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Effects of Fraser Fir Death on Population Dynamics in Southern Appalachian Boreal Ecosystems

Rex Randall Boner
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by Rex Randall Boner entitled "Effects of Fraser Fir Death on Population Dynamics in Southern Appalachian Boreal Ecosystems." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

H.R. DeSelm, Major Professor

We have read this thesis and recommend its acceptance:

Edward R. Buckner, J. Rennie

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

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

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and recommend its acceptance:

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Accepted for the Council:

L. Evans Roth

Vice Chancellor
Graduate Studies and Research

EFFECTS OF FRASER FIR DEATH ON POPULATION DYNAMICS IN SOUTHERN APPALACHIAN BOREAL ECOSYSTEMS

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

Rex Randall Boner

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ABSTRACT

High elevation fir and spruce-fir forests of the Southern Appalachians were sampled in the Black Mountains, North Carolina and in the Great Smoky Mountains, Tennessee and North Carolina. Both absolute and relative data were collected on the composition of the overstory and understory strata; the ground cover stratum was sampled for relative data. Both stands infested by the balsam woolly aphid and uninfested stands were sampled to determine the effects of the opened canopy caused by the death of Fraser fir on the population dynamics of these boreal ecosystems. Comparison of stand composition and use of correlation and regression analysis revealed trends in changes.

Overstory density in uninfested fir and spruce-fir forests at 6000 feet elevation or above averaged 354.7 stems per acre with a basal area total of 205.6 square feet per acre. In lower elevation uninfested stands overstory density averaged 280.4 stems per acre and basal area averaged 232 square feet per acre. Those stands infested by the balsam woolly aphid displayed decreasing overstory densities and basal areas in response to Fraser fir death.

Sapling densities are believed to have varied more as a result of sampling error than in response to fir death. Uninfested stands at or above 6000 feet elevation averaged 119.9 sapling stems per acre (77.3% fir), lower elevation stands averaged 168.6 stems per acre (67.4% fir).

Stems less than one inch DBH and more than two feet tall exhibited the greatest response to aphid-caused Fraser fir death. These stems averaged 1110.5 stems per acre (50.2% fir) in the high elevation uninfested stands, 2828.3 stems per acre (24.1% fir) in the lower elevation stands sampled and 6238.5 stems per acre (18.8% fir) in the stands with the longest period of time since the death of fir occurred. Not only did the total subsapling density increase significantly in those stands infested by the balsam woolly aphid, but the relative composition of this stratum changed drastically also. As demonstrated by simple comparison of stand composition and by correlation and regression analyses, the densities of thornless blackberry (*Rubus canadensis*), red raspberry (*Rubus idaeus* var. *canadensis*) and Fraser fir increased significantly in response to overstory fir death. However, the densities of mountain cranberry (*Vaccinium erythrocarpum*) and hobblebush (*Viburnum alnifolium*) decreased.

Changes in the composition of the ground cover layer in response to the death of fir were also significant. *Oxalis acetosella* cover and total moss cover decreased as the canopy opened due to the death of fir.

Based on regression analysis results, the amount of aphid-caused fir death was a good predictor of increased densities of thornless blackberry and subsapling fir. Increased fir death was a predictor of less mountain cranberry and hobblebush densities.

Correlation of site and vegetation variables revealed that *Oxalis acetosella* and thornless blackberry increased toward dry sites and toward increased exposed surface rock. Pteridophyte cover increased toward mesic sites and as surface rock cover decreased.

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I. INTRODUCTION

The composition and structure of the Southern Appalachians boreal forest system were investigated for two reasons: 1) to obtain baseline data concerning existing fir and spruce-fir stands and 2) to compare these stands to those infested by the balsam woolly aphid (*Adelges piceae* Ratz.) in order to relate time of aphid-caused death of Fraser fir (*Abies fraseri* (Pursh.) Poir.) and other ecological variables to vegetation succession and understory and ground cover composition.

Argument still exists concerning the taxonomic validity of the species, *Abies fraseri* (Pursh.) Poir. Certain investigators contend that it is a true species (Myers and Bormann, 1963; Little, 1971), others maintain that Fraser fir should be considered simply a variety of the more northern balsam fir (*Abies balsamea* (L.) Mill) (Thor and Barnett, 1974).

Regardless of its level of taxonomic distinctness, Fraser fir is limited in distribution to high elevations in the Southern Appalachians of southwest Virginia, western North Carolina and eastern Tennessee (Little, 1953). Several authors have reported a similarity between the flora of these southern fir and spruce-fir forests and the flora of the northern counterpart where Fraser fir is replaced by balsam fir (Oosting and Billings, 1951; Ramseur, 1960; Hoffman, 1964b; Norris, 1964). These similarities suggest a past more continuous distribution of the eastern boreal forest system.

Whittaker (1956) and Mark (1958) maintained that during Pleistocene glaciation the boreal forest occurred farther south than its present range and was continuous through the Southern Appalachians. They further contend that post-Wisconsin xerothermic or hypsithermal periods provided sufficiently warm climates to force the fir and, in some places, the spruce-fir forests off the lower elevation peaks in the southern portion of this range, thereby decimating the seed source needed for reinvasion during periods of cooler climates that followed. Bryoecological information based on the distribution of _Hylocomium splendens_ (Hedw.) B.S.G. appears to support this contention (Norris, 1964).

Zavarin and Snajberk (1972) reported chemical evidence to support this hypothesis. In fact, they contend that balsam fir spread to its present range from refugia in the West and in the South that now harbor populations of subalpine fir (_Abies lasiocarpa_ (Hook) Nutt.) and Fraser fir, respectively.

During this xerothermic or hypsithermal period, Mark (1958) reports that balsam fir suffered a reduction in biotypes during these xeric times yielding Fraser fir. Due to its restricted distribution and to the length of time it has been isolated, Fraser fir has probably lost much of its original genetic variability. This reduction in ability to produce new diverse genotypes has resulted in a lower resistance to diseases and infestations. Therefore, when the balsam woolly aphid was accidentally introduced into the U.S.

States about 1900 (Balch, 1952) and spread to the Southern Appalachians, Fraser fir was demonstrated to be one of the true firs with least resistance to the attack (Silen and Woike, 1959). Amount of aphid infestation per fir tree appeared directly related to diameter size of the tree (Johnson, 1977).

In the present investigation, uninfested fir and spruce-fir stands in the Great Smoky Mountains were sampled to provide a permanent record of their composition and structure in the event that Fraser fir is eliminated from this system. Infested stands in the Great Smoky Mountains and in the Black Mountains were sampled for comparison.

II. THE STUDY AREA

Location and Topography

The Great Smoky Mountains and Black Mountains study areas are in the southern section of the Blue Ridge Province of the Appalachian Highlands (Fenneman, 1938). The mountains which comprise the Great Smoky Mountains National Park are part of the Unaka Range at the western edge of the Blue Ridge Province, the Black Mountains are in the interior of the Blue Ridge Range.

The Black Mountains in Yancey County in western North Carolina, so named because of the dense coniferous forests of the high elevations (Pinchot and Ashe, 1897), lie approximately 20 miles northeast of Asheville, 35^{o} 45' north and 82^{o} 15' west and northward. Study areas are on the Mt. Mitchell and Celo 7.5 minute quadrangles of the United States Geological Survey.

The Great Smoky Mountains comprise approximately 508,000 acres in parts of five counties in eastern Tennessee and western North Carolina. That portion of the Great Smoky Mountains included in this study lies northeast of Clingmans Dome, 35^{o} 33' north and 83^{o} 30' west. Study areas are on the Clingmans Dome, Mt. LeConte, Bunches Bald, Mt. Guyot, Luftee Knob and Cove Creek Gap 7.5 minute quadrangles of the United States Geological Survey.

The mountains of both areas are very old and have been subjected to much weathering resulting in the many rounded summits and the "subdued" appearance (Fenneman, 1938). The higher slopes, commonly with 20% to 60% slopes, are less steep than the valley sides (Fenneman, 1938). The Black Mountains drain in the Mt. Mitchell area on the north and west into the Cane and Toe Rivers, tributaries to the Nolichucky River, and to the Swannanoa and French Broad Rivers on the south and east. The Great Smoky Mountains drain into the Pigeon River on the north and east, the Little Tennessee River on the south and the Little Pigeon River on the north and west.

Climate

Although some areas in the Great Smoky Mountains receive more precipitation than the Black Mountains due to the moist Gulf air masses which reach the Great Smoky Mountains before reaching the Black Mountains, the overall climate of both study areas can still be discussed jointly as trends appear similar for the high elevation sites. However, the terrain of these areas doubtlessly causes microclimatic differences similar to those found by Shanks and Norris (1950) due to the effects of aspect.

Official collection of climatic data began on Mt. Mitchell in 1873 when a party of Signal Service observers spent the months of May, June, July and August on the summit recording temperature, rainfall, barometric pressure and other features of the weather (Message from the President, 1902). They described the high elevation climate as follows:

> The highest temperature observed on the summit of the mountain during the four months was 72° in July; the lowest, 41° in June. The monthly mean temperatures for the four months were as follows: May, 49.3°; June, 54.1°; July, 56.4°; and August, 55.3°. The rainfall was very heavy, 36.8 inches being recorded while the observers were on the summit. Rain fell on 21 days in May, 22 in June, 15 in July, and 21 in August. There was a great abundance of foggy and cloudy weather, the fog and clouds being frequently below the summit. The prevailing winds were from a westerly quarter.

Shanks (1954) reported that the spruce-fir forests of the Southern Appalachians are warmer and wetter than their Acadian Boreal counterparts and classified those of the Great Smoky Mountains as more humid than the most humid climatic categories of Thornthwaite (1931, 1948). At 6300 feet in the Great Smoky Mountains, precipitation peaks occur in late winter and late summer as January averages 11.86 inches and August 10.14 inches; the remaining months average between 4.97 inches in October and 8.36 inches in June (Stephens, 1969). An annual average of 90.48 inches at 6300 feet elevation was reported by Stephens (1969) and 90.9 inches was reported by Shanks (1954). Precipitation decreases downslope to 89.0 inches at 5000 feet elevation and 78.8 inches at 3800 feet elevation (Shanks, 1954). This increase in precipitation with an increase in altitude is accompanied by a greater increase in water surplus since evapotranspiration decreases with elevation (Shanks, 1954).

Total precipitation is less in the Black Mountains with an annual average at 6635 feet elevation of 71.2 inches with a high of 8.94 inches in August, 8.12 inches in July and 6.34 inches in March (Carney, 1955).

In general, precipitation increases with increased elevation; Smallshaw (1953) reported an increase of approximately nine inches for each 1000 feet of elevational increase in the Southern Appalachians. However, he also reported that the effect of elevation appeared to be somewhat less pronounced above elevations of 3000-3500 feet. He further observed the significant effect of other factors on the amount of rainfall such as updraft, carry-over of moisture-laden air and funneling of winds which results in less total rainfall at an elevation of 5600 feet on Snake Mountain, North Carolina than at lower surrounding elevations.

Intensity of rainfall is also apparently greater at higher elevations in the Great Smoky Mountains as Bogucki (1972) reported the occurrence of 194 intense rainfalls over a 30 year period at elevations above 4000 feet while elevations below 4000 feet experienced only 56 such storms. Clingmans Dome, the location of the highest rain gauge in the Park at 6250 feet elevation, accounted for 122 of the 194.

Mean monthly temperature reaches an average low of 28.7^{o}F in February and an average high of 56.5^{o}F in July in the Great Smoky Mountains at these highest elevations (Stephens, 1969). The average January low at Mt. Mitchell is 28.7^{o}F and the average high in July is 59.2^{o}F (Carney, 1955).

Although measurements of temperature changes throughout the year are important, perhaps the essence of these measurements concerns those that dictate the length of the growing season. Wang (1963) considered the growing season as the number of days between the last killing frost in spring and the first one in autumn. However, although such temperature extremes will indeed retard or limit plant growth, certain plant physiological processes may decrease to a minimum at higher temperatures. Stephens (1969) measured the length of growing seasons at four elevations in the Great Smoky Mountains at temperatures of 32^{o}F, 36^{o}F and 40^{o}F. Surprisingly, the growing season based on the 32^{o}F and 36^{o}F limits in the spruce-fir zone measured at 6300 feet elevation were 152.25 days and 136.25 days, respectively, which did not differ significantly from that at Park Headquarters located at 1460 feet elevation. This latter growing season length at 36^{o}F was actually longer than that found at all lower elevation weather stations. However, the growing season defined by 40^{o}F at 6300 feet elevation was only 96.50 days. Dickson (1959) found the growing season on Mt. Mitchell to be 126 days at 32^{o}F.

