feet elevation. They swim in the cold water in search of immature aquatic insects. Dominant vegetation may be spruce, fir, hemlock, willow, yellow birch, and rhododendron. The water shrew may occur in the George Washington, Jefferson, Pisgah, and Cherokee National Forests. Due to the paucity of data concerning the status and distribution of this shrew, it has been designated as Endangered in Virginia (Handley, In: Linzey, 1979), Status Undetermined in North Carolina (Cooper, Robinson, and Funderburg, 1977), Deemed in Need of Management in Tennessee (Eagar and Hatcher, 1980), and Rare and Of Scientific Interest in West Virginia.

It was not until 1950 that this species was recorded as a member of the Park fauna. In that year, Conaway and Pfitzer took several individuals along Walker Prong of the Little Pigeon River less than a mile below the confluence with Alum Cave Creek. These specimens represented a new state record for Tennessee. They also represented a southward range extension of 200 miles from a site in West Virginia. They have since been found living beneath overhanging banks and in rock crevices along Walker Prong and other tributaries of the Little Pigeon River from 3700 feet to 4700 feet elevation.

CURRENT STATUS OF WATER SHREW

The second part of the study for the U. S. Fish and Wildlife Service involved the northern water shrew. To study this species, Sherman live traps baited with potted meat were used. Traps were set in suitable habitat throughout the five state study area. Within the Park, trapping was carried out along

such waterways as Walker Prong, Kanati Fork, Beech Flats Creek, the Oconaluftee River, Bunches Creek, Cosby Creek, and several areas in the Greenbrier section including the Middle Prong of the Little Pigeon River and Porter's Creek.

In 1965, I was successful in rediscovering these shrews along Walker Prong. However, no specimens appeared to be present during 1980. Extensive trapping was conducted along Beech Flats Creek in 1965, but no shrews were taken. In 1980, however, one specimen was secured at an elevation of approximately 4000 feet. This record is especially significant because it represents the first record of this species in the North Carolina section of the Park and the first record for the Deep Creek watershed. It is only the second record of this species from the state of North Carolina. Also in 1980, a specimen was taken along a tributary of the Middle Prong of the Little Pigeon River near Ramsey Cascades. This record was unique because the specimen was taken at an elevation of between 1925 and 2000 feet and represents the lowest elevation on record for this species in the southern Appalachians. It significantly expands the area that could be inhabited by this species and that should be searched for its presence.

The problem of isolated populations and speciation addressed in the flying squirrel account holds true for the water shrew as well.

MANAGEMENT RECOMMENDATIONS

At the present time, the northern water shrew is known to be living in only two small areas within the Park. Although further trapping would undoubtedly reveal a more widespread distribution, the small, isolated populations would continue to be vulnerable. Since these areas are within a National Park, they will probably not undergo sudden alterations, but if any changes are planned, a thorough investigation should be made to determine whether water shrews are present.

The situation in the Park is obviously unique. Elsewhere the situation is quite different. In Virginia, for example, the water shrew has been taken at only one locality. It was discovered during the environmental survey for Virginia Electric Power Company's huge pumped storage reservoir project in Bath County (Pagels and Tate, 1976). This project is now approximately two-thirds complete and the shrew habitat has been completely destroyed. Thousands of trap nights in nearby areas and surrounding counties have failed to reveal the presence of any other populations. Extensive logging operations in West Virginia have the capacity to destroy considerable habitat for this species. Lowman (1975) noted that siltation caused by logging operations, off-road vehicles, and road construction can destroy mountain streams as suitable habitat for water shrews, as well as human waste, trash, and garbage from improperly located camping areas. Three new ski resorts are planning to begin operations during the latter part of 1983 in West Virginia. The construction of buildings and roads associated with these resorts could be extremely detrimental to shrew populations inhabiting these areas.

The precise distribution and abundance of this shrew within the southern Appalachians remains unknown. In Virginia, Handley (1979) stated: "It seems likely that the water shrew no longer occurs at the single locality where it

has been found in Virginia.....It is possible that other surviving isolated populations will be found, but at best numbers must be very low.....The remnants should be jealously protected." In addition, he proposed the following protective measures: "If there are remnant populations of water shrews to be protected in Virginia, they first must be located. Then it will be necessary to protect inhabited streams from clearing, siltation, pollution (particularly with insecticides), and other destructive disturbance."

CONCLUSION

The disjunct, island-like distribution of these three forms and their great distance from the center of their species' range in the northern United States and Canada suggest that they are relict forms which have become isolated in small patches of suitable habitat by changing climatic and vegetational conditions since the last glacial period of the Pleistocene. Handley (1971) noted that disjunctions in their ranges probably could be accounted for by irregularities in elevation of the mountains and oscillations in temperature.

The small, isolated populations of these forms in the southern Appalachians deserve protection. There is little we can do about natural climatic and vegetational changes. However, we can and should provide protection from such human activities as logging, bulldozing, siltation, and pollution. Our initial efforts need to concentrate on locating additional populations.

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SOILS IN THE SPRUCE-FIR REGION OF THE GREAT SMOKY MOUNTAINS

M. E. Springer¹

Abstract. Schematic diagrams were used to relate kinds of soil to elevation, aspect, parent material, and vegetation. Mean annual soil temperatures are superimposed on these diagrams. Also, a simplified diagram predicted Spodosols or Inceptisols under four combinations of spruce-fir and northern hardwood vegetation with coarse and fine textured parent material. Soils were unstable because of tree throw, creep, and landslides, but general patterns were predictable.

At high elevations, all the soils were low in base saturation and extremely acid. Major vegetation types were ranked in the following sequence of decreasing pH of the O horizon: northern hardwoods, spruce-fir, heath bald. This sequence was also a gradient of increasing distinctness of horizons and depth of O horizon layers.

INTRODUCTION

Soils of the spruce-fir region at elevations of 1500 to 1900 m in the Smoky Mountains are similar to those of spruce-fir regions farther north in the Appalachians but differ from soils at nearby lower elevations where conditions are warmer and dryer. Surveys and research studies in Great Smoky Mountains National Park (GRSM) and other parts of the Unaka mountains indicate that at high elevations all the soils are extremely acid and low in base saturation. They are mainly Inceptisols with lesser areas of Spodosols. Schematic diagrams relate the kind of soil to elevation, aspect, parent material, and vegetation. However, more precise information on the nature and location of the different soils is needed for decisions in management research.

LITERATURE REVIEW

Coile (1938) described well-defined Podzols in West Virginia and in Tazewell County, Virginia, and less well-developed Podzols at elevations above 1400 or 1500 m in southwestern North Carolina and eastern Tennessee. Near a Podsol in West Virginia, he described a brown forest soil under northern hardwood forest type and suggested that "The two contrasting types of soil, developed along the tension zone of the red spruce and birch-beech-maple forest types are believed to have been influenced in their development primarily by the widely different forest vegetation types."

Early soil surveys of Cocke (1955), Sevier (1956), and Blount (1959) Counties in Tennessee classified the spruce-fir region as Ramsey or Ashe soils and stony roughlands or rough mountainous land. Soils were described as strongly acid and low in fertility. A survey of Swain and Haywood Counties in North Carolina, listed the soils as Burton, Porters, and Ramsey. Delineation of the different soils was too general for detailed research management.

¹Professor Emeritus, Department of Plant and Soil Science, University of Tennessee, Knoxville, Tenn.

At 1580 m, McGinnis (1958) reported that in the O layers under spruce-fir, organic matter of 98,000 kg/ha was 14 times greater than under beech gap forest. However, in the mineral soil under spruce-fir, organic matter content of 151,000 kg/ha was only slightly more than under beech gap. Concentration of Ca and pH values were less under spruce-fir.

Properties of soils at elevations from 1370 to 2000 m in the Great Smoky Mountains were reported by McCracken et al. (1962). They grouped the soils into those "lacking A2 horizons with thin A1 and 'color B' horizons" and others "with A2 horizons, B1 horizons, and relatively thick mor layers." Soils of the first group were described on well drained sites under both spruce-fir and northern hardwood vegetation and were ascribed to the Sols Bruns Acides great soil group. The second group described on "less well-drained sites under heath bald or rhododendron understory of spruce-fir, with some indication that they tend to form from more quartzose conglomeratic rock" were interpreted as Podzols. They emphasized that the prevailing soils at higher elevations in the Smoky Mountains as represented by two of their soils are "characterized by duff mull surficial horizons, relatively thick and granular A1 horizons, and B horizons differentiated by color but not by relative accumulation of layer silicate clay or of iron. They are extremely weathered, are very low in base status and show surface incorporation of organic carbon which decreases with depth."

Over feldspathic sandstone and under spruce-fir in GRSM, Wolfe (1967) suggested that three soils appeared to represent Umbric Dystrochrepts, incipient Spodosols, and Spodosols. He compared these with soils from medium-textured parent material and those under beech gap vegetation. Soils under both kinds of vegetation are highly acid and low in base saturation. Exchange acidity was greater in soils under spruce-fir than under adjacent beech stands, but decreased with depth under both. Under heath vegetation, pHw values were even less. Wolfe suggested that bedrock differences were not responsible for sudden changes in vegetation. Leaf litter produced by beech was less acid, contained slightly more bases, and formed looser, less persistent layers of organic matter than did the spruce-fir litter. Roots were distributed to greater depths and soil horizons were less distinct under beech.

In the Balsam Mountains, Weaver (1972) recognized Inceptisols only, even though parent materials were mica-gneiss and mica schists and soils were somewhat coarser than in the Smokies. Concentration of Ca in the forest floor under yellow birch was two or three times higher than under spruce-fir, although there was little difference in total content. By treating forest floor apart from the soil, he suggested that vegetation and the forest floor are the major nutrient sinks and the proportion in the soil is generally low. Nutrients in the litter fall are returned at rates of one kg/40-60 kg in yellow birch stands and one kg/90-100 kg in spruce-fir stands.

Springer and Elder (1980) generalized the soils of the spruce-fir region of GRSM with the steep and very steep loamy and stony soils at high elevations from metamorphic and igneous rocks and colluvium (Dystrochrepts, Haplumbrepts, Spodosols). They stated "The soils are loamy, vary in content of stones, and range from shallow on the crests and upper slopes of the mountains to deep on the long talus slopes with thick accumulations of downslope creep. Most of the surface layers, especially on north facing slopes, are dark and high in

organic matter. On the lofty peaks, temperatures are cool, annual precipitation is 60 to 80 inches (150–200 cm), vegetation is heath or coniferous, and some of the soils have a highly bleached layer beneath an organic layer."

They placed the Tennessee part of the GRSM spruce–fir region in Ditney Jeffrey–Brookshire: Steep and very steep, shallow to deep, loamy and stony soils from sandstone, graywacke, schist, slate, and colluvium. In describing the soils they state that rocks high in weatherable minerals make up the bed rock. "Because of the high altitude and cool climate most of the soils have dark surface layers high in organic matter. The soils range from 1 to 3 feet (0.3 – 1 m) deep on the crests and upper parts of the mountain slopes to as much as 7 or 8 feet (2 m) deep in coves and on the lower slopes of mountains where there are thick accumulations of downslope creep. The soils vary in stone content and have loamy permeable subsoils.

"Ditney and Jeffrey soils are on the upper slopes of the mountains. Jeffrey soils are higher and darker than Ditney soils. Brookshire and Spivey soils are in the coves and on the lower parts of the slopes where thick deposits of colluvium have accumulated....The soils are loamy, mixed Umbric and Typic Dystrochrepts, with small areas of loamy, mixed Haplumbrepts and Spodosols at the highest elevations."