The average temperature was 2.23°F lower for every 1000 feet increase in elevation in the Southern Appalachians according to Shanks (1954). This gradual decrease in temperature with increase in elevation results in the spruce-fir zone of the Great Smoky Mountains and the Black Mountains averaging 10°F to 15°F colder than the base of the mountains during the growing season.

Dickson (1959), using the Thornthwaite method, calculated potential evapotranspiration for Mt. Mitchell where it ranged from zero in December through March to a monthly high of 3.4 inches in July. Shanks (1954) reported similar trends in the Great Smoky Mountains; the potential evapotranspiration at 6300 feet elevation ranged from zero in January to a monthly high of 3.9 inches in July resulting in a large water surplus.

Soil temperatures vary according to elevation and according to environmental differences within the same elevation (Shanks, 1956). A lag appears in the spring warming of the soil at 6000 feet elevation as the soil temperature ranges from a low of approximately 30°F in March to a high of approximately 52°F in August (Shanks, 1956).

Geology

Black Mountains. This area is almost completely underlain by Carolina gneiss of Archean age (Keith, 1905). Although the origin of Carolina gneiss is not completely known, it is a very old metasedimentary series that apparently was much metamorphosed and invaded by granitic material during Precambrian time then subjected to further deformation and regional metamorphism during Paleozoic time (Hadley and Goldsmith, 1963). This formation consists mainly of mica-gneiss and mica-schist combinations with smaller amounts of garnet-schist, garnet-gneiss, cyanite-gneiss and fine granitoid layers. The Black Mountains area in particular contains a considerable amount of cyanite which, due to its resistance to weathering, is largely responsible for the great height of this range (Keith, 1905). Apparently no true measure of the thickness of this formation has been obtained but it appears to be extremely thick.

Great Smoky Mountains. Most of the eastern portion of the Great Smoky Mountains consists of variably metamorphosed sandstone, conglomerate and siltstone, many thousands of feet thick known as the Ocoee Series of late Precambrian Age (Hadley and Goldsmith, 1963). These rocks are underlain by a complex assemblage of granitic and metasedimentary gneisses much older than the Ocoee Series (Hadley and Goldsmith, 1963).

Rocks in the study area are all part of the Great Smoky Group, Thunderhead sandstone being predominant and the Anakeesta Formation outcropping over small areas. Thunderhead Sandstone is characterized by 6000-12,000 feet of thick-bedded, medium to coarse grained feldspathic sandstone and fine arkosic conglomerate with metamorphic biotite generally present (Hadley and Goldsmith, 1963). The Anakeesta Formation includes a greater variety of rocks than does the Thunderhead Sandstone, including a small pebbled arkosic conglomerate, graywacke, fine to coarse grained feldspathic sandstone, gray chloritoidal slate and argillite, very dark carbonaceous slate and phyllite and dark carbonate rocks (Hadley and Goldsmith, 1963). It characteristically contains dark carbonaceous and sulfide-bearing pelitic and arenitic rocks and thin dolomite beds that often intertongue with the Thunderhead Sandstone making the boundary between these two formations often indistinct (Hadley and Goldsmith, 1963).

Soils

Black Mountains. Soils in the Mt. Mitchell area are composed primarily of the rough stony phase of the Porters series (Perkins and Gettys, 1952). They are classified as lithosolic Gray-Brown Podzolic soils characterized by weakly developed horizons: the A horizon is friable and brown to dark brown in color while the B horizon is very permeable and brown to yellowish-brown in color. Composed of residuum from granite, gneiss or schist, these soils are further characterized by many small angular rock fragments, boulders and many outcrops of bedrock, very rapid external drainage and moderate to rapid internal drainage (Perkins and Gettys, 1952). Holmes (1911) characterized these soils as black loams with sandy subsoils varying from a few inches to two feet thick. Keith (1905) further observed that the clay cover on the decayed rocks was thin. Due to stoniness and shallowness to bedrock, these soils were given a fifth class rating indicating their poor agricultural potential (Perkins and Gettys, 1952).

Great Smoky Mountains. Soils of this area have been termed rough mountainous land or stony rough land and are composed mainly of soils of the Ramsey and Porters series (Hubbard, et al., 1956; Goldston, et al., 1954). They are characterized by the occurrence of numerous large angular rock fragments, rapid external drainage, moderate internal drainage, low pH, low base status, high exchangeable aluminum and decreasing amounts of organic carbon with increasing depth (Goldston, et al., 1954; Cain, 1931; McCracken, et al., 1962).

Due to shallowness and poorly developed profiles, these soils were classified by Goldston, et al., (1954) as lithosols, later as Sol Brun Acides (McCracken, et al., 1962) and finally as Inceptisols with these specific soils in the Great Smoky Mountains belonging to the Umbic Dystrochrept Subgroup (Wolfe, 1967). Likewise, Coile (1938) described the formation of Podzols within certain high elevation forests of the Southern Appalachians and Wolfe (1967) further classified those in the Great Smoky Mountains as Spodosols belonging to the Entic Normorthod Subgroup.

McGinnis (1958) described a soil profile under spruce-fir vegetation on a southeast-facing slope near Newfound Gap in the Great Smoky Mountains at 5200 feet elevation. He found the parent material to be graywacke with thin L, F, H_1 and H_2 layers present. The A horizon consisted of 5.1 cm of A_1 and 3.4 cm of AB while the B was 5.4 cm thick and undifferentiated.

Subsoil within the spruce-fir zone of the Great Smoky Mountains, and presumably in the Black Mountains as well, was found to be less acidic than the surface soil as Cain (1931) reported the pH of the subsoil to be 3.8 as compared to 3.6 in the surface soil at an elevation of 6500 feet. Generally he discovered that soil pH decreases with an increase in elevation. Soils in heath balds, sampled at elevations of 6600 and 5000 feet, displayed more acidic soils than those of the spruce-fir stands.

Flora

Black Mountains. Ramseur (1960) compiled the vascular flora of the high elevation vegetation of the Southern Appalachians above 5500 feet elevation and collected 391 species and varieties, of which 139 occurred in the Black Mountains of North Carolina. This number included *Betula papyrifera* var. *cordifolia* (Regel.) Fern., occurring at the southern extent of its range. Ramseur (1960) found it to be limited to the Black Mountains where it occurs as a rare canopy tree. He also reported a southern range extension to the Black Mountains for Agrostis borealis Hartm., from its previous southernmost extent on Roan Mountain on the Tennessee-North Carolina border.

Southern Appalachian vascular plant endemics are numerous as Harper (1947) listed 188 such species. Such plant endemics occurring in the spruce-fir forests of the Black Mountains include Abies fraseri, Rhododendron catawbiense, Diervilla sessilifolia, Vaccinium erythrocarpum, Chelone lyoni and Solidago glomerata. Other species widespread in Canada and the northern United States but limited to the uplands and mountains in the Southern Appalachians occurring in the Black Mountains include Picea rubens, Betula lutea, Prunus pensylvanica, Sorbus americana, Acer spicatum, Acer pensylvanicum, Viburnum alnifolium, Sambucus pubens, Rubus canadensis, Rubus idaeus var. canadensis, Carex brunnescens, Clintonia borealis, Oxalis acetosella and Aster acuminatus (Ramseur, 1960).

Great Smoky Mountains. Hoffman (1964a, 1966) completed a checklist of the vascular plants of the entire Great Smoky Mountains National Park and Ramseur (1960) worked intensively in the high elevation plant communities of the Great Smoky Mountains. Ramseur (1960) reported 185 vascular species and varieties from the spruce-fir forests above 5500 feet elevation in the Great Smoky Mountains. Included in this number were Senecio rugelia, an endemic to these mountains, and Calamagrostis cainii, a narrow endemic to the Great Smoky Mountains which occurs only near the summit of Mt. LeConte. Other Southern Appalachians vascular plants endemic to the spruce-fir forests of the Great Smoky Mountains include Abies fraseri, Rhododendron catawbiense, Diervilla sessilifolia, Vaccinium erythrocarpum, Chelone lyoni and Solidago glomerata. Species occurring in the spruce-fir forests of the Great Smoky Mountains that have ranges widespread in Canada and northern United States but limited to the uplands and mountains in the Southern Appalachians include Picea rubens, Betula lutea, Prunus pensylvanica, Sorbus americana, Acer spicatum, Acer pensylvanicum, Viburnum alnifolium, Viburnum cassinoides, Sambucus pubens, Rubus canadensis, Rubus idaeus var. canadensis, Carex brunnescens, Circaea alpina, Clintonia borealis, Polygonum cilinode, Oxalis acetosella and Aster acuminatus (Ramseur, 1960). Oosting and Billings (1951) reported an unusually high proportion of species common to both spruce-fir forests of the Southern Appalachians and of the White Mountains in New Hampshire. Likewise, Hoffman (1964b) reported that 36 families of plants, 78 genera and 109 species and varieties were common to the boreal forests of Canada, Alaska and the Great Smoky Mountains.

Black spruce, Picea mariana (Miller) BSP., has been reported in the Great Smoky Mountains (Gattinger, 1901; Ayres and Ashe, 1905; House, 1913; Cain, 1930) but undoubtedly this was in reference to red spruce, Picea rubens. Both red spruce and Fraser fir, Abies fraseri, were thought to reach the westernmost and southernmost extent of their ranges in the Great Smoky Mountains approximately three miles west of Clingmans Dome (Stupka, 1964). However, a population of Fraser fir has been reported to occur approximately 35 miles southwest of this range limit on the summit of Haw Knob at an elevation of 5472 feet (DeVore, 1972). Whether this is a naturally occurring stand is not known.

Cain (1930, 1937, 1943, 1945) has contributed immensely to the understanding of the Great Smoky Mountains. He reports that the woody taxa of the spruce-fir forests are definitely northern in their affinities as 59% of the woody taxa such as *Betula lenta*, *Viburnum alnifolium*, *Prunus pensylvanica*, *Acer spicatum* and *Acer pensylvanicum* are extraneous and contain northern elements which find their southern distributional limits in the Great Smoky Mountains or vicinity (Cain, 1930).

Cain (1945) classified 301 flowering plant taxa occurring above 4500 feet elevation in the Great Smoky Mountains according to their life form (Raunkiaer, 1934). Hemicryptophytes were the predominant life form comprising 56.5% of the taxa while phanerophytes comprised 21.2%, cryptophytes 17.2%, therophytes 2.6% and chamaephytes 2.3%, a spectrum quite similar to the entire Great Smoky Mountains National Park which displayed 52.1%, 19.5%, 15.1%, 11.5% and 1.7% respectively.

The bryophyte flora of the Park is also large; Norris (1964) reported over 200 species within the spruce-fir zone.

He also sampled the bryophytes of the Adirondacks and discovered that 132 species occur there in the spruce-fir forests, of which 105 occur in the Southern Appalachians. One species in particular, Hylocomium splendens (Hedw.) B.S.G., is quite restricted in the Southern Appalachians to spruce-fir forests and is replaced by other species at lower elevations.

Vegetation

Black Mountains. Because of a higher degree of human disturbance, the Black Mountains have been less fully investigated than the Great Smoky Mountains. Descriptions by Harshberger (1903), Davis (1930), Oosting and Billings (1951), Ramseur (1960) and Weaver (1972) generally confirm vegetational patterns reported in the Great Smoky Mountains.

Great Smoky Mountains. Composition and structure of the spruce-fir forests in the Great Smoky Mountains have been intensively investigated (Cain, 1930; Cain, 1931, Cain, 1935; Cain, 1937; Cain and Sharp, 1938; Oosting and Billings, 1951; Whittaker, 1948, 1956; Crandall, 1958; Ramseur, 1960; Schofield, 1960; Norris, 1964). Oosting and Billings (1951) considered these forests as the best developed and most extensive virgin forests of spruce-fir in the Southern Appalachians and found them to be closely related to the Northern Appalachian spruce-fir forests to which these southern stands were undoubtedly geographically connected during the Pleistocene. Norris (1964) noted the physiognomic, floristic and vegetational similarities of the Southern Appalachian spruce-fir forests to those of the Adirondack Mountains in New York. Whittaker (1948) also observed the similarity in composition and structure of the Southern Appalachian spruce-fir forests to thcse of Canada but noted that the floristic differences between the two were significant enough to merit recognition of this southern assemblage as a separate division of the boreal forest system in eastern North America.

Although isolated spruce-fir stands occur as low as 4000 feet elevation within the Great Smoky Mountains National Park (Cooley, 1954), they generally occur at elevations greater than 5000 feet from Mt. Sterling in the northeast to Clingmans Dome in the southwest portion of the Park. These stands contain mixtures of Fraser fir and red spruce that vary in number with elevation and site as red spruce density decreases with an increase in elevation whereas Fraser fir density increases with an increase in elevation attaining nearly pure stands on certain high peaks in the Park.

Oosting and Billings (1951) reported that Fraser fir was three to five times more abundant in spruce-fir stands than red spruce (all stems greater than one inch DBH). Fir seedlings less than one inch DBH averaged 108.3 stems per 100 square meters compared to 26.1 stems per 100 square meters of red spruce seedlings. However, although Fraser fir was more abundant, red spruce had a higher basal area than fir. They also found that red spruce occurred in small numbers in each of a wide range of diameter size classes while Fraser fir occurred in higher numbers in fewer size classes.

Due to overstocking and overtopping, the age and amount of growth based on number of growth rings per diameter size at breast height, of both red spruce and Fraser fir, showed little correlation, although near Clingmans Dome a red spruce that was 21 inches DBH had 359 annual rings and a 15.3 inch DBH fir had 168 rings (Oosting and Billings, 1951). In general, red spruce attains larger size than Fraser fir, reaching 120 feet in height and 40 inches DBH, while mature fir trees only reach approximately 40 feet in height. Korstian (1937) reported a 57 inch DBH, 162 feet tall red spruce in the Southern Appalachians but the largest known red spruce in the Great Smoky Mountains has a diameter of 52.5 inches and a height of 106 feet (Stupka, 1964). The largest known Fraser fir in these mountains has a diameter of 30.2 inches and a height of 44 feet (Stupka, 1964).

Commonly associated canopy trees include *Sorbus americana*, *Prunus pensylvanica*, *Betula lutea* and *Acer spicatum*. Whittaker (1948) observed that the elevational distribution of *Sorbus americana* was similar to that of

Fraser fir as it increased in abundance with an increase in elevation. Prunus pensylvanica, Betula lutea and Acer spicatum displayed trends similar to red spruce as they decreased in abundance with an increase in elevation within the spruce-fir zone (Whittaker, 1948).

Common shrubs include Acer pensylvanicum, Ilex ambigua var. montana, Vaccinium erythrocarpum, Viburnum alnifolium, Rhododendron catawbiense and Rhododendron maximum. Whittaker (1948) reported that the undergrowth of spruce forests in the Great Smoky Mountains consisted of five layers: ground moss, low herb, fern, low heath and high shrub represented by Hylocomium splendens, Oxalis montana, Dryopteris campyloptera, Hugeria (Vaccinium) erythrocarpa and Viburnum lantanoides (V. alnifolium), respectively. On the other hand, the fir forest undergrowth was composed of only three layers: ground moss, Oxalis and ferns which often total more than 200% coverage when combined. He also observed that these undergrowth elements were favored by mesic sites and that all strata decreased in coverage toward xeric sites where heath became more important.

Crandall (1958) further investigated these undergrowth layers and described eight site types in fir and spruce-fir forests above 5500 feet elevation. These types include: 1) Oxalis-Hylocomium, 2) Oxalis-Dryopteris, 3) Viburnum-Vaccinium-Dryopteris, 4) Senecio, 5) Rhododendron,

6) Hylocomium-Vaccinium, 7) Viburnum-Vaccinium-Senecio and 8) Rhododendron-Viburnum.

Common ground cover species present include Hylocomium splendens, Athyrium asplenioides, Dryopteris intermedia, Oxalis acetosella and Senecio rugelia which often total more than 100% coverage. Crandall (1958) found that many of the same species of herbaceous plants occur throughout the altitudinal range of the Southern Appalachian boreal forests, but certain species are more characteristic of specific forest types. She further observed that Senecio rugelia, a Great Smoky Mountains endemic, is of low frequency but often of high coverage when present. Whittaker (1948) distinguished between mesic herbs such as Solidago glomerata, Senecio rugelia, Chelone lyoni, Aster acuminatus and Aster divaricatus, occurring in moist sites in valleys near springs from the mesic herbs such as Oxalis montana and Clintonia borealis which were best developed on north slopes and flats.

Cain and Sharp (1938) studied the bryophytic unions within the forest types of the Great Smoky Mountains. Within the spruce-fir zone they reported a Hylocomium splendens union in the terrestrial communities and a Polytrichum ohioense union and a Sphagnum union from the epilithic communities. They also found four unions in the epixylic communities and three unions from the corticolous communities. Norris (1964) further investigated the bryoecology of the spruce-fir zone of the Great Smoky Mountains and reported 22 bryophytic unions from these high elevation forests. Although moss coverage is generally high in the spruce-fir forests of the Great Smoky Mountains, Whittaker (1948) noted that this coverage increased with an increase in elevation.

III. METHODS

Field work was begun in July 1974 and continued through September 1974 in the Great Smoky Mountains National Park, Tennessee and North Carolina, and in the Black Mountains of North Carolina in Mt. Mitchell State Park and adjacent Pisgah National Forest. Locations to be sampled within the Great Smoky Mountains were chosen on the basis of amount and dates of infestation of the balsam woolly aphid as best determined from U. S. Forest Service mapping projects (Ciesla, et al., 1965; Rauschenberger and Lambert, 1969; Rauschenberger and Lambert, 1970), from personal communication with Park personnel and from personal reconnaissance. Stand changes within the Great Smoky Mountains ranged from none in the Central portion to extreme in the Mt. Sterling and Spruce Mountain areas. Changes in the Mt. Mitchell area of the Black Mountains were extreme in all stands sampled. The summit of Mt. Mitchell and the area bordering the road approaching the summit were sprayed to control the aphid infestation to attempt to save the high elevation forests for the tourists, but no plots were established in these areas.

Stands chosen were first located on topographic maps; representative stands of similar exposure in several areas were chosen for field sampling. Stands that were sampled ranged from 5120 feet elevation to 6600 feet elevation.

Since stands were predetermined from known information concerning aphid infestation, but plot location was random, the overall design was considered stratified random.

The terms disturbed and undisturbed are used throughout this investigation to refer to stands infested by the balsam woolly aphid and stands not infested, respectively. Stands were chosen so that other perturbations were minimized.

Within each sampling area, a series of 0.1 acre circular plots were established. These plots were corrected for slope according to Bryan (1956) and within each plot, all stems one inch DBH and greater were tallied by species. All stems five inches DBH or greater, hereafter referred to as overstory stems, were tallied by species and number and were placed in two inch DBH size classes. All stems 1-4.9 inches DBH, hereafter referred to as sapling stems, were counted by species.

Transects six feet wide were walked along the north-south and the east-west diameters of the 0.1 acre circular plots (area totalled approximately 0.02 acre) to sample all stems between two feet tall and one inch DBH, hereafter referred to as subsapling stems, which were counted by species. In order to avoid repetitive sampling in the center of the plots, the second transect in each plot began and ended three feet outside the perimeter of the 0.1 acre plot and skipped the area of the first transect.

Also within the 0.1 acre circular plots, eight smaller rectangular plots one foot wide and 10.9 feet long were established to sample all individuals less than two feet tall, hereafter referred to as ground cover (area totalled approximately 0.02 acre). Two ground cover plots were located on each radius from the center of the 0.1 acre plots outward toward the four cardinal points on the periphery of the circular plots with the exact locations determined by a random numbers table to avoid sampling bias. Within these eight plots, percent cover of each taxon was estimated.

Circular 0.1 acre plots were used because data collection by one person was easy and the plot size was easily corrected for slope differences. Plot size of 4356 square feet (404.6 square meters) was considerably larger than the 50 square meter plot size found by Cain (1935) to be the minimum quadrat sampling size in the fir forest and the 200 square meter minimum size in the spruce-fir stands of lower elevations. The data from these 0.1 acre plots are also easily converted to totals per acre for convenient comparison to results of other investigations in the high elevation forests of the Southern Appalachians.

Site characteristics recorded on each plot included: elevation from the topographic map, slope angle (percent), local slope position, slope form on a vertical basis, aspect, estimated surface rock exposed (percent), estimated canopy closure (percent) and estimated conditions of overstory fir stems. The degree and probable date of aphid infestation were also recorded at each plot. This estimate of date of fir death was based on the approximate known time of attack by the aphids (Speers, 1958; Nagel, 1959; Ciesla, et al., 1965; Aldrich and Drooz, 1967; Rauschenberger and Lambert, 1968, 1969, 1970) as well as certain on-site examinations and measurements of growth rings of saplings and recently killed fir stems.

Slope angle was measured with an Abney level and determined by obtaining an average of the upslope and downslope readings. Local slope position was determined by examining the immediate landscape surrounding the plot. Slope form (vertical) was recorded as flat, concave or convex. Aspect was recorded for each plot based on readings of a Silva compass.

Individual plant species were determined in the field where possible; all unknown specimens were collected and compared with specimens in The University of Tennessee Herbarium. Nomenclature follows that of Radford, et al., (1969) except for that of the byrophytes which follows Crum, et al., (1973).

Plot data were then calculated to obtain absolute and relative measures of overstory density and basal area, sapling and subsapling density and percent coverage of individual and total ground cover taxa. These plot totals were then combined into six separate classes based on amount of time since infestation by the balsam woolly aphid.

In addition to simple comparison of group totals, a correlation and regression analysis was completed on both the vegetation and site characteristics of the plot data using a multiple regression, maximum R-square improvement technique of the Statistical Analysis System (SAS) as described by Service, (1972). These calculations were performed on the IBM 360/65 computer at The University of Tennessee Computer Center.

IV. RESULTS AND DISCUSSION

General

The assumption was made at the beginning of the investigation that all stands were similar to the undisturbed stands prior to the onset of the aphid attack. Whether all of the differences noted between undisturbed stands and the various aged disturbed stands are due to death of fir will be considered more fully. The following text and tables detail the characteristics of the plots, grouped by time since initial aphid attack and averaged, used in the study.

Undisturbed Stands

Below 6000 feet elevation. Spruce-fir stands sampled below 6000 feet elevation in the Great Smoky Mountains (n=27) averaged 280.4 overstory stems per acre, 163.7 (58.4%) of which were Fraser fir (*Abies fraseri*), 81.5 (29.1%) red spruce (*Picea rubens*) and 16.7 (6.0%) yellow birch (*Betula lutea*) (Table 1, column 0[a]). Six other arborescent species contributed to the total overstory density resulting in an overstory species diversity of nine. Oosting and Billings (1951) reported an overstory diversity of eight species in seven spruce-fir stands sampled in the Great Smoky Mountains below 6000 feet elevation.

Distribution of density by diameter size classes reveals that over 46% of all sapling and overstory density in

TABLE 1

OVERSTORY DENSITY OF DISTURBED AND UNDISTURBED STANDS (STEMS/ACRE)

Taxa	Years Since Opening of Canopy						
	0[a]	0[b]	0[c]	5-6	7-10	11-15	16-20
Abies fraseri	163.7	280.0	258.0	2.9		56.7	33.1
Acer spicatum	1.5			1.4	2.3	1.1	
Amelanchier arborea var. laevis	1.9				1.4		
Betula lenta	8.1				1.8		
Betula lutea	16.7	2.1	4.0	14.3	42.3		
Fagus grandifolia	2.2	0.5					
Picea rubens	81.5	65.3	48.0	60.0	76.4	25.6	16.2
Prunus pensylvanica	1.5		4.0	1.4		2.2	
Sorbus americana	3.3	6.8	12.0	5.7		16.7	10.0
Total	280.4	354.7	326.0	85.7	124.2	102.3	59.3

[a]Undisturbed stands < 6000 feet elevation.

[b]Undisturbed stands ≥ 6000 feet elevation.

[c]Disturbed stands, fir dying.

these spurce-fir stands was accounted for by Fraser fir stems one inch to 8.9 inches DBH (Table 2). Red spruce stems were less abundant in these small size classes but were present in a wider range of size classes than Fraser fir, a characteristic of these high elevation forests reported previously by Oosting and Billings (1951). Of the total density, however, 83.5% of all stems occurred in diameter size classes below 13 inches DBH.

Basal area of the overstory averaged 232 square feet per acre in these spruce-fir stands (Table 3, column 0^a). Of this, 118.2 (50.9%) was of red spruce and 84.5 (36.4%) Fraser fir indicating red spruce dominance that is not apparent when considering only density. This figure compares with a previously reported high basal area total of approximately 325 square feet per acre at 5100 feet elevation in the spruce-fir forests of the Great Smoky Mountains (Cain, 1935), 227.4 square feet per acre in other spruce-fir stands of the Great Smoky Mountains (Shanks, 1953) and 247 square feet per acre in a red spruce stand at 5000 feet elevation in the Great Smoky Mountains (Cain, 1937). Oosting and Billings (1951) reported that Fraser fir occurs at higher densities than red spruce but that red spruce stems, on the average, are larger thereby yielding a larger basal area. In seven stands sampled above 5400 feet elevation, they reported red spruce comprised 50.4% of the total overstory basal area and Fraser fir 34.4%, totals similar to those of the present investigation.