Their description of Tennessee soils north of GRSM is applicable to some of the North Carolina part of the spruce–fir region. A description of Unaka–Ashe: Steep and very steep, deep and moderately deep, loaming and stony soils from gneiss, granite, and colluvium, follows. "The soils formed from these rocks or from downslope creep. They are well drained, loamy, and friable from the surface to bedrock and contain few to common fragments of granite and gneiss. Soil thickness ranges from 1 to 4 feet (0.3 to 1.2m) on the upper slopes to more than 6 feet (2 m) on the lower slopes and in coves. In many places the upper few feet of the bedrock are weathered or softened to saprolite. Small flakes of mica are common throughout the soils. At the lower elevations the soils have pale surface layers, but the surface layers are darker at elevations above 3000 to 4000 feet (900 to 1200 m), especially on the north– and east–facing slopes. The soils are medium acid and strongly acid and moderately high in natural fertility....The soils are loamy, mixed Umbric and Typic Dystrochrepts with some loamy, mixed Haplumbrepts and Spodosols."

In a soil survey of Monroe County, Tennessee, Hall et al. (1981) delineated and described soils comparable to those under northern hardwoods in GRSM. Citico, Sylco, and Ditney are Typic Dystrochrepts. Spivey is a Typic Haplumbrept. Brookshire and Jeffrey are Umbric Dystrochrepts.

DISCUSSION

With results of research in the literature as background, numerous transects from the spruce–fir region to lower elevations reveal patterns that relate soils to parent material, aspect, elevation, and vegetation. The most probable kinds of soil at different elevations and aspects are indicated by Figures 1 to 3. The dashed lines show that annual soil temperatures decline as elevation increases and are lower in sheltered than in exposed positions.

In the Great Smoky Mountains, greater rainfall at high elevation also adds to the moister conditions. Figure 1 shows that soils are darker colored and higher in organic matter in the cooler and wetter conditions at high elevations and sheltered positions. With exposure and decreasing elevations, surface horizons are lighter colored, and clay content in B horizons is greater.

If parent material is coarse and the soil surface is stable, leaching through the organic layer under spruce-fir produces bleached E horizons and Bh or Bir horizons in the mineral soil (Figure 2). Nearby, under northern hardwoods or under unstable conditions in spruce-fir, horizons are less distinct.

Under rhododendron or other heath vegetation, organic layers are thicker, acidity is greater, and soil horizons are more distinct than under either spruce-fir or northern hardwoods. Spodosols are far more common and may extend to elevations as low as 1000 m (Figure 3). In places, organic layers are so thick that the soils are Histosols.

Above 1500 m, Inceptisols are by far the most common, but the kind of Inceptisols and the presence of Spodosols form a predictable pattern. A simplified vegetation-soil relationship for stable topography at 1700 m (Figure 4) relates kind of soil to parent material and vegetation. Where parent material was medium textured, both northern hardwoods and spruce-fir are on Inceptisols. Under northern hardwoods, the organic distribution is mull type. Under spruce-fir it is mor. Where parent material was coarse, Spodosols with distinct organic and mineral horizons are under the spruce-fir. Adjoining these under northern hardwoods, horizons are less distinct, organic distribution is mull type, and the soils are mainly Umbric Dystrochrepts or Umbrepts. Tree-throw, creep, landslides, and changing vegetation are continually shifting these patterns.

In the spruce-fir region the geological maps and tremendous amount of ecological information can be related to fragmentary knowledge of soils. Where either research or intensive management is conducted, more precise location of the soils by detailed surveys is definitely needed. In other areas, at least semidetailed soil maps would help relate soils to other parts of the environment as a basis for wiser management.

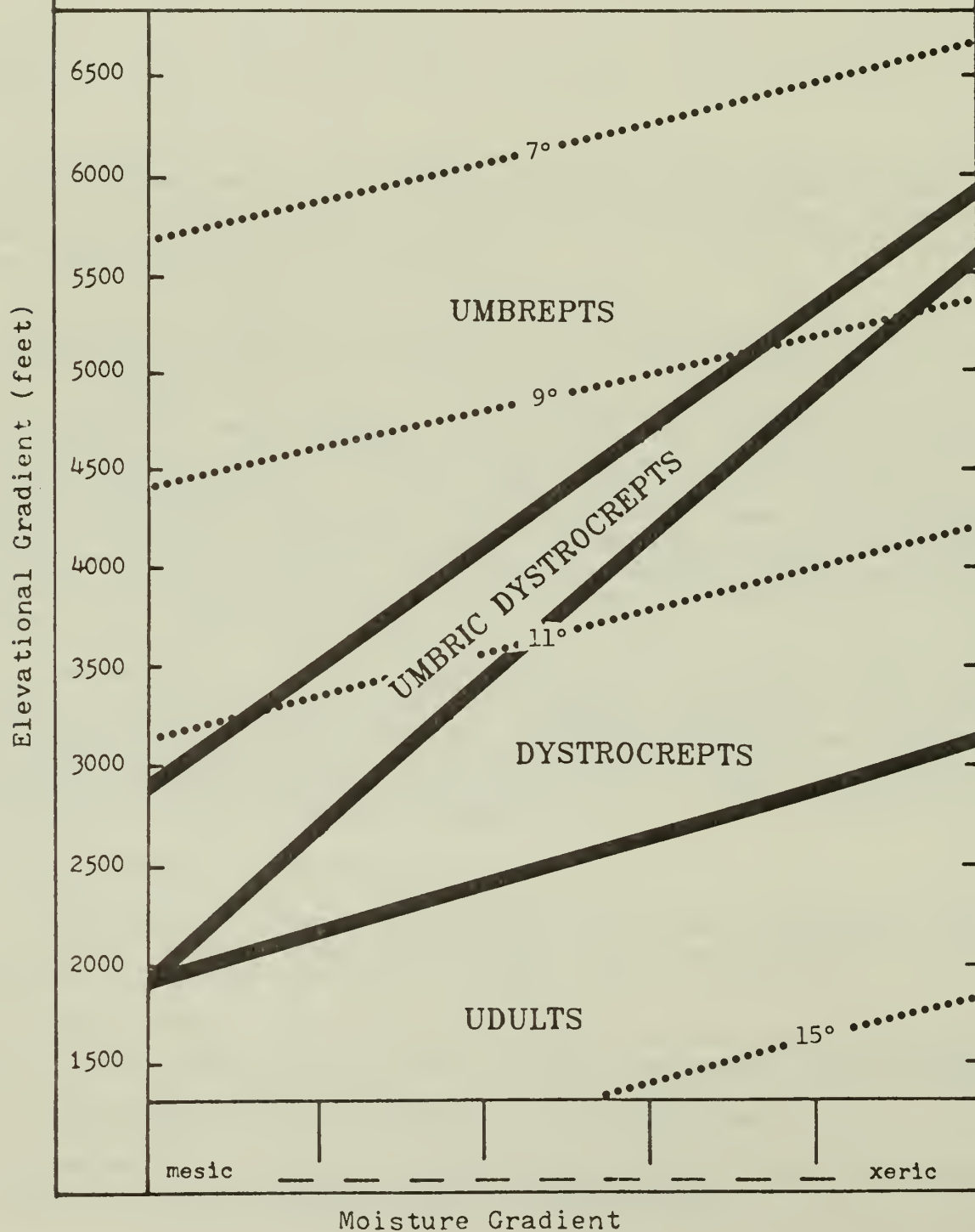
A few studies that deserve priority are:

1. Delineate and classify the different kinds of soil and display them on a soil map. Survey critical areas in detail. Use the results in preparation of a general soil map of the whole park.
2. Relate natural runoff and leachate to kind of soil and kind of vegetation; e.g., heath versus northern hardwood, heath versus cove hardwood.
3. Coordinate soils with research in other disciplines.
4. Relate natural runoff and leachate to kind of soil and kind of vegetation eg. heath vs. northern hardwood, heath vs. cove hardwood.

SUMMARY

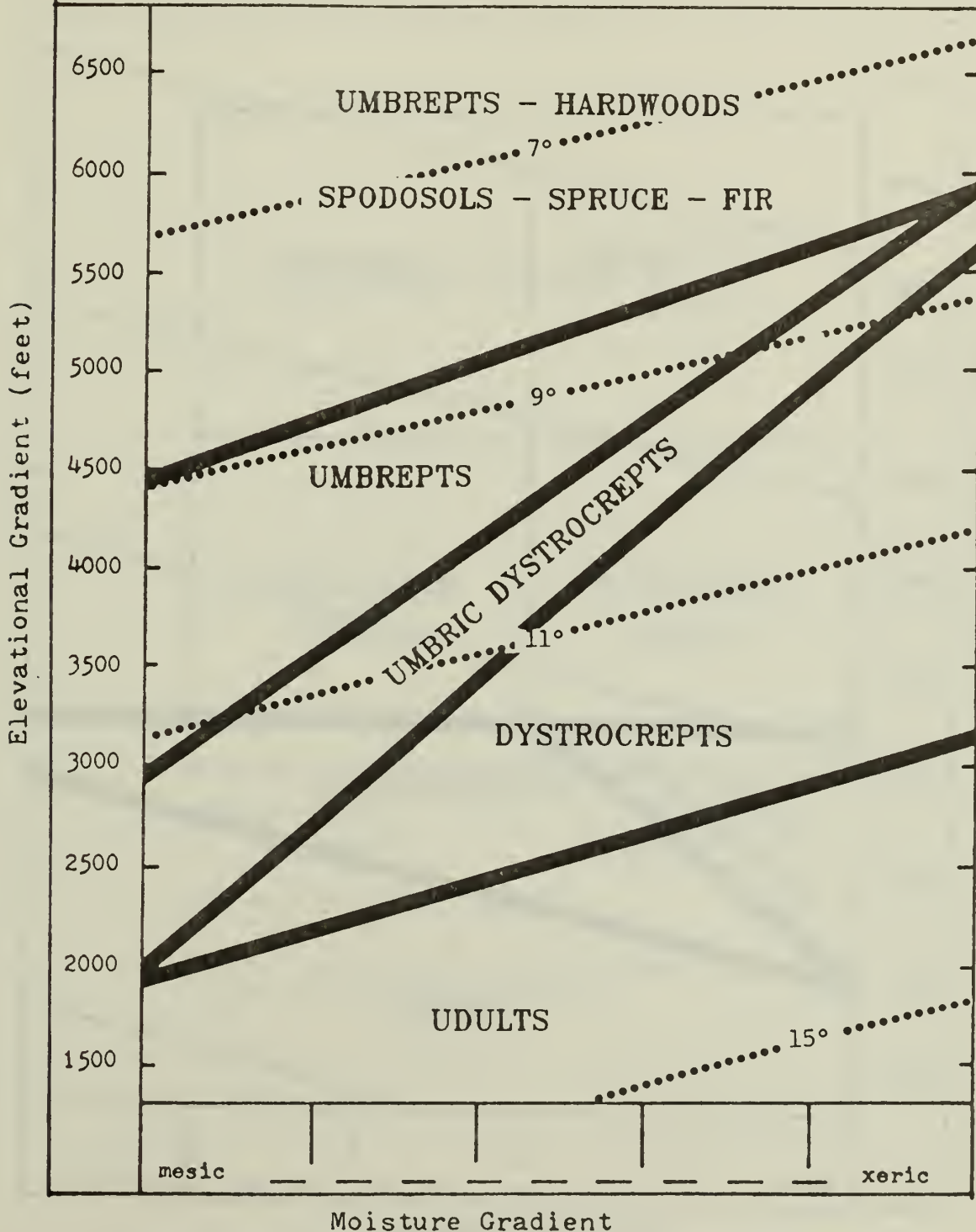
At high elevations, all the soils are low in base saturation and extremely acid. Under different vegetation, pH of the O horizons ranks northern hardwoods > spruce-fir > heath. Distinctness of horizons and thickness of O layers is in the order: northern hardwoods < spruce-fir < heath.