TABLE 2

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN UNDISTURBED STANDS < 6000 FEET ELEVATION[a]

Taxa	Diameter Size Classes in Inches DBH								
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9	29-32.9	>33
Abies fraseri	25.3	21.2	10.9	2.9	1.3	0.2			
Acer spicatum	1.9	0.3							
Amelanchier arborea var. laevis	0.1	0.3			0.1				
Betula lenta	0.6	0.3	0.3	0.3	0.9		0.1		
Betula lutea	2.0	1.8	0.9	0.6	0.3	0.1		0.1	
Fagus grandifolia		0.3	0.1	0.2					
Picea rubens	6.5	5.1	3.2	2.6	3.4	2.2	1.4	0.2	0.1
Prunus pensylvanica	0.1	0.3	0.1						
Rhododendron catawbiense	0.2								
Sorbus americana	0.2	0.7							
Viburnum alnifolium	0.7								
Viburnum cassinoides	0.1								
Total	37.7	30.3	15.5	6.6	6.0	2.5	1.5	0.3	0.1

[a]1223 stems among 27 plots.

93.82 → ≈1/acre

TABLE 3

OVERSTORY BASAL AREA OF DISTURBED AND UNDISTURBED STANDS (SQ. FT./ACRE)

Taxa	Years Since Opening of Canopy						
	0[a]	0[b]	0[c]	5-6	7-10	11-15	16-20
Abies fraseri	84.5	140.0	136.5	0.5		38.9	20.8
Acer spicatum	0.4			0.3	0.7	0.2	
Amelanchier arborea var. laevis	1.1				0.3		
Betula lenta	12.3				5.6		
Betula lutea	12.7	2.4	0.8	26.7	42.1		
Fagus grandifolia	1.5	0.9					
Picea rubens	118.2	60.2	17.7	117.0	75.8	25.2	10.5
Prunus pensylvanica	0.6		1.4	1.1		0.6	
Sorbus americana	0.7	2.1	4.8	1.1		4.1	2.5
Total	232.0	205.6	161.2	146.7	124.5	69.0	33.8

[a]Undisturbed stands $<$ 6000 feet elevation.

[b]Undisturbed stands $\geq$ 6000 feet elevation.

[c]Disturbed stands, fir dying.

Sapling density of these spruce-fir stands below 6000 feet elevation averaged 168.6 stems per acre (Table 4, column 0^a). Fraser fir accounted for 113.7 (67.4%) of these stems, red spruce only 29.3 (17.4%). The remainder was mainly yellow birch, mountain maple (Acer spicatum), hobblebush (Viburnum alnifolium) and sweet birch (Betula lenta). Five other species were represented by only a few individuals.

Based on sampling in seven stands above 5400 feet elevation in the Great Smoky Mountains, Oosting and Billings (1951) reported an average of 833.6 total stems per acre greater than one inch DBH, 516 (61.9%) of which were Fraser fir and 180 (21.6%) red spruce. The present investigation observed 449 stems greater than one inch DBH per acre in spruce-fir stands between 5260 and 5960 feet elevation. Of these, 227.4 (61.8%) were Fraser fir and 110.8 (24.7%) were red spruce.

In spruce-fir stands sampled below 6000 feet elevation, subsapling density averaged 2828.3 stems per acre (Table 5, column 0^a). Hobblebush accounted for 924.1 (32.7%) of these, Fraser fir 681.5 (24.1%), mountain cranberry (Vaccinium erythrocarpum) 433.4 (15.3%), thornless blackberry (Rubus canadensis) 374.1 (13.2%) and red spruce 213 (7.5%). Fifteen subsapling taxa were present in the sampled portions of these spruce-fir stands.

Ground layer coverage, represented by 43 taxa, averaged 107.1% in these stands (Table 6, column 0^a). This total

TABLE 4

SAPLING DENSITY OF DISTURBED AND UNDISTURBED STANDS (STEMS/ACRE)

Taxa	Years Since Opening of Canopy						
	0[a]	0[b]	0[c]	5-6	7-10	11-15	16-20
Abies fraseri	113.7	92.6	108.0	8.6	25.5	105.6	58.5
Acer pensylvanicum				1.4			
Acer spicatum	8.5		4.0	28.6	4.1	3.3	
Amelanchier arborea var. laevis	0.4			8.6	.5		
Betula lenta	2.6						
Betula lutea	8.9	4.7	54.0	12.9	17.7	7.8	
Ilex ambigua var. montana				5.7	4.1		
Picea rubens	29.3	13.7	34.0	22.9	46.4	14.4	10.8
Prunus pensylvanica	0.4	0.5			0.5	11.1	
Rhododendron catawbiense	0.7				32.3		
Sambucus pubens					2.3	3.3	
Sorbus americana	0.7	8.4	18.0	7.1	0.5	55.6	14.6
Tsuga canadensis					0.9		
Viburnum alnifolium	3.0			5.7			
Viburnum cassinoides	0.4						
Total	168.6	119.9	218.0	101.5	134.8	201.1	83.9

[a]Undisturbed stands < 6000 feet elevation.

[b]Undisturbed stands ≥ 6000 feet elevation.

[c]Disturbed stands, fir dying.

TABLE 5

SUBSAPLING DENSITY OF DISTURBED AND UNDISTURBED STANDS (STEMS/ACRE)

Taxa	Years Since Opening of Canopy						
	0[a]	0[b]	0[c]	5-6	7-10	11-15	16-20
Abies fraseri	681.5	557.9	120.0	43.0	329.5	889.0	1173.0
Acer pensylvanicum	13.0			7.0	9.0		
Acer spicatum	37.1		100.0	228.5	72.5	16.5	
Amelanchier arborea var. laevis	9.3			7.0			
Betula lenta	42.6						
Betula lutea	46.3	2.7	20.0	71.5	47.5	5.5	
Cornus alternifolia				7.0			
Diervilla sessilifolia		7.9					
Fagus grandifolia	1.9						
Hydrangea arborescens				21.5			
Ilex ambigua var. montana	9.3			7.0	13.5		
Menziesia pilosa				14.5			146.0
Picea rubens	213.0	26.3	60.0	43.0	84.0	22.0	42.5
Prunus pensylvanica					68.0	16.5	4.0
Rhododendron catawbiense	5.6	2.7			2.5		
Rhododendron maximum					2.5		
Rhododendron sp.							15.5
Ribes glandulosum						16.5	23.0
Ribes rotundifolium		5.3		14.5	4.5		88.5
Rubus canadensis	374.1	5.3	220.0	1000.0	1179.5	2972.0	900.0
Rubus idaeus var. canadensis			40.0			950.0	3254.0
Sambucus pubens	7.4	34.2		35.5	1127.5	178.0	223.0
Sorbus americana	29.7	21.1		14.5	79.5	105.5	307.5
Tsuga canadensis					2.5		
Vaccinium erythrocarpum	433.4	189.5	150.0	835.5	254.5	28.0	19.0
Viburnum alnifolium	924.1	257.9	180.0	1600.0	68.0	11.0	42.5
Total	2828.3	1110.8	890.0	3950.0	3345.0	5210.5	6238.5

[a]Undisturbed stands < 6000 feet elevation.

[b]Undisturbed stands ≥ 6000 feet elevation.

[c]Disturbed stands, fir dying.

TABLE 6

PERCENT COVER OF GROUND COVER TAXA OF DISTURBED AND UNDISTURBED STANDS

Taxa	Years Since Opening of Canopy						
	0[a]	0[b]	0[c]	5-6	7-10	11-15	16-20
Abies fraseri	0.2	0.3	3.0	0.3	0.5	0.7	
Acer spicatum	0.1		0.04				
Agrostis stolonifera	0.03	0.01	0.04			0.1	0.4
Angelica sp.						0.04	0.1
Arisaema triphyllum	0.04	0.01			0.1	0.4	
Aster acuminatus	1.0	4.5	20.5	6.1	16.0	11.3	20.6
Aster divaricatus	0.1	0.02	1.2			1.1	2.9
Athyrium asplenioides	13.6	25.6	14.8	5.4	3.2	38.7	13.1
Atrichum undulatum			2.1			1.0	
Betula lenta	0.004						
Brotherella recurvans	11.7	3.0	6.2	18.6	6.8	1.9	4.5
Carex aestivalis							0.1
Carex brunnescens	0.02	0.7	0.2	0.1	0.3	0.03	0.1
Carex debilis var. rudgei	0.03		0.2	0.01		0.1	0.3
Carex intumescens	0.004	0.02	0.1		0.01	1.6	0.02
Chelone lyonii	0.1	0.4	7.7			4.7	19.7
Cimicifuga racemosa		0.1				0.03	
Circaea alpina	0.004			0.1	1.2		
Clintonia borealis	1.7	1.6	0.8	2.6	0.5	0.8	1.7
Dennstaedtia punctilobula	0.3				0.3		
Dicranodontium denudatum	0.5	0.3	2.1	0.9	0.7	0.5	0.3
Dicranum fuscescens	0.2	0.5		0.01	0.1		
Dryopteris intermedia	15.6	12.7	11.4	15.5	29.3	13.0	7.6
Epifagus virginiana	0.004						
Eupatorium rugosum	0.03				0.1		0.2
Galium triflorum			0.02				
Glyceria striata	0.01						
Houstonia serpyllifolia	0.02				0.02	0.04	
Hylocomium splendens	11.5	10.4	1.2	8.6	11.3	7.3	1.1
Impatiens pallida	0.1	0.9	0.4	0.6		1.0	0.8
Laportea canadensis	0.3	0.1					
Liverwort	2.5	2.4	0.2	1.1	0.4	0.2	0.3
Luzula sp.		0.01	0.1		0.03	0.6	

TABLE 6 (continued)

Taxa	Years Since Opening of Canopy						
	0[a]	0[b]	0[c]	5-6	7-10	11-15	16-20
Lycopodium lucidulum	2.7			0.1	0.1		
Medeola virginiana	0.01						
Monotropa uniflora		0.01					
Oxalis acetosella	33.8	29.0	33.2	39.0	27.9	7.5	4.5
Picea rubens	0.04			0.3	0.04		
Polygonum cilinode					4.7	0.4	0.1
Polypodium virginianum				0.04		0.01	
Polytrichum ohioense	0.5	1.6			0.01		
Ptillium crista-castrensis		0.3					
Rhytidiadelphus triquetrus		0.2	2.0		0.05	0.1	0.02
Rubus canadensis	0.1	0.01	0.02		0.2		
Sambucus pubens	0.02				0.1		
Saxifraga michauxii		0.1	0.1				1.2
Senecio rugelia	8.2	12.5			4.2		
Smilicina racemosa		0.01					
Solidago glomerata	0.5	0.8	3.9			9.2	13.7
Sorbus americana	0.03	0.04	0.02				
Sphagnum subnitens	1.2	1.2	0.9	2.1	1.5	1.0	3.2
Stachys clingmanii		0.2					
Trillium erectum	0.01		0.3		0.01		
Vaccinium erythrocarpum	0.3	0.1					
Veratrum viride						0.1	0.2
Viburnum alnifolium			0.02				
Viola sp.	0.01		0.8		0.01	0.01	0.01
Total	707.1	109.6	113.6	101.5	109.7	103.5	96.8

[a]Undisturbed stands < 6000 feet elevation.

[b]Undisturbed stands ≥ 6000 feet elevation.

[c]Disturbed stands, fir dying.

included 33.8% Oxalis acetosella, 15.6% Dryopteris intermedia, 13.6% Athyrium asplenioides, 11.7% Brotherella recurvans, 11.5% Hylocomium splendens, 25.9% total moss cover and 31.9% pteridophyte cover. Thirty-five herbaceous species were recorded representing an increase in the previously reported total of 27 herbaceous species occurring in spruce-fir forests between 5500 and 6000 feet elevation in the Great Smoky Mountains (Crandall, 1958). Based on site counts, Whittaker (1948) reported that the percent coverage of Oxalis montana in spruce-fir forests of the Great Smoky Mountains between 5600 and 6100 feet elevation varied from 1% on southwest-facing slopes to 66% on northeast-facing slopes. He also reported that total moss coverage ranged from 7% on southwest-facing slopes to 64% on northeast-facing slopes and total fern coverage varied from 3% on southwest-facing slopes to 65% on northeast-facing slopes. Oosting and Billings (1951) reported that Oxalis montana averaged 52% coverage and Dryopteris dilata cover averaged 29%.

Six thousand feet elevation and above. Fir and spruce-fir forests sampled at or above 6000 feet elevation in the Great Smoky Mountains (n=19) averaged 354.7 overstory stems per acre, 280 (78.9%) of which were Fraser fir and 65.3 (18.4%) red spruce (Table 1, column 0^b, page 29). Only three other species were present in the overstory of these high elevation forests: Mountain ash (Sorbus americana), yellow birch and American Beech (Fagus grandifolia).

Distribution of density by diameter size classes indicates that over 52% of all stems one inch DBH and greater were Fraser fir stems in the one inch to 8.9 inches DBH size classes (Table 7). Another 20% were Fraser fir stems 9-12.9 inches DBH resulting in over 72% of all sapling and overstory density accounted for by Fraser fir in these small diameter size classes. Cain (1937) referred to these high elevation stands as pole stands reflecting the density and small sizes of fir. Considering all overstory stems, 89.2% occurred in diameter size classes smaller than 13 inches DBH.

The dominance of Fraser fir in these high elevation forests was also demonstrated by the basal area totals of all overstory stems (Table 3, column 0^b, page 32). The basal area of the stands sampled averaged 205.6 square feet per acre, 140 (68.1%) of which were Fraser fir and 60.2 (29.3%) red spruce. These figures compare with 69.9% Fraser fir basal area and 28.8% red spruce at 6300 feet elevation in the Great Smoky Mountains (Oosting and Billings, 1951). Other basal area totals reported for fir and spruce-fir stands of the Great Smoky Mountains include 167.2 square feet per acre at 6500 feet elevation (Crandall, 1958), 288.1 square feet per acre (90.7%) Fraser fir and 4.2% red spruce) at 6300 feet elevation (Cain, 1935, 1937) and 291.8 square feet per acre (87.8% Fraser fir and 5.6% red spruce) at 6300 feet elevation (Cain, 1935, 1937).

In these stands sampled at elevations of 6000 feet or more, sapling density averaged only 119.9 stems per acre

TABLE 7

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN UNDISTURBED STANDS ≥ 6000 FEET ELEVATION[a]

Taxa	Diameter Size Classes in Inches DBH						
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9
Abies fraseri	19.5	32.9	20.4	4.8	0.7	0.2	
Betula lenta	1.0	0.1	0.2			0.1	
Fagus grandifolia					0.1		
Picea rubens	2.9	4.8	4.1	2.2	1.4	1.0	0.2
Prunus pensylvanica	0.1						
Sorbus americana	1.8	1.1	0.3	—	—	—	—
Total	25.3	38.9	25.0	7.0	2.2	1.3	0.2

[a]911 stems among 19 plots.

(Table 4, column 0^b, page 34). Fraser fir accounted for 92.6 (77.2%) of these and red spruce 13.7 (11.4%). Mountain ash, yellow birch and fire cherry (Prunus pensylvanica) comprised the remaining density resulting in representation of only five species in the sapling stratum compared to 11 taxa at lower elevations. Fraser fir saplings were relatively more abundant than in stands sampled below 6000 feet elevation in which Fraser fir accounted for only 67.4% of the total.

Subsapling density in these high elevation forests was also less than that of the spruce-fir stands of lower elevations (Table 5, column 0^b, page 35). At 6000 feet elevation and above, the subsapling density averaged 1110.5 stems per acre, 557.9 (50.2%) of which were Fraser fir, 257.9 (23.2%) hobblebush and 189.5 (17.1%) mountain cranberry. Only 11 species were present in the subsapling stratum of stands sampled compared to 15 species in stands at lower elevations.

Ground cover in these higher elevation stands averaged 109.6%; 34 species were present (Table 6, column 0^b, page 36). Thirty species were herbaceous which represented an increase in diversity from a previous study which reported only 16 herbaceous species from the 6000-6600 feet elevation band in the Great Smoky Mountains (Crandall, 1958). Oxalis acetosella was the most dense ground cover species and had a coverage of 29%, Athyrium asplenioides had 25.6%, Dryopteris intermedia 12.7%, and Hylocomium splendens 10.4%. Moss coverage averaged 30% and ferns 38.3%. Crandall (1958) reported 38.1% moss coverage, 49.9% Oxalis cover and 94.1% fern cover in fir forests near Clingmans Dome in the Great Smoky Mountains.

In fir forests above 6200 feet elevation in the Great Smoky Mountains, Whittaker (1948) reported that the cover of mosses ranged from 30% on southwest-facing slopes to 95% on northeast-facing slopes. He also noted that Oxalis ranged in cover from 2% on southwest-facing slopes to 70% on northeast-facing slopes and fern cover varied from zero on south and southwest-facing slopes to 60% on northeast-facing slopes.

Zero Year Age, Fir Dying

Those stands attacked by the balsam woolly aphid in the past few years without complete death of all overstory Fraser fir stems comprise this group (n=5). Since four of the samples in this group were above 6000 feet elevation (Table 8), the results are most comparable to those of uninfested stands above 6000 feet.

Overstory density in these recently infested stands averaged 326 stems per acre, 258 (79.1%) of which were Fraser fir, 48 (14.7%) red spruce and 12 (3.7%) mountain ash (Table 1, column 0^c, page 29). Yellow birch and fire cherry comprised the remaining density. This total was slightly less than the absolute densities observed in undisturbed stands but approximates the relative totals of 78.9% fir, 18.4% red spruce and 1.9% mountain ash observed in uninfested stands.

TABLE 8

NUMBER OF SAMPLE PLOTS IN ELEVATIONAL ZONES

Elevation (Feet)	Years Since Opening of Canopy					
	0[a]	0[b]	5-6	7-10	11-15	16-20
≥ 6500	2	3			5	5
6000-6499	17	1			5	8
5500-5999	18	1	8	19		
5000-5499	9			3		
Total	46	5	8	22	10	13

[a]Undisturbed stands.

[b]Disturbed stands, fir dying.

Size and presumably age distribution in these stands approximated that of undisturbed stands above 6000 feet elevation; 71.7% of the total density occurred in diameter size classes smaller than nine inches DBH (Table 9) compared to 64.2% in undisturbed stands (Table 7). Of the remaining density in the infested stands, 22.8% occurred in the 9-12.9 inch DBH size class compared to 25% in that size class in uninfested stands (Table 7).

Overstory basal area in stands of this group averaged 161.2 square feet per acre, 136.5 (84.7%) of which were Fraser fir and 17.7 (11%) red spruce (Table 3, column 0^c, page 32). This total is less than that of the uninfested stands. A total of 167.2 square feet per acre at 6500 feet elevation was reported by Crandall (1958).

Sapling density in these recently infested stands was 218 stems per acre, much higher than in undisturbed stands which averaged 119.9 stems per acre (Table 4, column 0^c, page 34). Percent composition of this sapling layer also differed from the undisturbed stands as 108 (49.5%) were Fraser fir, 54 (24.8%) yellow birch, 34 (15.6% red spruce, 18 (8.3%) mountain ash and 4 (1.8%) mountain maple.

Subsapling density was somewhat less in these stands than in undisturbed stands; the average number of stems per acre was 890 (Table 5, column 0^c, page 35) compared to 1110.5 stems per acre in the uninfested stands above 6000 feet elevation (Table 5, column 0^b). In the former set, thornless

TABLE 9

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN DISTURBED STANDS, FIR DYING[a]

Taxa	Diameter Classes in Inches DBH								
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9	29-32.9	>33
Abies fraseri	20.1	23.1	19.1	5.1					
Acer spicatum	0.7								
Betula lutea	9.9	0.7							
Picea rubens	6.2	5.9	2.6		0.4				
Prunus pensylvanica		0.7							
Sorbus americana	3.3	1.1	1.1	—	—				
Total	40.2	31.5	22.8	5.1	0.4				

[a]272 stems among five plots.

blackberry accounted for 220 (24.7%) of these, hobblebush 180 (20.2%), mountain cranberry 150 (16.9%), Fraser fir 120 (13.5%), mountain maple 100 (11.2%) and lesser densities of red spruce, red raspberry and yellow birch.

Total coverage by ground cover taxa was about the same as in undisturbed stands, the mean was 113.6% (Table 6, column 0^c, page 36). This represents a slightly higher cover of *Oxalis acetosella*, 33.2%; *Aster acuminatus* cover was much higher at 20.5%; *Brotherella recurvans* was higher at 6.2%; *Chelone lyoni* was higher at 7.7% and *Solidago glomerata* was higher at 3.9%. *Dryopteris intermedia* approximated the cover it displayed in undisturbed stands, as it averaged 11.4%; *Athyrium asplenioides* cover and *Hylocomium splendens* cover were significantly less at 14.8% and 1.2%, respectively.

Five-Six Years After Fraser Fir Death

Stands attacked by the balsam woolly aphid followed by the death of the overstory Fraser fir approximately 5-6 years prior to this investigation comprise this group (n=8). All stands sampled were between 5500 and 6000 feet elevation (Table 8), and were sampled in the Black Mountains. Results are compared to those of the undisturbed stands below 6000 feet elevation.

Overstory density in these stands was 85.7 stems per acre, much less than in undisturbed stands (Table 1, page 29). This lower density reflects the loss of Fraser fir stems as red spruce and yellow birch averaged 60 and 14.3 stems per acre, respectively, compared to 81.5 and 16.7 in undisturbed stands at similar elevations. Fraser fir, mountain maple and fire cherry comprised the remaining density.

Comparison of diameter class distribution in this release class (Table 10) with undisturbed stands below 6000 feet indicates that in the five-six year release class, higher percentages occurred in the 1-4.9 inches size class and lower percentages in the 5-12.9 inch classes. In the 1-4.9 inch class, mountain maple and red spruce were more numerous and in the 1-12.9 inch classes, fir was less numerous.

The death of Fraser fir was also reflected in the overstory basal area, the mean was only 146.7 square feet per acre (Table 3, page 32). Red spruce basal area was 117 square feet per acre, similar to that of undisturbed stands below 6000 feet. Basal area of yellow birch was 26.7 square feet per acre, considerably higher than in undisturbed stands. Relative basal area totals of 79.8% and 18.2% in red spruce and yellow birch, respectively, suggest increased growth or replacement of overstory Fraser fir.

Sapling density in these stands was also less than in undisturbed stands at similar elevations as the mean was 101.5 stems per acre (Table 4, page 34). This included 28.6 (28.2%) mountain maple stems, 22.9 (22.6%) red spruce, 12.9 (12.7%) yellow birch, 8.6 (8.5%) Fraser fir and 8.6 (8.5%) serviceberry (Amelanchier arborea var. laevis). Four additional species contributed to the composition of the sapling

TABLE 10

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN DISTURBED STANDS RELEASED 5-6 YEARS[a]

Taxa	Diameter Classes in Inches DBH								
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9	29-32.9	>33
Abies fraseri	4.6	1.5							
Acer pensylvanicum	0.8								
Acer spicatum	15.3	0.8							
Amelanchier arborea var. laevis	4.6								
Betula lutea	6.9	0.8	0.8	2.3	2.3	0.8		0.8	
Ilex ambigua var. montana	3.1								
Picea rubens	12.2	5.4	6.1	5.4	3.1	6.9	3.1	2.3	
Prunus pensylvanica			0.8						
Sorbus americana	3.8	3.1							
Viburnum alnifolium	3.1								
Total	54.4	11.6	7.7	7.7	5.4	7.7	3.1	3.1	

[a]131 stems among eight plots.

layer: striped maple (Acer pensylvanicum), mountain holly (Ilex ambigua var. montana), mountain ash and hobblebush. The density of mountain maple represents a three-fold increase over that in undisturbed stands at similar elevations.

Subsapling density in these disturbed stands averaged 3950 stems per acre, significantly higher than the lower elevation undisturbed stands (Table 5, page 35). Composition of this stratum differed considerably from that of undisturbed stands as hobblebush was the most prevalent taxon with 1600 (40.5%) stems per acre, thornless blackberry 1000 (25.3%), mountain cranberry 835.5 (21.2%) and mountain maple 228.5 (5.8%). These subsapling densities which were different from those of the undisturbed stands were due to the decrease of Fraser fir and red spruce stems from 681.5 (24.1%) to 43 (1.1%) and 213 (7.5%) to 43 (1.1%) stems per acre, respectively.