Figure 1. Soils patterns of the Great Smoky Mountains--
Medium textured parent material or unstable
surface (heath vegetation excepted)



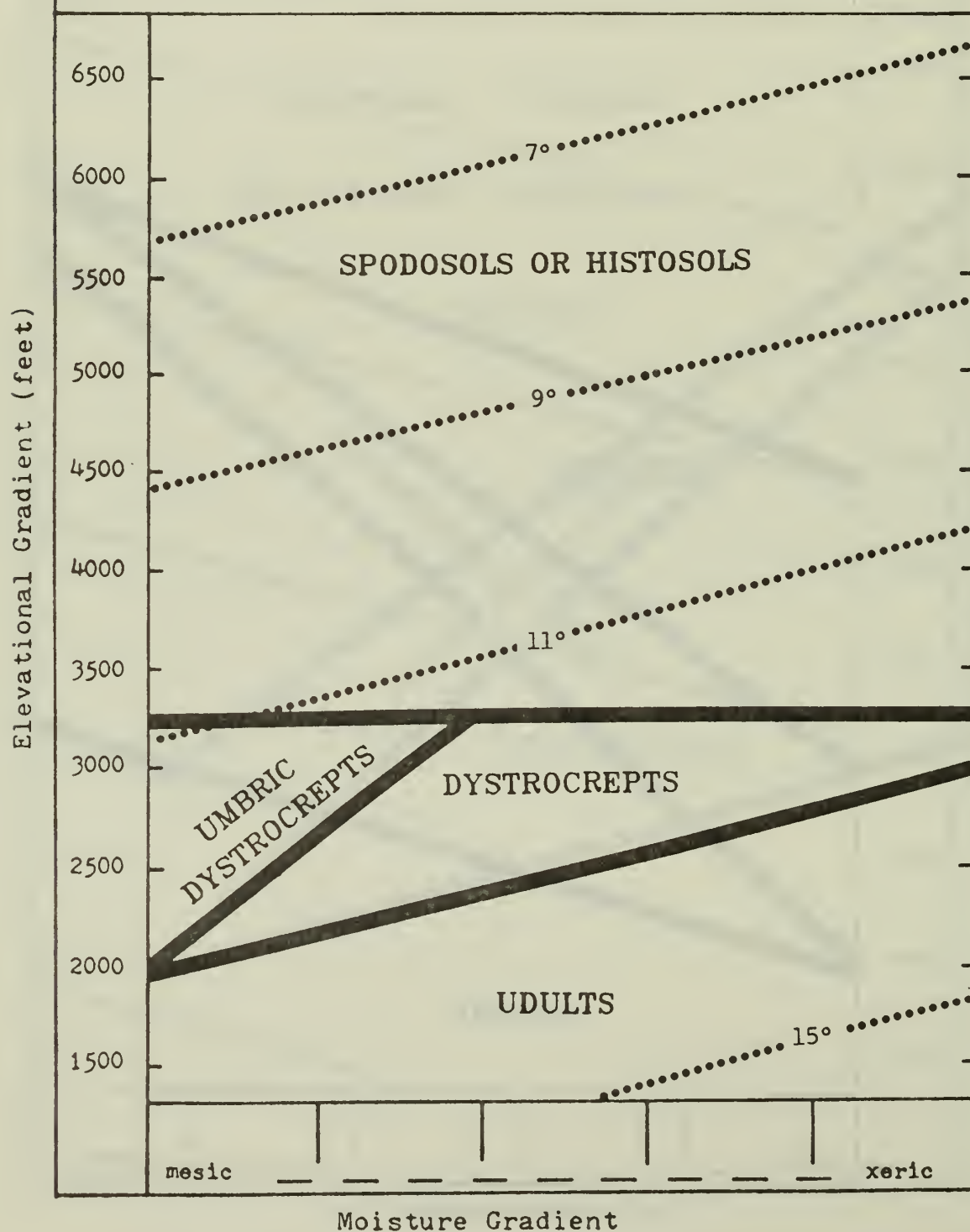
Annual soil temperatures are shown by thin dashed lines

Figure 2. Soils patterns of the Great Smoky Mountains--
Coarse textured parent material and stable
surface (heath vegetation excepted)



Annual soil temperatures are shown by thin dashed lines

Figure 3. Soils patterns of the Great Smoky Mountains--
Heath vegetation



Annual soil temperatures are shown by thin dashed lines

SPODOSOLS	INCEPTISOLS (MOR)	Spruce-fir
INCEPTISOLS (MULL)	INCEPTISOLS (MULL)	Northern Hardwoods

PARENT MATERIAL:

coarse

medium

STABLE TOPOGRAPHY AT 1700 m

Figure 4. Simplified vegetation-soil relationship
for the Great Smoky Mountains

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LEAD IN VEGETATION, FOREST FLOOR MATERIAL, AND SOILS
OF THE SPRUCE-FIR ZONE, GSMNP

Mary Anna Bogle and Ralph R. Turner^{1/}

Abstract.--Based on a survey during 1982, lead concentrations in vegetation, litter and soils of the spruce-fir zone of the Great Smoky Mountains National Park are generally less than values reported for similar sites in the northeastern United States and western Europe. As expected, lead concentrations increased with increasing age of spruce and fir foliage, and with increasing degree of decomposition of litter. Fir bole wood was higher in lead than spruce bole wood, but both species were far below acutely phytotoxic levels. Although the results of this study indicated no immediate cause for concern, periodic monitoring of lead and other metals in the spruce-fir zone should be continued to provide early detection of significant changes.

The biogeochemistry of lead in forest ecosystems continues to be of considerable interest. Among numerous metals studied, lead stands out in showing a very strong tendency to accumulate in the forest floor (Reiners et al. 1975; Heinrichs and Mayer 1980; Smith and Siccama 1981; Siccama et al. 1980; Andresen et al. 1982; Friedland et al. in press). This behavior is consistent with its strong affinity for organic matter and with its low solubility in forest soil even at low pH (Tyler 1978, 1981). High elevation sites, such as the spruce-fir zone of the Appalachians, although remote, are especially likely to show high concentrations of lead due to their unique orographic conditions; in general they exhibit higher concentrations in foliage and forest floor material than low elevation sites of the same region (Reiners et al. 1975; Wiersma and Brown 1980; Johnson et al. 1982). In fact, some lead values for forest floor material of montane forests approach values for urban areas and areas adjacent to roadways. The increased lead levels for high elevation sites (compared to lower elevation sites) have been attributed to four features of the sites: (1) increased precipitation due to orographic effects, (2) addition of cloud and fog interception, (3) higher wind speeds favoring higher impaction of small particles on surfaces of vegetation and higher diffusion rates of submicron particles across the boundary layer, and (4) predominance of coniferous foliage with higher leaf area indices and year-round persistence (Reiners et al. 1975; Lovett et al. 1982). This increases the likelihood that such high elevation sites, although remote from industrial sources, receive high exposure to certain pollutants.

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Prior to this study, published data on lead concentrations in the spruce-fir ecosystem of the Appalachians had been limited to work done primarily in the White and Green Mountains of New England and to the work of Wiersma and colleagues in the Great Smoky Mountains National Park (GSMNP). Wiersma et al. (1979) reported very high concentrations (378-879 $\mu\text{g/g}$; $\bar{X}=506 \mu\text{g/g}$) of lead in the forest floor at one spruce-fir site in the GSMNP. These values are higher than any previously reported for montane ecosystems unimpacted by smelters or urban automobile traffic and raise questions concerning the magnitude of Pb contamination in the GSMNP and the possible adverse effect on the spruce-fir ecosystem. Lead is not only directly toxic to plants and animals but has also been implicated in reduced decomposition rates of forest floor material (Tyler 1972; Ruhling and Tyler 1973; Jackson and Watson 1977), thus interfering with the cycling of essential nutrients in the forest ecosystem. Vogelmann (1983) has also suggested a synergistic effect between Pb and acid rain, resulting in the death or sharp decline in growth rate of spruce trees and other plants. The high natural resource value of the GSMNP is unquestioned, and thus it is imperative that any potential threat by a contaminant, such as lead, be detected early. Our study was conducted with the following objectives: (1) to determine whether lead concentrations in the forest floor horizons of the spruce-fir zone of the GSMNP are comparable with reported values for forest floor material from other spruce-fir sites (e.g., in New England and West Germany), (2) to expand the data base for Pb for the spruce-fir zone by determining lead concentrations in foliage and bole wood of spruce and fir, in forest floor subunits (Oi, Oe, and Oa horizons), and in soil subunits (A and B horizons), (3) to determine if there is evidence of root or foliar absorption of Pb in vegetation, (4) to determine if Pb concentration in the forest floor increases with increasing degree of decomposition, as expected, and (5) to determine if there is evidence of appreciable movement of Pb from organic to mineral horizons. Complete results of our study, including data for two hardwood sites, are given in Turner et al. (in press).

MATERIALS AND METHODS

Study Sites

Five high elevation (>1700 m), spruce-fir sites were sampled between August and November 1982. Site descriptions are as follows:

- (1) Double Springs Gap--35°33'50" N Lat, 83°30'06" W Long; 1740 m elevation; located 0.75 km east of the Double Springs Gap shelter and approximately 50 m south of Appalachian Trail on a gentle south-facing slope; forest canopy is dominated by red spruce (Picea rubens Sargent) and Fraser fir (Abies fraseri Poiret) with scattered yellow birch (Betula allegheniensis Britton), mountain ash (Sorbus americana Marshall) and mountain maple (Acer spicatum Lam.); shrub layer consists of blackberry (Rubus spp.), witch hobble (Viburnum alnifolium Marshall), and wood fern (Dryopteris campyloptera Clarkson).

- (2) Clingmans Dome Road--35°33'32" N Lat, 83°30'38" W Long; 1900 m elevation; located 0.2 km north of entrance to parking lot and approximately 50 m east of Clingmans Dome Rd on a steep east-facing slope; forest canopy is dominated by red spruce with scattered yellow birch and Fraser fir; shrub layer consists of blackberry, witch hobble, and wood fern. Site was chosen because of its relative proximity to a heavily travelled road.
- (3) Mt. Collins--35°35'35" N Lat, 83°28'25" W Long; 1790 m elevation; located 50 m west (uphill) from spring on trail west of Mt. Collins shelter on a gentle north-facing slope; forest canopy is dominated by red spruce with scattered yellow birch and Fraser fir; shrub layer consists of blackberry, witch hobble, and wood fern. Forest floor material from this Mt. Collins site was previously reported (Wiersma et al. 1979) to have elevated levels of Pb.
- (4) Mt. LeConte, West Peak--35°39'18" N Lat, 83°27'05" W Long; 1920 m elevation; located approximately 1 km west of LeConte Lodge along the crest of an east-west trending ridge; red spruce and Fraser fir are canopy dominant with scattered mountain ash, pin cherry (Prunus pensylvanica L.) and yellow birch; blackberry, witch hobble, and wood fern constitute the main shrub layer species.
- (5) Mt. Kephart--35°37'50" N Lat, 83°23'25" W Long; 1880 m elevation; located near the crest of Mt. Kephart on a moderately steep southwest slope near the junction of the Appalachian Trail with the Boulevard Trail; red spruce is canopy dominant with scattered Fraser fir, yellow birch, and mountain ash; dead and/or fallen Fraser fir have left large openings in the canopy; blackberry, wood fern, and witch hobble comprise the shrub layer.