Total ground coverage approximated that of uninfested stands at similar elevations, the mean was 101.5% (Table 6, page 36). Oxalis acetosella cover peaked in these stands at 39%; Brotherella recurvans cover also peaked here at 18.6%; Dryopteris intermedia cover was similar at 15.5%; and cover of Hylocomium splendens was less at 8.6%. Coverage of Athyrium asplenioides averaged 5.4%, considerably less than in undisturbed stands. Only 19 ground cover taxa occurred in the samples taken in these stands compared to 43 in uninfested stands at similar elevations. Senecio rugelia, a

Great Smoky Mountains endemic, did not occur in these Black Mountains stands.

Seven-Ten Years After Fraser Fir Death

Those stands whose canopy opened as a result of the death of Fraser fir approximately seven-ten years prior to this investigation were on Mt. Sterling in the Great Smoky Mountains (n=22). Since these sampled stands were all below 6000 feet elevation (Table 8, page 43), the results are compared to those of the uninfested stands below 6000 feet elevation.

Overstory density in these stands averaged 124.2 stems per acre, much less than in undisturbed stands (Table 1, page 29). Red spruce and yellow birch comprised most of this density, averaging 76.4 (61.5%) and 42.3 (34.1%) stems per acre respectively. Absolute density of red spruce was slightly lower than the 81.5 stems per acre in undisturbed stands, but relative density was much greater due to the absence of Fraser fir. Both absolute and relative density of yellow birch were much greater than in uninfested stands. Mountain maple, serviceberry and sweet birch comprised the remaining overstory density.

Distribution of density by diameter size classes in these stands reveals that 70% of all sapling and overstory stems occurred in the 1-8.9 inch DBH diameter size classes (Table 11). This is similar to the distribution of density in undisturbed stands below 6000 feet elevation (Table 2,

TABLE 11

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN DISTURBED STANDS RELEASED 7-10 YEARS[a]

Taxa	Diameter Classes in Inches DBH								
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9	29-32.9	>33
Abies fraseri	9.5								
Acer spicatum	1.6	0.7	0.2						
Amelanchier arborea var. laevis	0.2	0.5							
Betula lenta				0.2		0.3		0.2	
Betula lutea	6.9	5.8	5.6	1.6	1.9	0.7	0.5		0.2
Ilex ambigua var. montana	1.6								
Picea rubens	18.0	10.9	7.2	5.3	3.3	1.9	0.9		
Prunus pensylvanica	0.2								
Rhododendron catawbiense	12.5								
Sambucus pubens	0.9								
Sorbus americana	0.2								
Tsuga canadensis	0.3	0.2							
Total	51.9	18.1	13.0	7.1	5.2	2.9	1.4	0.2	0.2

[a]569 stems among 22 plots.

page 31). The percentages in the 1-4.9 inch size class are higher and in the 5-8.9 inch class are lower than in uninfested stands below 6000 feet but are similar to percentages in stands released five-six years.

Overstory basal area in these disturbed stands reflected the density pattern as red spruce and yellow birch averaged 75.8 (60.9%) and 42.1 (33.8%), respectively, of the total 124.5 square feet per acre (Table 3, page 32). Sweet birch comprised most of the remaining basal area, mountain maple and serviceberry contributed least.

Sapling density was less than that of the uninfested stands as the mean was 134.8 stems per acre (Table 4, page 34). Composition of this layer was also different from that of the undisturbed stands as red spruce comprised 34.4% of the total, catawba rhododendron (Rhododendron catawbiense) 24%, Fraser fir 18.9% and yellow birch 13.2%.

The subsapling density of 3345 stems per acre was similar to the total in the five-six year group of stands sampled and was significantly higher than in the uninfested stands (Table 5, page 35). Thornless blackberry was the most prevalent taxon as it contributed 1179.5 (35.3%) stems per acre to the total, red-berried elder (Sambucus pubens) 1127.5 (33.7%), Fraser fir 329.5 (9.9%) and mountain cranberry 254.5 (7.6%). Subsapling Fraser fir stems apparently were not affected by the infestation as they appeared to be maintaining a high density. Red-berried elder appeared to be an invading species as its density increased more than 100-fold over that in uninfested stands. Thornless blackberry was maintaining its high density; it averaged approximately four times as many stems as in uninfested stands at similar elevations.

Total ground cover in these infested stands averaged 109.7%, including 29.3% Dryopteris intermedia, 27.9% Oxalis acetosella, 16% Aster acuminatus and 11.3% Hylocomium splendens (Table 6, page 36). Thirty taxa occurred in the ground cover layer compared to 43 in the more heavily sampled undisturbed stands at similar elevations. Aster acuminatus and Dryopteris intermedia had much higher cover and Athyrium asplenioides, Oxalis acetosella and Senecio rugelia had less cover than in uninfested stands. Solidago glomerata did not occur in these sampled areas. Polygonum cilinode, which did not occur in uninfested stands, comprised 4.7% of the total ground cover in these infested stands suggesting its light requirements.

Eleven-Fifteen Years After Fraser Fir Death

This group of sampled fir and spruce-fir stands contained Fraser fir stems which had died approximately 11-15 years prior to this investigation (n=10). Since all stands comprising this group were above 6000 feet elevation (Table 8, page 43) in the Black Mountains, results are compared to those of uninfested stands above 6000 feet elevation.

Overstory density in these stands was 102.3 stems per acre, considerably less than in undisturbed stands due primarily to the loss of Fraser fir (Table 1, page 29). Fraser fir averaged 56.7 (55.4%), red spruce 25.6 (25%) and mountain ash 16.7 (16.3%) stems per acre. Other species occurring in the overstory were fire cherry and mountain maple.

Based on the distribution of density by diameter size classes, these stands appeared much younger than any of the previous stands. Here, 80.1% of the total sapling and overstory density occurred in the 1-8.9 inch DBH diameter size classes (Table 12) compared to only 64.2% in undisturbed stands at similar elevations (Table 1). This distribution was due chiefly to the death of most of the mature fir. Percentage distribution of red spruce stems greater than nine inches DBH approximates that of uninfested stands. Overall size class distribution and perhaps age class distribution is similar aside from those due to the loss of Fraser fir.

As expected, mean overstory basal area of 69 square feet per acre was considerably less than the total in undisturbed stands (Table 3, page 32). Fraser fir accounted for 38.9 (56.4%) square feet of this total, red spruce 25.2 (36.5%) and mountain ash 4.1 (5.9%).

Sapling density of 201.1 stems per acre in these stands (Table 4, page 34) was higher than in all other stands except

TABLE 12

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN DISTURBED STANDS RELEASED 11-15 YEARS[a]

Taxa	Diameter Classes in Inches DBH								
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9	29-32.9	>33
Abies fraseri	34.8	5.2	9.9	3.7					
Acer spicatum	1.1	0.4							
Betula lutea	2.6								
Picea rubens	4.8	1.8	3.6	1.1	1.1	0.8			
Prunus pensylvanica	3.7	0.8							
Sambucus pubens	1.1								
Sorbus americana	18.3	5.5							
Total	66.4	13.7	13.5	4.8	1.1	0.8			

[a]273 stems among ten plots.

that of fir dying (Table 4, column O[c], page 34). Diversity also increased from five species occurring in the sapling layer of high elevation uninfested stands to seven species in these stands. Fraser fir accounted for 105.6 (52.5%) of this total, mountain ash 55.6 (27.6%), red spruce 14.4 (7.2%) and fire cherry 11.1 (5.5%). Yellow birch, serviceberry and red-berried elder comprised the remaining density.

Subsapling density averaged 5210.5 stems per acre, nearly five times the density of uninfested stands at similar elevations (Table 5, page 35). Over one-half of the total, 2972 (57%), were thornless blackberry, 950 (18.2%) red raspberry (Rubus idaeus var. canadensis), 889 (17.1%) Fraser fir, 178 (3.4%) red-berried elder and 105.5 (2%) mountain ash. Hobblebush and mountain cranberry displayed considerably lower densities than in the undisturbed stands. Skunk currant (Ribes glandulosum) occurred in these stands.

Total ground coverage averaged 103.5%, slightly less than in uninfested stands (Table 6, page 36). Cover of Aster acuminatus (11.3%), Athyrium asplenioides (38.7%), Chelone lyoni (4.7%), Solidago glomerata (9.2%) and all pteridophytes (51.7%) was greater than in undisturbed stands at similar elevations. Cover of Hylocomium splendens (7.3%), total moss coverage (11.8%) and Oxalis acetosella coverage (7.5%) were much less than in high elevation uninfested stands. Senecio rugelia again did not occur in these Black Mountain stands.

Sixteen-Twenty Years After Fraser Fir Death

The oldest infested stands sampled were those attacked by the balsam woolly aphid followed by the death of Fraser fir approximately 16-20 years prior to this investigation (n=13). These stands were located in the Black Mountains and represent the most advanced stages of succession following the opening of the canopy. Since the forests sampled were all above 6000 feet elevation (Table 8, page 43), the results are compared to those of uninfested stands above 6000 feet elevation.

Overstory density in these high elevation disturbed stands averaged only 59.3 stems per acre, represented by three species compared to five species that occurred in the undisturbed stands (Table 1, page 29). Fraser fir accounted for 33.1 (55.8%) of this total, red spruce 16.2 (27.3%) and mountain ash 10 (16.9%).

Distribution of density by diameter size classes in these stands was similar to that in the 11-15 year group as 80% of the total sapling and overstory density occurred in the 1-8.9 inch DBH diameter size classes (Table 13). The complete absence of stems greater than 21 inches DBH indicates that these stands may be younger than others sampled.

Overstory basal area averaged 33.8 square feet per acre (Table 3, page 32). Fraser fir comprised 20.8 (61.5%) of this total, red spruce 10.5 (31.1%) and mountain ash the remaining 2.5 (7.4%).

TABLE 13

PERCENTAGE DISTRIBUTION OF DENSITY BY DIAMETER SIZE CLASSES IN DISTURBED STANDS RELEASED 16-20 YEARS[a]

Taxa	Diameter Classes in Inches DBH								
	1-4.9	5-8.9	9-12.9	13-16.9	17-20.9	21-24.9	25-28.9	29-32.9	>33
Abies fraseri	40.2	9.0	10.1	2.7					
Picea rubens	7.4	5.3	3.2	2.1	0.5				
Rhododendron catawbiense	1.6								
Sorbus americana	10.1	6.4	0.5	—	—				
Total	59.3	20.7	13.8	4.8	0.5				

[a]189 stems among 13 plots.

Sapling density of 83.9 stems per acre was lower than in all other groups sampled (Table 4, page 34). Only three species occurred in this stratum compared to five species in the sapling layer of undisturbed stands at similar elevations. Of the total, Fraser fir contributed 58.5 (69.7%), mountain ash 14.6 (17.4%) and red spruce the remaining 10.8 (12.9%).

While the sapling layer displayed a low density in these stands, the subsapling stratum averaged 6238.5 stems per acre, the highest density of all stands sampled (Table 5, page 35). Thirteen species were represented in the subsapling layer of these stands compared to only 11 in high elevation undisturbed stands, and total density was over five times as great as in undisturbed stands. Red raspberry comprised the majority of this total with 3254 (52.2%) stems per acre, Fraser fir 1173 (18.8%), thornless blackberry 900 (14.4%), mountain ash 307.5 (4.9%), red-berried elder 223 (3.6%) and minnie-bush (Menziesia pilosa) 146 (2.3%).

Only 26 taxa occurred in the ground cover samples compared to 34 in uninfested stands at comparable elevations. Total ground coverage averaged 96.8%, slightly lower than in undisturbed stands (Table 6, page 36). Cover of Aster acuminatus (20.6%), Chelone lyoni (19.7%), and Solidago glomerata (13.7%) was much higher than in uninfested stands at similar elevations. Total coverage of mosses (9.1%), Hylocomium splendens (1.1%), Athyrium asplenioides (13.1%), Dryopteris intermedia (7.6%), pteridophytes (20.8%) and

Oxalis acetosella (4.5%) was significantly less than in undisturbed stands. Senecio rugelia was absent from these Black Mountains stands.

Summary of Vegetation Analysis Results

Southern Appalachian fir and spruce-fir stands infested by the balsam woolly aphid and uninfested stands were sampled to determine structure and composition. In the uninfested stands at or above 6000 feet elevation, overstory density averaged 354.7 stems per acre. Fraser fir accounted for 78.9% of these and red spruce 18.4%. Only three other species occurred in the overstory of these sampled stands.

Overstory density in uninfested fir and spruce-fir stands below 6000 feet elevation averaged 280.4 stems per acre but nine species contributed to this total. Fraser fir accounted for 58.4% of this total and red spruce 29.1%.

Total overstory density decreased significantly over time since balsam woolly aphid infestation (Table 14). This was due mainly to the decrease in density of overstory fir.