Sample Collection and Preparation

Because this was largely an exploratory study, samples were of the "grab" type, with many being composites of several grab samples. In contrast to earlier studies conducted in the GSMNP, more effort was made to reduce variability among replicates by dividing samples into more homogeneous subunits.

One of two sampling patterns was followed at each site, depending on site topography. A linear pattern of replicates taken at 5-10 m intervals was used at steep sites including Clingmans Dome Road (parallel to road), Mt. LeConte, and Mt. Kephart. A circular pattern with replicates taken at equal intervals around a 15-m-radius circle was used at flatter sites, i.e., Double Springs Gap and Mt. Collins. Table 1 gives an inventory of the samples collected at each site and the number of replicates. In all cases samples were handled using polyethylene gloves and double-bagged in polyethylene collection bags. During sample preparation, extreme care was taken by the use of a laminar-flow clean bench to prevent possible contamination of samples or cross-contamination between samples. All processed samples were stored in acid-cleaned bottles.

Table 1.--Inventory of sample types and number of replicates at each site in the GSMNP.
Numbers in () under bole cores are the number of cores analyzed.

Sample type	Double Springs Gap	Clingmans Dome	Mt. Collins	Mt. Le Conte	Mt. Kephart	Total
Soil						
A	5	3	5	6	5	24
B	5	3	5	6	5	24
Roots						
Red spruce	5					5
Fraser fir	5					5
Yellow birch	5					5
Forest floor						
Oi (Litter)	5	3	5	7	5	25
Oe (Fermentation)	5	3	5	5	5	23
Oa (Humus)	5	3	5	5	5	23
Foliage						
Red spruce Old	5			5	2	12
Current	5			5	2	12
Fraser fir Old	3			5	2	10
Current	3			5	2	10
Yellow birch	2					2
Bole cores						
Red spruce	5(5)			5(1)	4(1)	14(7)
Fraser fir	3(3)			5(1)	2(1)	10(5)
Yellow birch	2(2)					2(2)

Branches of red spruce and Fraser fir foliage were collected with a pole pruner from near the top of canopy-dominant trees or from solitary trees growing in exposed areas (i.e., ridge crests). Deciduous foliage of yellow birch was collected from lower branches of trees at one site, Double Springs Gap. Unwashed foliage from spruce and fir was separated in the laboratory into "old" (i.e., 2- to 4-year-old and "current" (i.e., 1982 growth) needles before oven drying at 75° to 100°C. Dried needles were then removed from their stems and stored. Unwashed yellow birch leaves were also oven dried and broken into small fragments before storage. All foliage samples were put into solution by nitric-perchloric acid digestion without further processing (Jackson 1964).

Xylem cores were taken with a 46-cm steel (Ni-plated) increment corer with a 12-mm I.D. After removal of the outer 1-2 mm of wood with a stainless steel scalpel, each core was cut into sections. Core sections were dried to a constant weight at 95°C, dry ashed (450°C) in 25-ml beakers, and dissolved in 1N HNO₃ (Baker 'Ultrex') and 100 µl of 30% H₂O₂.

Roots were collected at only one site, Double Springs Gap, by uprooting saplings of red spruce and Fraser fir or by excavating at the base of large yellow birches. A sample consisted of root segments ranging up to approximately 1 cm in diameter. Roots were cleaned with distilled water while in the original collection bags using an ultrasonic cleaner. Water was changed repeatedly until it remained clear upon sonification of the sample. Roots (oven dried at 100°C) were put into solution by dry ashing (450°) followed by dissolution in 1N HNO₃ ('Ultrex') and 30% H₂O₂.

Forest floor samples were obtained by sequential removal and separation of the Oi, Oe, and Oa layers (Soil Conservation Service, 1981) using a stainless steel spatula or trowel. Individual samples were assembled by compositing material from several locations within an ~20 m² area. The criteria for separation of these layers correspond to those used in many previous studies of forest floor material, but as recently noted by Federer (1982) the actual separation is somewhat subjective. In the laboratory, samples were oven dried at 75° to 100°C and then ground in a Wiley mill with stainless steel grinding components. Loss-on-ignition (LOI) values were determined on all forest floor material in this study as a convenient way of comparing consistency of sampling a horizon within a site and between sites and to permit assessment of Pb concentrations on an organic matter (ash-free) basis. Ashed (450°C) samples were dissolved in 1N HNO₃ and 30% H₂O₂.

Mineral soil samples were obtained by coring or excavation and separated qualitatively into A and B horizons in accordance with the standard definitions of these horizons (field classification based on stratigraphic position, color, and texture). After drying at 75° to 100°C, samples were finely crushed using a mortar and pestle, sieved through a stainless steel U.S. Standard Sieve No. 18 (1.00 mm), and digested in a 1:1 mixture of concentrated HNO₃ and HCl using the procedure described by Anderson et al. (1974).

All lead analyses were performed with either flame (AA) or graphite furnace (FAA) atomic absorption spectrophotometry on solutions prepared by wet oxidation or by dry ashing and dissolution in acid. Instrument calibration was by the method of standard additions for FAA and by standard curve for AA.

Quality Assurance

Since the reliability of much of the extant data on lead in the environment has been seriously questioned (NAS 1980), the quality of the analytical data generated in this study was monitored in several ways to assess and improve precision and accuracy of results. The centralized analytical facility at ORNL, which performed all atomic absorption analyses, maintains its own Quality Assurance program. In addition, the measures listed below were taken to assure the reliability of our data.

- (1) Use of Standard Reference Material (SRM)--At least one sample of SRM having a similar matrix and lead concentration as the sample was run with every batch of 10 to 25 samples. SRMs run included NBS 1571 (orchard leaves), NBS 1573 (tomato leaves), NBS 1575 (pine needles), NBS 1645 (river sediment), CCMET SO-2 ('B' soil), and CCMET SO-4 ('A' soil). The latter soil SRMs were obtained from the Canadian Centre for Mineral and Energy Technology.
- (2) Replicates--Selected samples were digested and analyzed in duplicate or triplicate to assess procedural precision. With one exception, coefficients of variation for replicates were $<\pm 10\%$ and frequently $<\pm 5\%$.
- (3) Reanalysis of Selected Samples--As an indication of day-to-day variability, a few samples were reanalyzed with later batches of samples. Initial and subsequent values agreed within $\pm 10\%$.
- (4) Cross Method Check of Analysis--Digestion of samples by independent methods (wet oxidation or dry ashing) was done to reveal problems with sample digestion. Values for forest floor samples prepared both ways agreed within $\pm 10\%$, and the more convenient method, i.e. dry ashing, was used. Trial runs with foliage indicated potential low recovery of Pb when dry ashing was used. Although the addition of 100 μl of 30% H_2O_2 to foliage ash resulted in good recovery of Pb, it was decided that all foliage samples would be run by wet oxidation to avoid uncertainty.
- (5) Spike Recovery--All analyses performed by FAA entailed sample spiking as part of the calibration procedure. Selected samples ($\sim 10\%$) run by AA were also spiked. Spiking allowed for differences in sample matrices, which may cause suppression or enhancement, to be taken into account.
- (6) Use of Field Sites in Common with Earlier Studies--Among the five spruce-fir sites selected for sampling, two (Mt. Collins and Double Springs Gap) were chosen because earlier studies of Pb in litter had been conducted at these sites by Wiersma et al. (1979) and Breckenridge and Wiersma (1982).

RESULTS AND DISCUSSION

Vegetation

Foliage samples were not washed and thus analytical results for foliage reflect the sum of internal tissue levels and surface contamination. Concentrations of Pb in red spruce, Fraser fir, and yellow birch generally follow the relationship: roots > foliage > bole. This pattern is consistent with other published data (Van Hook et al. 1977; Nilsson 1972; Heinrichs and Mayer 1980; Smith and Siccama 1981). Lead concentrations in foliage, averaged by site and for all sites, for the three species sampled are given in Table 2. Average concentrations range from 0.38 $\mu\text{g/g}$ dry weight (D.W.) for current foliage of Fraser fir collected at Double Springs Gap to a high of 4.1 $\mu\text{g/g}$ D.W. for old needles of Fraser fir collected at the same site. This range of concentrations for Fraser fir is consistent

Table 2.--Average concentrations ($\mu\text{g/g}$ dry wt) of lead in foliage from the spruce-fir zone of GSMNP. Values in () are S.D. (or range if $N = 2$). X = average for all three sites.

	Double Springs	Mt. Le Conte	Mt. Kephart	X
Red spruce				
Current	0.69 ^{a,x} (0.18)	0.62 ^{a,x} (0.24)	0.61 ^{a,x} (0.60-0.61)	0.65 ^x (0.18)
Old	0.66 ^{a,x} (0.26)	1.03 ^{a,b,x} (0.33)	1.45 ^{b,x} (1.1-1.8)	0.95 ^y (0.42)
Fraser fir				
Current	0.38 ^{a,x} (0.05)	0.81 ^{a,x} (0.61)	0.61 ^{a,x} (0.49-0.73)	0.64 ^x (0.46)
Old	4.1 ^{a,x} (3.6)	1.9 ^{a,y} (0.61)	2.6 ^{a,y} (2.6-2.6)	2.69 ^y (2.02)
Yellow birch	2.4 (2.2-2.6)			2.4

*For a given row averages followed by the same letter (a,b) are not significantly different at the 5% level (Walker-Duncan K-ratio or Student's t-test). For a given column and species, old and current averages followed by the same letter (x,y) are not significantly different at the 5% level (Student's t-test).

with values reported by Wiersma and Brown (1980) for Fraser fir foliage collected in GSMNP in 1978. However, lead concentrations in needles of red spruce in our study are three to four times lower (see Table 3) than concentrations reported by Johnson and Siccama (1983) for red spruce from the boreal forest of Camels Hump, Vermont and almost eight times lower than red spruce needles collected in the Hubbard Brook Experimental Forest located in central New Hampshire (Smith and Siccama 1981).

Intersite comparisons of coniferous foliage were made using the Duncan-Waller k-ratio t-test or Student's t-test (see Table 2). As might be expected due to similar orographic conditions at all five spruce-fir sites, no between-site differences in the lead concentrations of Fraser fir or current red spruce needles are observed. However, there is a significant difference in Pb concentration of old red spruce needles from Double Springs Gap and Mt. Kephart. This apparent difference may be an artifact of the low number of replicate samples ($N=2$) at the Mt. Kephart site.

A comparison (Table 2) of average Pb concentrations in old needles with current needles reveals that, with one exception, old needles are higher in Pb. Although the difference is not always significant on a site-by-site

Table 3.--A comparison of spruce-fir foliage and forest floor Pb concentrations ($\mu\text{g/g}$ dry wt.) from selected studies.

Locality		Foliage		Forest Floor			Reference
		New	Old	Oi	Oe	Oa	
GSMNP	Spruce	0.65	0.95	52	130	132	This study
	Fir	0.64	2.69				
	Fir		0.2-3.1	-	-	-	Wiersma and Brown 1980
		-	-	-----	210	-	Breckenridge and Wiersma 1982
		-	-	59.3	132	-	Wiersma, personal communication
Green Mountains, Vermont (Camels Hump)	Spruce		~3	-	-	-	Johnson and Siccama 1983
		-	-	225	266	175	Friedland et al., in press
Vermont		-	-	-----	188-----		Johnson et al. 1982
White Mountains, New Hampshire	Fir	-	-	246	202	82	Reiners et al. 1975
	Spruce-fir	-	-	110	114	60	Reiners et al. 1975
Hubbard Brook, New Hampshire	Fir		7.4	-	-	-	Smith and Siccama 1981
	Spruce		13.8	-----	193-----		Smith and Siccama 1981
Solling Forest, West Germany	Spruce	5.4	12.0	300	450	465	Heinrichs and Mayer 1980
Skane, Sweden	Spruce	2.1	3.7	46	71	86	Nilsson 1972

basis, it is significant when comparing averages for all sites. Numerous researchers, including Nilsson (1972) and Heinrichs and Mayer (1980), have reported similar results for old and new needles of coniferous trees (Table 3). These findings are reasonable considering the longer exposure time of old needles to surface deposition and to possible uptake of lead.

Average Pb concentration in foliage of yellow birch is $2.4 \mu\text{g/g}$ D.W. This concentration in deciduous leaves seems high when compared to 1-year-old needles of Fraser fir and red spruce but is consistent with the reputation of birch (*Betula* spp.) as an accumulator of Pb (Cannon 1976; Smith and Siccama 1981).

Bole wood Pb values for red spruce and Fraser fir are low, averaging $0.03 \mu\text{g/g}$ D.W. and $0.25 \mu\text{g/g}$ D.W., respectively. An interspecific comparison of average lead concentrations in foliage and in bole wood lends some insight into the possible site of lead accumulation, i.e., whether the lead represents surface-deposited lead and/or tissue-incorporated lead. Fraser fir and red spruce Pb concentrations for current needles ($0.64 \pm 0.46 \mu\text{g/g}$ and $0.65 \pm 0.18 \mu\text{g/g}$ D.W., respectively) are not

significantly different ($P > 0.05$). However, the average value of old Fraser fir needles (2.69 ± 2.02 g/g D.W.) is significantly higher ($P < 0.01$) than that of old red spruce needles (0.95 ± 0.41 μ g/g D.W.). This observation, combined with the fact that Fraser fir bole wood values are approximately ten times that of red spruce bole wood, suggests that more lead is incorporated by Fraser fir into foliage and bole tissue through root and/or foliar uptake than by red spruce; i.e., Fraser fir is an 'accumulator'.

Consistent with birch's reputation as an 'accumulator' of Pb are bole wood values averaging 5.1 μ g/g D.W. and root concentrations as high as 91 μ g/g D.W. ($X=51$ μ g/g D.W.), contrasted with an average concentration in roots of both red spruce and Fraser fir of 30 μ g/g D.W.

Forest Floor

The average concentrations of lead in the Oi, Oe, and Oa horizons of the forest floor are 52, 128, and 132 μ g/g D.W. respectively, with the composite average of the three layers being 105 μ g/g D.W. (126 μ g/g ash-free weight). These concentrations are difficult to compare with earlier results from spruce-fir sites in GSMNP (Wiersma et al. 1979; Breckenridge and Wiersma 1982) because of differences in sampling methods (e.g., forest floor material was not separated into subunits in the earlier two studies) and in sampling sites. However, a comparison of our results for average Pb concentrations at two sites in common with the earlier studies (summarized in Table 4) demonstrates that our values are lower at both sites for all forest floor horizons. More recent data from Wiersma (personal communication) for Double Springs Gap are consistent with our findings. The very high Pb values reported earlier for Mt. Collins material suggest a contamination or analytical problem. In general, our Pb data for forest floor material are also less than recent published values for spruce-fir sites in the northeast (Table 3). Because of the measures we took to assure 'good' data during analysis of our samples (see Quality Assurance section) as well as the recent communication of comparable values from Wiersma, we feel confident of our values.

Table 4.--Comparison of forest floor Pb values at two spruce-fir sites, GSMNP.

	Double Springs Gap Breckenridge and			Mt. Collins	
	This study	Wiersma 1982	Wiersma ^a	This study	Wiersma et al. 1979
Forest floor, Oi	69 $\pm$ 16(5)	210 $\pm$ 66(9) ^b	59.3(10)	47 $\pm$ 8(5)	506 $\pm$ 155(9) ^b
Oe	125 $\pm$ 20(5)		132.0(10)	120 $\pm$ 34(5)	
Oa	125 $\pm$ 34(5)			105 $\pm$ 40(5)	
X	106			91	

^aPersonal communication, 1983.

^bUnincorporated litter $\approx$ Oi and Oe horizons.

Intrasite comparisons of forest floor horizons reveal a nearly consistent trend toward increasing Pb concentration in forest floor horizons with increasing degree of decomposition. This trend is especially striking if ash-free concentrations for the three forest floor horizons are compared. With the exception of the Clingmans Dome Road site (where $O_e \approx O_a$), average Pb concentrations are significantly different at all sites for all three horizons with $O_i < O_e < O_a$ (Fig. 1). Reiners et al. (1975) in their study on trace metals in forest floor material conducted on Mt. Moosilauke, New Hampshire reported the opposite trend, decreasing Pb concentrations in forest floor layers with increasing degree of decomposition, and suggested that this finding indicated that the rate of dissemination of Pb aerosols was accelerating during the time of their study (early 70's). Several recent papers (e.g., U.S. EPA, 1983; Smith and Siccama 1981; Lindberg and Turner 1983; Turner et al. submitted) suggest that the rate of input of anthropogenic Pb into the atmosphere, and hence deposition of atmospheric Pb to the earth, has decreased over the last few years. Reconstructing historical trends in metal loadings from forest floor profiles is complicated, if not impossible, at present (see e.g. Friedland et al., in press). Nonetheless, our data do not seem to contradict the idea that atmospheric inputs of Pb to the GSMNP have been decreasing over the last few years.

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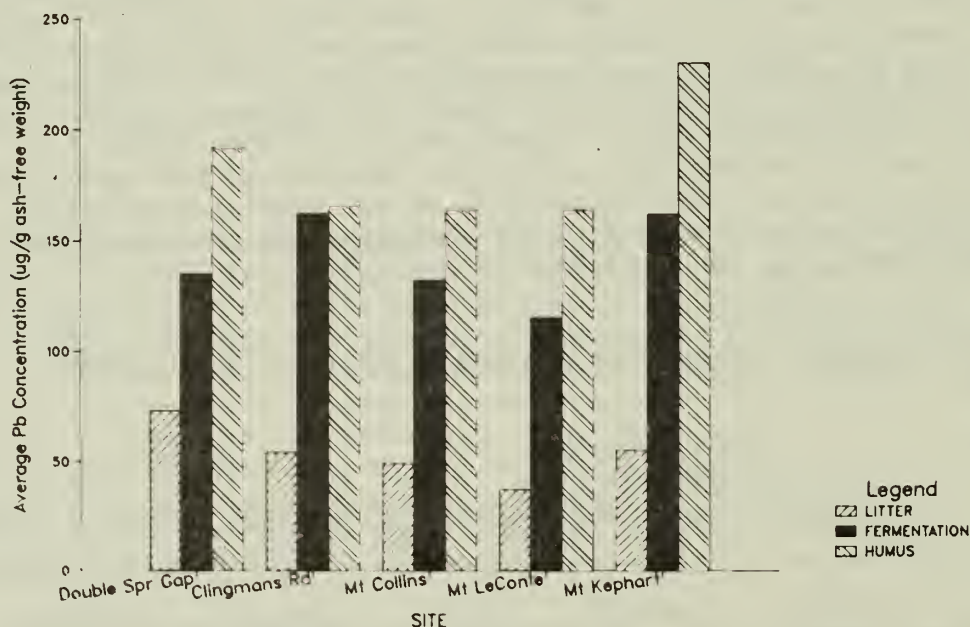


Figure 1.--Lead concentration (ash-free basis) in forest floor horizons of five spruce-fir sites (GSMNP).

McGinnis (1958) determined the standing pool of forest floor material from a spruce-fir site near Newfound Gap (GSMNP) to be 844, 2496, and 12702 kg/hectare for the Oi, Oe, and Oa horizons, respectively. Using these values and our values for Pb concentrations in the forest floor layers, a very rough estimate of 0.20g/m² can be calculated for the total Pb content of the spruce-fir forest floor. It should be cautioned that this estimate may well be low because other researchers, including Reiners et al. (1975), have found forest floor biomass to be considerably higher than that reported by McGinnis.

Soils

Average concentrations of Pb in soil horizons (A=33 µg/g D.W. and B=24 µg/g D.W.) are similar to values reported by others for soils of the GSMNP (Boergen and Shacklette 1981; Wiersma et al. 1979) and are typical for soils developed on low-grade metamorphic bedrock, suggesting little appreciable movement of Pb into the soil. Our values for pH of A horizon soils range from 3.2 to 3.5, for B horizon soils from 3.3 to 3.7. These values agree well with data presented by McGinnis (1958) for soils of a spruce-fir site in the Smokies. Even at low pH, Tyler (1978) found Pb to be so tightly bound to organic material that it was essentially immobile except under conditions favoring the leaching of organic matter (Tyler 1981). As expected based on their higher content of organic matter and the affinity of Pb for organic matter, A horizon soils are higher in Pb than B horizon. The difference is significant ($P < 0.05$) at the Double Springs Gap, Mt. Collins, and Mt. LeConte sites.

CONCLUSIONS

The results of our study suggest that Pb concentrations are not exceptionally high in the spruce-fir zone of the GSMNP and in general are less than values reported for similar sites in the northeastern United States and western Europe. We suspect that our results are lower than the previously reported high values for Mt. Collins' forest floor material due to possible contamination or analytical problems in the earlier study and not because of differences in sampling methodology nor because Pb concentrations have declined greatly since 1978.

Comparison of our data with available data on acute toxicity of Pb to higher plants (almost exclusively agricultural species) suggests that Pb concentrations in the GSMNP are well below the level where such effects are noticeable. However, information on Pb toxicity to forest trees is virtually lacking. Likewise, even for agricultural species, information on the subtler effects of Pb either alone or in combination with other contaminants, is scarce; thus it would be premature to conclude that current Pb levels in the spruce-fir zone pose no ecological threat. If studies at spruce-fir sites in the northeastern United States and in western Europe, where Pb deposition and concentrations are higher, validly implicate heavy metals in the forest declines in these areas, then Pb and other metals in the GSMNP should continue to be closely monitored. Recent data from a variety of sources, including this study, suggest that air concentrations and deposition of

Pb are decreasing primarily in response to reduced emissions from vehicles. While these emission reductions stem from regulations aimed at protecting catalytic exhaust systems and human health, in the long term they will likely also be beneficial to fragile high elevation ecosystems, such as the spruce-fir zone of the GSMNP.