Basal area totals of the higher elevation stands averaged only 205.6 square feet per acre, 68.1% of which was Fraser fir and 29.3% red spruce. Stands below 6000 feet elevation had an average basal area total of 232 square feet per acre comprised of 50.9% red spruce and 36.4% Fraser fir.

The basal area of overstory fir and total overstory basal area followed trends similar to overstory density (Table 14). Total basal area continued to decrease over time

TABLE 14

CHANGES IN STAND COMPOSITION OVER TIME

Stand Characteristic	Years Since Opening of Canopy 0[a]	5-10[b]	11-20[c]
Density of Overstory Fir (stems/acre)	233.9	1.5	44.9
Total Overstory Density (stems/acre)	320.4	105.0	80.8
Basal Area of Overstory Fir (square feet/acre)	120.3	.3	29.9
Total Overstory Basal Area (square feet/acre)	199.6	135.6	51.4
Density of Sapling Fir (stems/acre)	104.8	17.1	82.1
Total Sapling Density (stems/acre)	168.9	118.2	142.6
Density of Subsapling Fir (stems/acre)	453.1	186.3	1031.0
Density of *Rubus canadensis* (Stems/acre)	199.8	1089.8	1936.0
Density of *Vaccinium erythrocarpum* (stems/acre)	257.6	545.0	23.5
Density of *Viburnum alnifolium* (stems/acre)	454.0	834.0	26.8
Total Subsapling Density (stems/acre)	1609.7	3647.6	5724.5
Oxalis acetosella Cover (Percent coverage)	32.0	33.5	6.0
Total Moss Cover (Percent coverage)	19.2	25.3	10.5
Total Pteridophyte Cover (Percent coverage)	32.2	27.0	36.2
Total Ground Cover (Percent coverage)	110.1	105.6	100.2

[a]n=51.

[b]n=30.

[c]n=23.

since initial aphid infestation. Fir basal area decreased through the 5-10 year time period since initial fir death, then increased by the 11-20 year time period

Total sapling density averaged 119.9 stems per acre in stands at or above 6000 feet elevation and 168.6 stems per acre in the lower elevation stands. Of these totals, fir saplings averaged 92.6 (77.2%) and 113.7 (67.4%) respectively.

Both total sapling density and density of sapling fir decreased from uninfested stands through the 5-10 year period since initial fir death (Table 14). However, these totals increased from the 5-10 year period to the 11-20 year period. There was no apparent explanation for this trend.

Subsaplings displayed a more obvious and understandable response to aphid-caused Fraser fir death. Their total density averaged 1110.5 stems per acre in the high elevation uninfested stands and 2828.3 stems per acre in the stands sampled below 6000 feet elevation. Total subsapling density showed a direct increase over time since initial fir death (Table 14). Not only did the total subsapling density increase significantly as aphid-caused disturbance increased but the relative composition of this stratum changed drastically also. Mountain cranberry (*Vaccinium erythrocarpum*) and hobblebush (*Viburnum alnifolium*) densities each increased approximately twofold 5-10 years after aphid-caused fir death began, after which densities decreased with time (Table 14). Thornless blackberry (*Rubus canadensis*) displayed a continued increase in density suggesting its relatively high light requirements. Density of subsapling fir decreased immediately following aphid infestation but had increased 10 years following initial fir death.

Changes in the composition of the ground cover were also significant. With increased opening of the canopy, *Oxalis acetosella* and total moss cover increased slightly through the 5-10 year period since initial fir death (Table 14). However, the cover of these two groups had decreased by the 11-20 year measurements. In contrast, total pteridophyte cover decreased initially, then increased with increased opening of the canopy.

Correlations Between and Among Vegetation and Environmental Variables

Correlation is a statistical technique used to estimate or predict the degree or extent to which the dependent variables vary together (Sokal and Rohlf, 1969). This section examines the correlation among the variables listed in the Appendix.

Correlation coefficients were determined among site and vegetation variables. Matrices were developed and examined using data from all infested stands, all uninfested stands, and subsets of these based on elevation bands. All correlations included are significant at least at the 5% level of significance (Scedecor, 1956).

The mountains forming the Blue Ridge Province have subdued appearances due to the lack of rugged peaks and the presence of rounded summits and domes (Fenneman, 1938). As remnants of a former highland carved from an upraised lowland or peneplain (Fenneman, 1938), these mountains have been, and continue to be, subjected to much weathering and physical degradation. Since these degradation processes have been operative for millions of years, physical site characteristics measured in the boreal forests sampled should demonstrate the effects of these processes.

Correlations among site variables (Table 15) are indeed instructive. The correlation between elevation and aspect suggests small sample size resulting in location bias. The occurrence of both positive and negative correlations between elevation and surface rock suggests other unknown problems. However, the negative relationship between elevation and slope angle suggests the rounded summits of the high mountains and supports the degradation hypothesis. The negative elevation and slope form relationship suggests lack of dissection at higher elevations. Surface rock was positively correlated with north slopes where perhaps at present or in the past more boulder size colluvium has developed, and was positively correlated with slope angle indicating that boulders formed more abundantly on steep slopes or they have become more obvious by exposure due to the removal of soils which might otherwise cover them there. Perhaps more cliffs

TABLE 15

SIGNIFICANT CORRELATIONS AMONG SITE VARIABLES[a]

Site Variables	1	2	3	4	5
1 Elevation	1.00	0.35[b]	-0.49[f]	-0.30[e]	0.49[c] -0.44[f]
2 Aspect		1.00		-0.33[b]	0.46[c]
3 Slope Angle			1.00		0.59[b] 0.57[c] 0.65[d] 0.40[e] 0.55[f]
4 Slope Form				1.00	
5 Surface Rock					1.00

[a]All correlations are significant at P=0.05.

[b]All undisturbed stands, n=46.

[c]Undisturbed stands ≥ 6000 feet elevation, n=19.

[d]Undisturbed stands < 6000 feet elevation, n=27.

[e]All disturbed stands, n=58.

[f]Disturbed stands < 6000 feet elevation, n=31.

and ledges were present on these steeper slopes which allowed for greater colluvium development.

Significant correlations between site and vegetation variables (Table 16) indicate certain relationships. Both the density and basal area of overstory fir were positively correlated with elevation as expected. However, total overstory density and basal area were generally negatively correlated with elevation--apparently a response to the harsher environmental conditions at higher elevations caused by increased exposure, a function of less protection and less dissection at higher elevations. Density of sapling fir was positively correlated with elevation indicating a good seed source and survival rate in higher stands. Total sapling density and density of subsapling fir showed positive and negative relationships respectively with elevation for unknown reasons. Total subsapling density, density of _Rubus_, density of _Viburnum alnifolium_ and density of _Vaccinium erythrocarpum_ were negatively correlated with elevation indicating that the optimum range of these species is at lower elevations. In contrast to previous reports (Whittaker, 1956; Crandall, 1958), moss coverage was negatively correlated with elevation. The relationship of _Oxalis acetosella_ cover and elevation remains somewhat contradictory. Pteridophyte cover was positively correlated with elevation.

Basal area of overstory fir was weakly positively related to mesic aspect (north, northeast, east), total

TABLE 16

SIGNIFICANT CORRELATIONS BETWEEN SITE VARIABLES AND VEGETATION VARIABLES[a]

Site Variables	Vegetation Variables													
	Density of Over-story Fir	Total Over-story Density	Basal Area of Over-story Fir	Total Over-story Basal Area	Density of Sapling Fir	Total Sapling Density	Density of Sub-sapling Fir	Total Sub-sapling Density	Density of Rubus	Density of Viburnum alnifolium	Density of Vaccinium erythrocarpum	Moss Cover	Oxalis acetosella Cover	Pteridophyte Cover
Elevation	0.41[b] 0.49[e] 0.49[f]	-0.54[g]	0.53[b] 0.51[e] 0.56[f]	-0.31[b] -0.56[c] -0.41[e] 0.50[f] -0.61[g]	0.68[c] 0.32[e]	0.47[c] -0.36[g]	0.32[e] -0.62[g]	-0.39[b] -0.56[f]	-0.29[b] -0.57[f]	-0.30[b] -0.34[e] -0.50[f]	-0.34[e]	-0.30[b] -0.48[e] -0.49[g]	-0.61[c] -0.61[e] 0.46[f]	0.50[g]
Aspect			0.29[b]	-0.42[b] -0.57[c] -0.28[e]				-0.32[b] -0.46[c] -0.43[e] -0.52[g]	-0.38[e] -0.48[g]		-0.37[b] -0.50[c]	0.71[c] -0.42[g]	-0.30[b] -0.58[c]	0.56[e] 0.52[f] 0.62[g]
Slope Angle	-0.37[e] -0.42[g]	0.32[b]	-0.40[e] -0.38[f] -0.43[g]		-0.29[b] -0.43[d]	-0.42[d]	0.27[e] 0.49[f]				0.34[e] 0.40[f] 0.44[g]	0.43[d] 0.47[g]	-0.33[b] -0.39[d]	-0.38[b] -0.53[c]
Slope Position											0.65[f]			0.55[f]
Slope Form	-0.42[g]		-0.41[g]		-0.40[g]	-0.51[c] -0.38[g]	0.48[c] 0.40[f]					0.32[e]	-0.38[g]	
Surface Rock	0.45[b] 0.49[d]	0.40[b] 0.50[d] -0.39[f]	0.35[b]				0.30[e]		-0.29[b]	-0.39[b] -0.56[c]		0.39[b] 0.59[d]	-0.30[b] -0.48[c]	-0.35[b] -0.60[c]
Disturbance	-0.32[e] -0.79[f] -0.61[g]	-0.49[e] -0.79[f]	-0.71[f] -0.59[g]	-0.54[e] -0.72[f]			0.43[e]		0.30[e]	-0.37[e] -0.64[g]	-0.29[e] -0.37[g]	-0.40[e]	-0.61[e] -0.74[f] -0.48[g]	

[a]All correlations are significant at P=0.05.

[b]All undisturbed stands, n=46.

[c]Undisturbed stands ≥ 6000 feet elevation, n=19.

[d]Undisturbed stands < 6000 feet elevation, n=27.

[e]All disturbed stands, n=58.

[f]Disturbed stands ≥ 6000 feet elevation, n=27.

[g]Disturbed stands < 6000 feet elevation, n=31.

overstory basal area was negatively correlated with such aspects, perhaps a climatic phenomenon. Total subsapling density, Rubus density and Vaccinium erythrocarpum density were negatively correlated with mesic aspect suggesting their relation to aspect or their negative relationship to fir basal area. The contradictory relationships between moss cover and aspect is not fully understood. Oxalis acetosella cover was negatively related to mesic aspects in contrast to previous studies (Whittaker, 1956). Pteridophyte cover, especially in uninfested stands, was positively correlated with more northerly and easterly exposures.

Nearly all relationships with slope angle were opposite of those with elevation since they were negatively correlated. Factors associated with elevation are presumed to be controlling. Both density and basal area of overstory fir were therefore negatively related to slope angle; total overstory density was positively correlated with slope angle. Density of sapling fir and total sapling density were negatively related to slope angle, higher densities occurred at higher elevations. Density of subsapling fir and density of Vaccinium erythrocarpum, however, were positively related to slope angle in certain infested stands. At lower elevations where slope angle increased, moss cover also increased. Oxalis acetosella cover and pteridophyte cover were negatively correlated with slope angle, probably due to decreased slope angle at higher elevations.

Slope position showed little relationship with the vegetation variables measured. In high elevation infested stands the density of Vaccinium erythrocarpum increased downslope, perhaps a function of elevation position. Pteridophyte cover was also positively related to lower slope position (increased protection).

Slope form was negatively correlated with the density and basal area of overstory fir in lower elevation disturbed stands indicating that fir occurred there in more convex-shaped sites. Similarly, the density of sapling fir and total sapling density increased on flat to convex-shaped sites. The density of subsapling fir in high elevation stands, however, was positively correlated with slope form indicating that fir reproduction was greater in depressions. Moss cover displayed a similar trend.

Surface rock cover was positively correlated with elevation in certain uninfested stands and therefore displayed similar relationships to elevation. Both the density and basal area of overstory fir were positively correlated with surface rock, probably a phenomenon related to elevation. Total overstory density was positively related to surface rock in uninfested stands possibly due to elevation. Other relationships of note included the negative correlations of the density of Rubus and Viburnum alnifolium, Oxalis and pteridophyte cover with surface rock, suggesting their requirement for surface soil. Only the moss species of the ground cover displayed positive relationships with surface rock indicating the typical epilithic growth of mosses in the high elevation forests of the Southern Appalachians.