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POLLUTANT DEPOSITION IN MOUNTAINOUS TERRAIN

Gary M. Lovett¹

Abstract. Theoretical considerations suggest that the high elevation forests in mountainous areas receive substantially more atmospheric deposition than do the forests of the surrounding lowlands. Wet deposition should increase with elevation because of orographic enhancement of precipitation and increased deposition of snow, which may be more polluted than rain. Dry deposition should be greater in high-elevation forests because of greater wind speeds, higher relative humidities, greater surface area of vegetation present during the entire year, and greater filtering efficiency of needles compared to broad leaves. Somewhat lower concentrations of airborne particles and gases at remote high elevation sites may act to diminish the elevational increase of dry deposition to some extent. In addition to increased wet and dry deposition, cloud water deposition is likely to be significant at high elevations because of the frequent presence of wind-driven clouds. At low elevations, clouds and fogs are probably negligible as a deposition vector because they occur less frequently and are usually associated with still air.

Experimental verification of these expected trends is not easily found, but studies on cloud water deposition and lead accumulation suggest their accuracy. Additional data on air quality, meteorology, and precipitation chemistry are needed for high elevations before atmospheric deposition of any airborne substance can be determined with certainty.

INTRODUCTION

Several networks now exist for measuring pollutant deposition in rain and snow (called wet deposition) across the North American continent (EPA 1983). Although no similar network is yet operative for deposition of atmospheric particles and gases (dry deposition), such a network is being developed. The distances between monitoring stations in these networks is necessarily large, usually on the order of hundred of kilometers or more. Observational evidence suggests that the presence of mountain ranges can effect dramatic changes in deposition over spatial scales on the order of tens of kilometers, which is below the spatial resolution of the national monitoring networks. Very few studies have focused on elevational patterns of deposition, therefore few data are available to document the effect. This paper summarizes the factors that control wet and dry deposition, shows how those factors might change along an elevational gradient, and discusses some North American data that illustrate topographical effects on deposition. Data from the southern Appalachians are emphasized where possible.

1. Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831

WET DEPOSITION

Two processes control the rate of wet deposition of pollutants: the scavenging of the pollutant material by atmospheric liquid water and ice, and the delivery of the incorporated pollutants to the ground by precipitation. The latter process certainly changes with elevation; orographic enhancement of precipitation is a well-known phenomenon. Dingman (1979) calculated that precipitation increases 0.075 cm/y for every meter of elevational gain in the mountains of New Hampshire and Vermont. On the west slope of the Great Smoky Mountains, Shanks (1954) found a precipitation increase of over 50 percent in the elevational range from 445 to 1523 m. The rate of increase was 0.076 cm/y per meter elevation, remarkably close to the New England value. Shanks found that the rate of precipitation enhancement decreased in the 1520 to 1920-m range, but attributed this change to a different exposure of the highest station.

These increases in precipitation with elevation do not necessarily imply proportional increases in wet deposition of pollutants. Wet deposition of SO_4^{2-} and trace metals has been found to be positively, but nonlinearly, related to precipitation amount (Hicks and Shannon 1979, Lindberg 1982), presumably because the efficiency of precipitation scavenging processes decreases as the air is cleaned by precipitation. Therefore, elevational enhancement of precipitation should bring a disproportionately smaller enhancement of wet deposition.

Precipitation scavenging processes can alter this elevational effect in other ways as well. For example, if the pollutants are released at low elevations, they may not be dispersed to altitudes high enough to affect the precipitation high in mountainous areas. The height over which pollutants are thoroughly mixed varies substantially with geographic area and weather conditions (EPA 1983). Lack of thorough vertical mixing would imply cleaner air, and thus cleaner rain, at high elevations, and this could counteract the effect of an increased amount of precipitation. The Tennessee Valley Authority (1983) collected wet deposition at 1016, 1367, and 1822 m in Raven Fork Watershed in the Great Smoky Mountains, and the data showed no significant effect of elevation on concentrations of SO_4^{2-} , NO_3^- , and H^+ ion rain (analysis of variance, $p > 0.05$). These data were collected over only one growing season, however, and a longer-term record with more sites would be needed to prove conclusively that rain chemistry does not vary with elevation.

Compared to low elevations, a greater percentage of the precipitation at high elevations is delivered as snowfall. This can affect the total wet deposition because snow is generally considered to be more efficient than rain at scavenging particles and gases from the air (Raynor and Hayes 1983, Knutson and Stockham 1977). This would result in higher annual average concentrations of pollutants in precipitation at higher elevations.

Thus, competing trends govern the change in wet deposition with elevation: increased amounts of precipitation and greater percentages of snowfall tend

to cause an increase in wet deposition, while cleaner air at high elevations could cause a decrease. The relative importance of these processes probably varies between mountain systems, and should be determined experimentally. For the southern Appalachians, however, one might expect a moderate increase in wet deposition with elevation because, based on the limited TVA data (TVA 1983), rain chemistry does not appear to change significantly with elevation.

DRY DEPOSITION

Dry deposition of particulate and gaseous pollutants to vegetated surfaces is controlled by a large number of factors including air quality, wind speed, morphological characteristics of the vegetation, and relative humidity (Sehmel 1980, Hosker and Lindberg 1982). Many of the controlling factors, especially those listed above, can change with elevation; thus the rate of dry deposition may also change with elevation.

Air quality may improve with elevation, but conclusive data to support this are lacking. Skelly et al. (1983) and Duchelle et al. (1982) report SO₂ and O₃ measurements in the mountains of western Virginia, and Davidson et al. (in press) report atmospheric concentrations of trace elements on Clingman's Dome in the Great Smoky Mountains National Park. However, none of these high-elevation data sets is accompanied by a simultaneously measured low-elevation data set, so direct elevational comparisons are not possible. Davidson et al. note that the trace metal concentrations at Clingman's Dome are less than those measured by Stevens et al. (1980) at a lowlands site 13 km away, but suggest that the differences may be the result of sampling methodology and proximity of the lower site to pollutant sources--in this case roads and populated areas. This emphasizes that in many cases it may be difficult to distinguish between the effects of elevation and remoteness in controlling air quality in mountainous areas that are frequently distant from pollution sources.

Wind speeds generally increase with elevation. Near the top of Clingman's Dome (about 2080 m) in the Great Smoky Mountains National Park, the annual mean wind speed in 1981 was 3.2 m/s at a height just above the forest canopy (D. Holland, National Park Service, pers. comm.). At the NOAA Oak Ridge, Tennessee, weather station (300 m elevation), the annual mean wind speed is 2 m/s at the top of a 10-m tower in an open area (NOAA 1981). If the Clingman's Dome anemometer were also located 10 m above the momentum-absorbing surface (the zero-plane displacement height of the canopy), then the difference between the sites would be much more striking. Wind speeds affect dry deposition in several ways. For particles large enough for inertial impaction on vegetation surfaces, increases in wind speed cause increased particle momentum and thus increased efficiency of impaction (Chamberlain 1975). For smaller particles and gases, the wind speed effect is less dramatic, but involves reduction in the width of the aerodynamic boundary layer through which the depositing material must pass.

Humidity also affects dry deposition. Hygroscopic particles (including many common pollutants such as salts of SO_4^{2-} , NO_3^- , and Pb) swell in size in higher humidities, and are deposited more efficiently. Gaseous deposition to plants has also been shown to increase under high humidity regimes (McLaughlin and Taylor 1981). Because of decreases in temperature with increasing elevation, relative humidities tend to increase, although some low-elevation hollows may have higher humidities because of cold air drainage (Geiger 1965). Data to support this humidity trend in the southern Appalachians are not available.

The nature of the vegetation cover can also change with elevation and affect dry deposition. If upper slopes are dominated by needle-leaved, evergreen forests, and lower slopes by broad-leaved deciduous forests, dry deposition to the upper slopes could be greater for two reasons. First, evergreen forests present a high surface area for dry deposition throughout the year, as opposed to the winter season defoliation of deciduous trees. Second, needles have a higher capture efficiency for small particles than do broad leaves (Belot and Gauthier 1975).

Changes in wind speed, humidity, and vegetation type therefore suggest higher rates of dry deposition at higher elevations. If higher elevations have better air quality, this effect could be reduced. However, because of a lack of conclusive evidence of elevational effects on air quality, a higher dry deposition load at high elevations is hypothesized. The current state of measurement capability for dry deposition suggests that it may be some time before this hypothesis can be tested conclusively for all major pollutants. Taylor and Parr (1983) measured fluoride in white pine (Pinus strobus) and hemlock (Tsuga canadensis) foliage at elevations of 600, 850, and 1300 m on a west-facing slope in the Great Smoky Mountains National Park. This slope had a windward exposure to potential regional sources of particulate and gaseous fluorides, including coal combustion, aluminum smelting, and uranium enrichment. No significant differences in foliar fluoride were found between the two lower elevations for either species, but concentrations found at the 1300-m site exceeded those at 600 m by factors of 1.5 to 2.5 and varied with species and needle age. Another recent study suggests the importance of dry deposition in a high-elevation ecosystem in the western United States. Graustein and Armstrong (1983) used strontium isotope ratios to show that the spruce-fir forests of the mountains of northern New Mexico are growing on a mantle of material derived from the surrounding lowlands and transported as wind-blown dust. This is undoubtedly an extreme case, occurring in a windy, arid environment, but it indicates the potential significance of dry deposition at high elevations.

CLOUD WATER DEPOSITION

The deposition of cloud droplets does not fit well into either the wet or dry deposition categories. Pollutant material is delivered in solution,

but the mechanisms of deposition (turbulent transport, impaction, sedimentation) are more characteristic of large suspended particles than of precipitation. At low elevations, fogs (defined as ground-level clouds) are formed chiefly by radiative cooling of the surface. These fogs are associated either with no wind, in the case of level terrain, or with very slight winds in the case of cold air drainage on hillslopes. In contrast, high elevation fogs are usually either orographic (caused by air rising up the windward slope of a mountain) or are the result of low-level stratus clouds whose base is below the height of the mountains. In either case, the fogs are usually associated with the high winds characteristic of mountaintops. These winds add momentum to the droplets and increase their ability to impact on vegetation surfaces (Thorne et al. 1982). In addition, the fog frequency on eastern mountains can be very high; the summit of Mt. Washington, New Hampshire, is in clouds 50 percent of the time (Reiners and Lang 1979). The concentrations of dissolved substances in cloud water tend to be several times higher than those in rain of the same area (Waldman et al. 1982, Lovett et al. 1982, Falconer and Kadlecsek 1980), probably because the cloud droplets have a longer residence time in the atmosphere. Taken together, these factors suggest that cloud water is an important vector of pollutant deposition at high elevations.

Cloud water deposition has been measured by Lovett et al. (1982) on Mt. Moosilauke, New Hampshire. The upper slopes of Mt. Moosilauke are in clouds about 40 percent of the time, and average wind speeds at 1200 m elevation are about 5 m/s. Lovett et al. found that cloud water deposition was directly proportional to wind speed and the total annual deposition of SO_4^{2-} , NO_3^- , K^+ , Na^+ , and H^+ by cloud water was greater than the deposition by precipitation. Dry deposition was not measured. Deposition of H^+ at 1200 m was almost four times the deposition measured at a low elevation site 13 km away. In the southern Appalachians, Smathers (1982) and Holland (National Park Service, unpublished data) reported substantial cloud deposition in rain gauges fitted with fog-intercepting screens. Although it is difficult to extrapolate from these measurements to the amount of cloud water actually caught by the vegetation, these studies document the existence of the cloud deposition phenomenon in the southeastern mountains.

STUDIES OF LEAD DEPOSITION

Several studies have focused on the accumulation of lead in the organic layers of high-elevation forest soils. Lead is released as an aerosol from some smelters and from automobiles burning leaded fuel, and is deposited by wet, dry, and cloud water deposition. The deposited lead is efficiently bound to organic material and thus accumulates in the forest floor; the extent of this accumulation has been considered a long-term record of lead deposition. Reiners et al. (1975) found an increase in lead contents of forest floors along an elevational gradient on Mt. Moosilauke, New Hampshire, which they attributed to increases in atmospheric deposition (wet, dry, and cloud water) along this gradient. The lead contents increased about fourfold from the hardwoods zone at approximately 700 m to the top of the fir zone

at approximately 1400 m, but decreased in the higher elevation alpine tundra ecosystem. This decrease was attributed to the smaller interceptive surface area of tundra plants, and suggests the importance of dry and cloud deposition, which are dependent on vegetation surfaces for deposition. Johnson et al. (1982) found a similar increase in forest floor lead content in the elevational range 300 to 1200 m in the Taconic, Green, and White Mountains of New England. Their analysis of buried soil horizons indicated that the lead content of these forest floors may have increased five to tenfold in the last century. Graustein and Turekian (1983) used soil profiles to determine the long-term average deposition rate of the natural radioactive isotope ^{210}Pb along elevational gradients in New Mexico and New Hampshire. They found that deposition increased with elevation in both places. In the southern Appalachians, Turner et al. (1983) measured lead concentrations in forest floor horizons of the spruce-fir zone of the Great Smoky Mountains National Park. Their data indicate concentrations about one-half those reported from spruce-fir forests in the northeastern United States, suggesting that pollutant lead deposition may not have occurred in the Southern Appalachians to the extent it has in the Northeast. Lead contents of the forest floor were not reported, nor were elevational trends.

CONCLUSIONS

The studies discussed in this paper suggest an elevational increase in total pollutant deposition. The apportionment of this trend into components of wet, dry and cloud deposition cannot be clearly discerned from the available data; however, all three processes probably increase with elevation, and their relative importance may vary between different pollutants and different geographic areas. Further research will be necessary to assess fully the rates and processes of pollutant deposition in mountainous terrain. Data needs include high-elevation measurements of precipitation chemistry and amount, air pollutant concentrations, fog water chemistry, dry deposition rates, and meteorological variables such as fog frequency, wind speed, wind direction, and relative humidity. Because of their severe climate, mountain ecosystems may be fragile and especially susceptible to damage from pollutants. Although these ecosystems are frequently remote from large population centers, they are important to man as recreation areas, sources of water and reserves for unique species. The consequences of air pollution damage to these ecosystems are thus potentially severe. An accurate determination of pollutant deposition rates if necessary before any assessment of pollutant impacts can be made.

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APPENDIX I.

VASCULAR PLANTS OF SOUTHERN APPALACHIAN SPRUCE-FIR: ANNOTATED CHECKLISTS ARRANGED BY GEOGRAPHY, HABITAT, AND GROWTH FORM

P. S. White and L. A. Renfro

These lists are arranged by geographic area, habitat, and growth form. Three geographic categories are used: (1) Great Smoky Mountains National Park, (2) additional southern Appalachian high peak areas, and (3) northern Appalachians. For Great Smoky Mountains National Park, five habitat categories are used: (1) spruce-fir forest, (2) wet sites (seepage areas, wet thickets, streamsides), (3) high elevations cliffs, (4) heath balds, and (5) trailsides (within spruce-fir). Grassy balds are not covered here because they have been treated in detail elsewhere (for a recent compilation see D. A. Stratton and P. S. White, 1982, National Park Service, Southeast Regional Office, Res./Resource Manage. Rept. SER-58) and because they are not always adjacent to spruce-fir forest (which is the central habitat type for these lists). For all lists, five growth form categories are used: (1) trees, (2) small trees, (3) shrubs, (4) dwarf shrubs, and (5) herbs (the latter divided into pteridophytes, graminoids, and forbs).

The following annotations are used to show frequency in spruce-fir forest, geographical distributions, and 'listed' status:

- + Species characteristic of Appalachian spruce-fir (hence used only for the spruce-fir habitat category)
- () Species characteristic of northern hardwood forest or other vegetation type adjoining spruce-fir and usually found only at low elevations within spruce-fir dominated forests
- N Species found in the northern Appalachians
- S Species found in the southern Appalachians
- rare Species significantly rare in either north (N-rare) or south (S-rare)
- endemic Species endemic to the high elevations of the southern Appalachians (Note that this category includes only the high elevation endemics. For example, if a particular species is endemic to the southern

Appalachians but occurs throughout the elevation gradient it would be designated "S" only. If the species were endemic to the high elevations it would be designated "S-endemic".)

-listed Species found on state or national rare and endangered species lists (from unpublished data of P. S. White; this designation is applied to GRSM plants only)

* Introduced species

The continuous nature of compositional change with elevation means that an arbitrary line must be drawn between extraneous floristic elements only rarely present in spruce or spruce-fir communities and those that can be considered recurrent enough to warrant inclusion in these lists. For example, Fagus grandifolia (beech) stands occur adjacent to the lower elevation limit of spruce-fir forests and saplings of this species are occasionally seen in adjacent spruce-fir--hence this species appears as "(Fagus grandifolia)" in the checklist. On the other hand a number of lower elevation species have been excluded from the lists even though they may be seen, though rarely, within or immediately adjacent to spruce-fir forests. These include: Allium tricoccum, Aquilegia canadensis, Castanea dentata, Caulophyllum thalictroides, Crataegus macrosperma, Cryptotaenia canadensis, Erigeron pulchellus, Fraxinus americana, Geranium maculatum, Osmorhiza claytonii, Pinus pungens, Polystichum acrostichoides, Smilax rotundifolia, and Vicia caroliniana. Spruce or spruce-fir dominated stands adjoin several community types: northern hardwoods (on moist and protected sites), hemlock (on north facing open slopes and ridges), heath balds (on exposed ridges), pine-heath (on exposed ridges), and oak (on upper flats and some south facing slopes). Species from each of these community types may also be found occasionally in adjacent spruce-fir forests.

There are also northern species and high elevation southern Appalachian endemic species which, though found in GRSM, are not known to occur within the spruce-fir type. Some of these cannot be assigned a habitat because collection data are imprecise (e.g., Linnaea borealis and Lilium grayi). Others are found in the GRSM flora, but not in any of the habitat types considered here (e.g., Agrostis borealis, Carex trisperma, Coeloglossum virescens, Corylus cornuta, Hieracium scabrum, Ilex collina, Lilium canadense, and Lycopodium annotinum). These species are not listed below, despite their association in other parts of their ranges with the habitat categories we have used.

Species listed under "Northern Appalachian species not found in southern Appalachian spruce-fir" may be found in areas adjacent to the southern Appalachian high peaks but are not found in the high elevation areas we focus on here. The southern Appalachian high peaks are those areas that surpass 1,680 m (5500 ft) in elevation (see Saunders, this volume, Ramseur 1960). Some

species listed as not found in southern Appalachian spruce-fir are native in the state of Virginia (e.g., Trientalis borealis) or West Virginia (e.g., Cornus canadensis). Quite a few of the species are found in the central Appalachians (e.g., Shenandoah National Park, Virginia, where Abies balsamea is found). These northern species may also be found in the south in association with habitats other than spruce-fir forest (e.g., bogs near the glacial boundary). In any case, they are generally distributed in spruce-fir communities in the northeast. As in the Great Smoky Mountains National Park checklist, those that are typical of upland northern Appalachian slope forests are designated by a "+" sign.

If species designated with " -- S " occur in the north, but are not associated with spruce-fir vegetation there, then no "N" appears in the annotations (e.g., Euonymus obovatus).

These lists are compiled from unpublished data of P. White and the following published sources:

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A. CHECKLISTS FOR GREAT SMOKY MOUNTAINS NATIONAL PARK

1. SPRUCE-FIR FORESTS

TREES:

+Abies fraseri -- S-endemic; listed
Acer rubrum -- N,S
(Acer saccharum -- N,S)
(Aesculus octandra -- S)
Betula cordifolia -- N,S-rare; listed
+Betula lutea -- N,S
(Fagus grandifolia -- N,S)
+Picea rubens -- N,S
(Prunus serotina -- N,S)
Tsuga canadensis -- N,S

SMALL TREES:

Amelanchier laevis -- N,S
Acer pensylvanicum -- N,S
+Acer spicatum -- N,S
Prunus pensylvanica -- N,S
+Sorbus americana -- N,S

SHRUBS:

Aronia melanocarpa -- N,S
(Cornus alternifolia -- N,S)
Diervilla sessilifolia -- S-endemic
(Euonymus obovatus -- S; listed)
(Hydrangea arborescences -- S)
Ilex montana -- S
Lonicera canadensis -- N,S-rare; listed
Menziesia pilosa -- S-endemic; listed
+Rhododendron catawbiense -- S
Rhododendron maximum -- S
+Ribes glandulosum -- N,S
+Ribes rotundifolium -- S-endemic
+Rubus canadensis -- N,S
Rubus idaeus var. canadensis -- N,S-rare; listed
+Sambucus pubens -- N,S
Vaccinium constablaei -- S
+Vaccinium erythrocarpon -- S-endemic
+Viburnum alnifolium -- N,S
Viburnum cassinoides -- N,S

DWARF SHRUBS:

(Gaultheria procumbens -- N,S)
(Mitchella repens -- N,S)

HERBS:

Pteridophytes:

Asplenium montanum -- S
+Athyrium asplenioides -- S
Athyrium thelypteroides -- N,S
(Botrychium virginianum -- N,S)
Cystopteris protrusa -- S
+Dennstaedtia punctilobula -- N,S
+Dryopteris campyloptera -- N,S
+Dryopteris intermedia -- N,S
Lycopodium clavatum -- N,S
+Lycopodium lucidulum -- N,S
Lycopodium obscurum -- N,S
Osmunda cinnamomea -- N,S
Osmunda claytoniana -- N,S
Polypodium virginianum -- N,S
(Pteridium aquilinum -- N,S)
Thelypteris noveboracensis -- N,S
Thelypteris phegopteris -- N,S-rare; listed

Graminoids:

Brachyelytrum erectum -- N,S
Carex aestivalis -- N,S
+Carex brunnescens -- N,S
Carex communis -- N,S
+Carex debilis -- N,S
+Carex intumescens -- N,S
Carex laxiflora -- N,S
Carex misera -- S-endemic; listed
+Carex pensylvanica -- N,S
Carex projecta -- N,S
+Cinna latifolia -- N,S
(Danthonia compressa -- N,S)
(Festuca obtusa -- N-rare, S)
Glyceria melicaria -- N,S
Glyceria nubigena -- S-endemic-rare; listed
Luzula acuminata -- N,S
Luzula echinata -- S
Miliun effusum -- N,S-rare; listed
Poa alsodes -- N,S

Forbs:

Amianthemum muscaetoxicum -- S
+Anemone quinquefolia -- N,S
+Angelica triquinata -- S-endemic
Arabis laevigata -- S
Aralia nudicaulis -- N,S
+Arisaema triphyllum -- N,S
+Aster acuminatus -- N,S
+Aster chlorolepis -- S-endemic
Aster cordifolius -- N,S

+*Aster curtisii* -- S
 Aster macrophyllus -- N,S
 Cacalia atriplicifolia -- S
 +*Cacalia rugelia* -- S-endemic; listed
 Chelone lyoni -- S-endemic
 +*Cimicifuga americana* -- S
 Circaea alpina -- N,S
 Claytonia caroliniana -- N,S
 +*Clintonia borealis* -- N,S
 Cuscuta rostrata -- S
 (*Cypripedium acaule* -- N,S)
 Dentaria diphylla -- N,S
 (*Dicentra canadensis* -- N,S)
 (*Dicentra cucullata* -- N,S)
 Erythronium americanum -- N,S
 (*Eupatorium purpureum* -- S,N-rare)
 +*Eupatorium rugosum* -- N,S
 (*Galax aphylla* -- S)
 Galium triflorum -- N,S
 Goodyera repens var. *ophioides* -- N,S
 Heuchera americana -- S
 Heuchera villosa -- S
 Houstonia purpurea -- S
 +*Houstonia serpyllifolia* -- S-endemic
 +*Impatiens pallida* -- N,S
 +*Laportea canadensis* -- N,S
 Lilium superbum -- S
 Listera smallii -- S
 Maianthemum canadense -- N,S
 +*Medeola virginiana* -- N,S
 (*Melantium parviflorum* -- S)
 (*Monarda didyma* -- S)
 +*Monotropa uniflora* -- N,S
 +*Oxalis montana* -- N,S
 (*Phacelia fimbriata* -- S)
 Platanthera psycodes -- N,S
 (*Podophyllum peltatum* -- N,S)
 (*Polygonatum pubescens* -- N,S)
 Polygonum cilinode -- N,S-rare; listed
 (*Potentilla simplex* -- N,S)
 +*Prenanthes altissima* -- N,S
 Prenanthes roanensis -- S-endemic; listed
 (*Ranunculus recurvatus* -- N,S)
 Rudbeckia laciniata -- S
 Saxifraga michauxii -- S-endemic
 (*Smilacina racemosa* -- N,S)
 Smilax herbacea -- N,S
 +*Solidago curtisii* -- S
 +*Solidago glomerata* -- S-endemic
 Stachys clingmanii -- S-endemic; listed
 Streptopus amplexifolius -- N,S-rare; listed
 +*Streptopus roseus* -- N,S
 (*Tiarella cordifolia* -- N,S)
 (*Trautvetteria caroliniensis* -- S)
 +*Trillium erectum* -- N,S

Trillium undulatum -- N,S
(Uvularia perfoliata -- N,S)
+Veratrum viride -- N,S
+Viola mackloseyi ssp. pallens --N,S
+Viola papilionacea -- N,S
(Viola rotundifolia -- N,S)

2. SEEPAGE AREAS, STREAMSIDES, AND WET THICKETS

SHRUBS:

Aronia melanocarpa -- N,S
Salix humilis -- N,S
Salix sericea -- N,S
Sambucus pubens -- N,S
Viburnum cassinoides -- N,S

HERBS:

Graminoids:

Carex crinita -- N,S
Carex normalis -- N,S
Carex ruthii -- S-endemic; listed
Carex scabrata -- N,S
Carex stipata -- N,S
Carex tribuloides --N,S
Glyceria nubigena -- S-endemic-rare; listed
Glyceria striata -- N,S
Juncus effusus -- N,S

Forbs:

Aconitum uncinatum -- S
Aster puniceus -- N,S
Chelone lyoni -- S-endemic
Cardamine clematitis -- S
Chrysosplenium americanum -- N,S; listed
Cirsium muticum -- N,S
Diphylleia cymosa -- S
Eupatorium fistulosum -- N,S
Eupatorium maculatum -- N,S
Hypericum graveolens -- S-endemic; listed
Hypericum mitchellianum -- S-endemic; listed
Hypericum mutilum -- N,S
Impatiens capensis -- N,S
Lycopus virginicus -- N,S
Monarda didyma -- S
Parnassia asarifolia -- S
Platanthera clavellata -- N,S
Platanthera psycodes -- N,S
Rudbeckia laciniata -- S
*Rumex obtusifolius -- N,S
Saxifraga micranthidifolia -- S
Stachys clingmanii -- S-endemic

Thalictrum clavatum -- S
Thalictrum polygamum -- N,S
Veratrum viride -- N,S
Viola mackloskeyi ssp. pallens -- N,S
Viola papilionacea -- N,S

3. HEATH BALDS

SHRUBS:

Aronia melanocarpa -- N,S
Diervilla sessilifolia -- S-endemic
Clethra acuminata -- S
Ilex montana -- S
Kalmia latifolia -- S
Leiophyllum buxifolium -- S
Leucothoe editorum -- S
Lyonia ligustrina -- N,S
Menziesia pilosa -- S-endemic; listed
Pieris floribunda -- S
Rhododendron catawbiense -- S
Rhododendron maximum -- S
Rhododendron minus -- S
Vaccinium constablaei -- S
Viburnum cassinoides -- N,S

DWARF SHRUBS:

Epigaea repens -- N,S
Gaultheria procumbens -- N,S

HERBS:

Pteridophytes:

Lycopodium flabelliforme -- N,S
Lycopodium tristachyum -- N,S
Pteridium aquilinum -- N,S

Forbs:

Galax aphylla -- S
Melampyrum lineare -- N,S

4. HIGH ELEVATION CLIFFS

SHRUBS:

Diervilla sessilifolia -- S-endemic
Leiophyllum buxifolium -- S
Menziesia pilosa -- S-endemic; listed
Rhododendron catawbiense -- S
Rhododendron minus -- S
Vaccinium angustifolium -- N,S-rare; listed

HERBS:

Pteridophytes:

Asplenium montanum -- S
Asplenium trichomanes -- N,S
Lycopodium selago -- N,S-rare; listed
Polypodium virginianum -- N,S

Graminoids:

Calamagrostis cainii -- S-endemic-rare; listed
Carex misera -- S-endemic; listed
Carex ruthii -- S-endemic; listed
Glyceria nubigena -- S-endemic-rare; listed
Juncus trifidus var. monanthos -- S-endemic-rare; listed
Scirpus caespitosus -- N,S-rare; listed

Forbs:

Cardamine clematitis -- S
Chelone lyoni -- S-endemic
Gentiana linearis -- N,S-rare; listed
Geum radiatum -- S-endemic-rare; listed
Hypericum graveolens -- S-endemic; listed
Hypericum mitchellianum -- S-endemic; listed
Krigia montana -- S-endemic-rare; listed
Parnassia asarifolia -- S-rare
Saxifraga michauxii -- S-endemic
Solidago glomerata -- S-endemic

5. TRAILSIDES WITHIN SPRUCE-FIR FORESTS

HERBS:

Graminoids:

Agrostis perennans -- N,S
*Holcus lanatus -- N,S
Juncus tenuis -- N,S
*Poa annua -- N,S
*Poa pratense -- N,S

Forbs:

*Achillea millefolium -- N,S
*Barbarea vulgaris -- N,S
*Chrysanthemum leucanthemum -- N,S
Fragaria virginiana -- N,S
Plantago rugelii -- N,S
*Prunella vulgaris -- N,S
Ranunculus spp -- N,S
*Rumex acetosella -- N,S
*Trifolium spp -- N,S
*Veronica officinalis -- N,S

B. ADDITIONAL SOUTHERN APPALACHIAN HIGH ELEVATION SPECIES NOT
FOUND IN GREAT SMOKY MOUNTAINS NATIONAL PARK

TREES:

Tsuga caroliniana -- S

SHRUBS:

Alnus crispa -- N,S-rare; listed
Comptonia peregrina -- N,S-rare; listed
Diervilla lonicera -- N,S-rare; listed
Potentilla tridentata -- N,S-rare; listed
Rhododendron vaseyi -- S-endemic-rare; listed

HERBS:

Pteridophytes:

Selaginella tortipilla -- S-rare

Graminoids:

Agrostis borealis -- N,S-rare; listed
Calamagrostis canadensis -- N,S-rare; listed
Carex biltmoreana -- S-endemic-rare
Deschampsia flexuosa -- N,S
Trisetum spicatum var. *molle* -- N,S-rare; listed

Forbs:

Arenaria groenlandica -- N,S-rare; listed
Cardamine pensylvanica -- N,S-rare; listed
Corallorhiza maculata -- N,S-rare
Epilobium angustifolium -- N,S-rare; listed
Gentiana andrewsii -- S-endemic-rare
Geum geniculatum -- S-endemic-rare; listed
Houstonia montana -- S-endemic-rare; listed
Hypericum buckleyi -- S-endemic-rare; listed
Hypericum canadense -- N,S-rare
Liatris helleri -- S-rare
Sedum telephioides -- S-rare
Sedum rosea var. *roanensis* -- S-endemic-rare
Solidago spithamea -- S-rare

C. NORTHERN APPALACHIAN SPRUCE-FIR FOREST SPECIES NOT FOUND IN
SOUTHERN APPALACHIAN SPRUCE-FIR

TREES:

+*Betula papyrifera*
Larix laricina
Picea mariana
Pinus banksiana

Pinus resinosa
Populus balsamifera
Populus tremuloides

SMALL TREES:

Betula populifolia
+Sorbus decora

SHRUBS:

Amelanchier bartramiana
Aralia hispida
Diervilla lonicera
Kalmia angustifolia
Ledum groenlandicum
+Nemopanthus mucronata
Prunus virginiana
Rhododendron canadense
Ribes hirtellum
+Ribes lacustre
Ribes triste
+Rubus pubescens
Salix bebbiana
Salix discolor
Salix pyrifolia
Salix rigida
+Vaccinium myrtilloides

DWARF SHRUBS:

Chimaphila umbellata
+Chiogenes hispidula
+Linnaea borealis

HERBS:

Pteridophytes:

Equisetum sylvaticum
Cystopteris fragilis
Gymnocarpium dryopteris
+Lycopodium annotinum

Graminoids:

Carex canescens
Carex trisperma
Oryzopsis asperifolia
Schizachne purpurascens

Forbs:

+Actaea rubra
Arenaria lateriflora

Conioselinum chinense
+Coptis groenlandica
Corallorhiza trifida
+Cornus canadensis
Dalibarda repens
+Goodyera tessellata
Mitella nuda
Moneses uniflora
Platanthera macrophylla
Platanthera orbiculata
Pyrola asarifolia
+Pyrola elliptica
+Pyrola minor
+Pyrola secunda
Smilacina trifolia
+Solidago macrophylla
+Trientalis borealis
Viola renifolia

APPENDIX II.

BIBLIOGRAPHY OF RESEARCH ON SOUTHERN APPALACHIAN SPRUCE-FIR VEGETATION

P. S. White and C. Eagar

Vegetation is the key component of this ecosystem: the analysis of forest decline, balsam woolly aphid effects, ecosystem effects of pollutants, and habitat change for a variety of plant and animal populations centers on changes in forest composition, structure, and dynamics. We have compiled this bibliography in order to provide easy access to the already extensive literature on southern Appalachian spruce-fir vegetation. We have included population, community, and ecosystem oriented research; for more specialized topics see individual chapter bibliographies in this volume. This bibliography was compiled from DeYoung et al. (1982), from the contributors to this volume, and from unpublished files of the authors.

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