Stand changes over time since death of overstory fir stems due to balsam woolly aphid attack showed significant trends. As expected, density of overstory fir, total overstory density, basal area of overstory fir and total overstory basal area were all negatively related to length of time since initiation of balsam woolly aphid disturbance. No significant relationships with time since disturbance were demonstrated by sapling stems since they had not had time to respond to the effects of the open-canopy stands. Subsapling fir density showed a positive correlation with time since disturbance, indicating the increased fir reproduction as a result of increased light in the presence of a partial canopy (Hart, 1959). Density of Rubus increased with an increase in time since disturbance as expected due to its invading characteristics and its shade intolerance. Other subsapling densities, such as Viburnum alnifolium and Vaccinium erythrocarpum, demonstrated negative relationships with disturbance indicative of their shade tolerance and their inability to reinvade the open sites. Both moss cover and pteridophyte cover showed negative correlations with time since balsam woolly aphid disturbance as these species require shading.

Significant correlations among vegetation variables in infested and uninfested stands (Table 17) suggest relationships of interest. Density of overstory fir was of course

TABLE 17

SIGNIFICANT CORRELATIONS AMONG VEGETATION VARIABLES[a]

Vegetation Variables	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Density of Overstory Fir	1.00	0.89[b] 0.91[c] 0.79[d] 0.79[e] 0.96[f]	0.78[b] 0.85[c] 0.51[d] 0.96[e] 0.95[f] 0.99[g]	0.33[e] 0.93[f]	0.29[e]			-0.50[b] -0.57[d] -0.33[e] -0.55[f]	-0.46[f]	-0.52[b] -0.54[d]		0.49[d]	0.90[f] 0.51[g]	-0.30[b] -0.43[d]
2 Total Overstory Density		1.00	0.59[b] 0.71[c] 0.73[e] 0.89[f]	0.51[c] 0.68[e] 0.85[f] 0.59[g]		0.29[e] 0.56[g]	0.39[g]	-0.37[b] -0.56[d] -0.47[e] -0.57[f]	-0.40[e] -0.46[f]	-0.42[b] -0.50[d]			0.85	-0.44[b] -0.59[c] -0.40[d]
3 Basal Area of Overstory Fir			1.00	0.32[e] 0.96[f]	-0.41[d] 0.30[e]	-0.37[b] -0.54[d]		-0.48[c] -0.49[d] -0.34[e] -0.57[f]	-0.49[f]	-0.42[b] -0.61[c]	-0.40[b] -0.48[c] -0.42[c]	0.51[c]	0.81[f] 0.49[g]	
4 Total Overstory Basal Area				1.00			0.54[g]	-0.30[b] -0.52[e] -0.60[f] -0.46[g]	-0.53[e] -0.49[f] -0.56[g]		0.52[b] 0.56[c] 0.56[d]	0.33[e]	0.40[b] 0.53[c] 0.43[e] 0.79[f]	-0.35[b] -0.42[d]
5 Density of Sapling Fir					1.00	0.92[b] 0.88[c] 0.94[d] 0.67[e] 0.87[f] 0.49[g]	0.27[e]				0.31[b]		0.55[d]	
6 Total Sapling Density						1.00					0.3[illegible][b] 0.42[d]		0.48[d]	
7 Density of Subsapling Fir							1.00	0.57[b] 0.92[c] 0.45[d]			0.62[c]		-0.31[e]	-0.31[b]
8 Total Subsapling Density								1.00	0.42[b] 0.94[e] 0.97[f] 0.93[g]	0.53[b] 0.46[d]	0.57[b] 0.83[c] 0.55[d] 0.28[e] 0.63[g]	-0.49[c] 0.49[g]	-0.37[e] -0.56[f] -0.41[g]	-0.37[e] -0.54[g]
9 Density of *Rubus*									1.00	0.43[b]	0.46[g]		-0.42[e] -0.50[f] -0.48[g]	
10 Density of *Viburnum alnifolium*										1.00	0.28[e]	-0.30[b] -0.51[d]	0.54[c]	0.33[b] 0.63[d]
11 Density of *Vaccinium erythrocarpum*											1.00	0.48[c] 0.40[e] 0.37[g]	0.33[b] 0.26[e]	-0.31[e] -0.45[g]
12 Moss Cover												1.00		-0.59[d] -0.46[e] -0.69[g]
13 [illegible] Cover													1.00	
14 Pteridophyte Cover														1.00

[a]All correlations are significant at P=0.05.

[b]All undisturbed stands, n=46.

[c]Undisturbed stands ≥ 6000 feet elevation, n=19.

[d]Undisturbed stands < 6000 feet elevation, n=27.

[e]All disturbed stands, n=58.

[f]Disturbed stands ≥ 6000 feet elevation, n=27.

[g]Disturbed stands < 6000 feet elevation, n=31.

positively related to total overstory density and to its own basal area. Certain infested stands displayed positive relationships between overstory fir density and total overstory basal area and between overstory fir density and sapling fir desnity. The cover of the shade tolerant Oxalis acetosella and mosses were positively related to the density of overstory fir. However, as fir died, Rubus and other subsaplings invaded the stands. Pteridophyte cover was negatively related to overstory fir density in uninfested stands.

Total overstory density displayed essentially the same relationships.

Basal area of overstory fir displayed relationships similar to those of the density of fir with few exceptions. One exception was the unexplained relationship between basal area of fir and the density of sapling fir as they were positively correlated in all infested stands sampled but negatively related in lower elevation uninfested stands. Basal area of fir was also negatively related to total sapling density in certain uninfested stands and negatively related to the density of Vaccinium erythrocarpum.

Total overstory basal area displayed relationships similar to those of fir basal area except total overstory basal area was positively related to the density of Vaccinium erythrocarpum.

Total sapling density decreased with an increase in basal area of fir.

Density of subsapling fir and total subsapling density displayed similar relationships as both were negatively related to overstory densities and basal area, increased as fir died, were positively related to the three major subsapling taxa: Rubus, Viburnum and Vaccinium, but apparently provided too much shade for Oxalis and the pteridophytes (negative relationships). Moss cover displayed a positive relationship with total subsapling density in infested stands sampled below 6000 feet elevation and a negative one in higher elevation uninfested stands.

Rubus density was negatively related to overstory variables due to its shade intolerance, and negatively related to Oxalis cover apparently due to the dense cover formed by the Rubus preventing light penetration. Vaccinium erythrocarpum and Viburnum alnifolium were weakly positively correlated--Viburnum scarcely sharing its niche with other taxa, although it was positively related to pteridophyte cover. Vaccinium density was positively related to sapling fir and other understory and ground cover taxa except pteridophytes which displayed a negative relationship.

Oxalis was positively related to the overstory variables, to densities of Viburnum and Vaccinium and negatively to density of Rubus and cover of pteridophytes. The moss-Oxalis relationships (Crandall, 1958) did not appear. The negative relationship between Rubus and Oxalis and between pteridophytes and other variables has not been well documented previously.

Regression of Environmental and Vegetation Variables on Vegetation Characteristics

Twelve independent variables and 14 dependent variables were chosen for examination using maximum R-square improvement, multiple regression techniques (Service, 1972) to indicate relationships among site characteristics and vegetation composition. Variables used in these analytical procedures and their respective codes appear in the Appendix Tables 18 and 19 -- independent variables (Table 18) and dependent variables (Table 19).

The regression analysis employed was performed on six data sets: all uninfested stands, uninfested stands at or above 6000 feet elevation, uninfested stands below 6000 feet, all infested stands, infested stands at or above 6000 feet and infested stands below 6000 feet. These computations were performed using four similar but separate procedures on all data sets. The first procedure tested the ability of seven independent variables: elevation (X1), aspect (X2), slope angle (X3), slope position (X4), slope form (X5), surface rock (X6) and time since disturbance due to balsam woolly aphid attack (X7), to predict the density of overstory fir (Y1), total overstory density (Y2), the basal area of overstory fir (Y3) and total overstory basal area (Y4). The maximum R-square improvement technique used on this set of variables calculated the regression equation with the best single variable predictor, the equation with the best combination of two variables, the equation with the best combination of three variables and the equation with the best combination of four variables as determined by the R-square of each equation. The regression equations selected for discussion are those which contain independent variables that contribute 5% or more to the total R-square.

The equations in the following discussion are numbered consecutively to refer to the following data sets respectively: 1) uninfested stands sampled at all elevations (U All), 2) infested stands at all elevations (I All), 3) uninfested stands at or above 6000 feet elevation (U > 6), 4) infested stands at or above 6000 feet elevation (I > 6), 5) uninfested stands below 6000 feet elevation (U < 6) and 6) infested stands below 6000 feet elevation (I < 6).

<u>Density of overstory fir (Y1)</u>.

			R^2	n	S.E.E.
1.	(U All)	Y1 = -47.82 + 0.14X6 + 0.01X1	.31	46	10.40
2.	(I All)	Y1 = -74.28 + 0.02X1 - 5.47X7	.68	58	4.90
3.	(U > 6)	Y1 = 261.10 + 0.26X6 - 0.04X1	.26	19	13.13
4.	(I > 6)	Y1 = -182.28 - 5.68X7 + 0.03X1	.68	27	6.40
5.	(U < 6)	Y1 = 25.35 + 0.16X6 - 3.87X5 - 0.15X3	.41	27	5.39
6.	(I < 6)	Y1 = 11.84 - 2.04X7 - 0.05X3 - 0.96X5	.54	31	1.51

Overstory fir density is best predicted in uninfested stands by a few variables. In equations 1, 3 and 5 fir density is predicted by surface rock cover (X6) and usually by elevation (X1). Above 6000 feet elevation (equation 3), elevation (X1) has a negative effect on density; below 6000 feet (equation 5), slope convexities (X5) and lower slope angles (X3) are important.

In the infested stands represented by equations 2, 4 and 6, time since aphid attack (X7) is important in each equation. Elevation (X1) is positive on overstory fir density in all infested stands (equation 2) and infested stands above 6000 feet (equation 4); slope angle (X3) and slope form (X5) are important predictors as before. R-square averaged higher in equations calculated for infested stands.

Total overstory density (Y2).

			R^2	n	S.E.E.
1.	(U All)	$Y2 = 26.12 + 0.14X6$	.16	46	10.60
2.	(I All)	$Y2 = -16.18 - 5.56X7 + 0.01X1$	.35	58	7.95
3.	(U > 6)	$Y2 = 316.60 + 0.29X3 - 0.05X1 + 0.15X6$	.31	19	12.54
4.	(I > 6)	$Y2 = 50.20 - 7.52X7$	.62	27	8.08
5.	(U < 6)	$Y2 = 24.67 + 0.11X6$	.25	27	6.28
6.	(I < 6)	$Y2 = 141.91 - 0.02X1 - 3.34X7 - 2.37X5$	.41	31	4.62

As was the case with overstory fir density, total overstory density increased in uninfested stands with an increase in surface rock cover (X6) but decreased as elevation (X1) increased in high elevation uninfested stands (equation 3).

Time since balsam woolly aphid disturbance (X7) was the most important factor in predicting total overstory density in infested stands (equations 2, 4 and 6) and they were negatively related. In such stands, total overstory density increased with an increase in elevation (X1), but decreased with an increase in elevation (X1) in lower elevation infested stands (equation 6) for unknown reasons.

<u>Basal area of overstory fir (Y3)</u>.

			R^2	n	S.E.E.
1.	(U All)	Y3 = -2.49 + 0.0001X1 + 0.003X6	.33	46	0.38
2.	(I All)	Y3 = -4.19 + 0.001X1 - 0.28X7	.62	58	0.30
3.	(U > 6)	Y3 = 8.42 + 0.01X6 - 0.001X1	.23	19	0.37
4.	(I > 6)	Y3 = -15.20 - 0.26X7 + 0.003X1	.62	27	0.39
5.	(U < 6)	Y3 = 0.49 + 0.003X6 + 0.09X2	.13	27	0.32
6.	(I < 6)	Y3 = 0.79 - 0.13X7 - 0.003X3 - 0.06X5	.51	31	0.11

Surface rock cover (X6) was the best predictor (a positive one) of the basal area of overstory fir in uninfested stands (equations 1, 3 and 5). Elevation (X1) predicted fir basal area positively in the whole uninfested sample (equation 1) but at high elevations (equation 3) it was negatively related. Basal area of overstory fir increased toward north aspect (X2) in lower elevation uninfested stands (also reported by Whittaker, 1956).

Basal area of fir in infested stands was influenced in all three equations by time since aphid disturbance (X7) and by elevation (X1) in two equations. In lower elevation infested stands (equation 6) the basal area of overstory fir again increased on lessened slope angles (X3) and on flatter slope forms (X5).

Total overstory basal area (Y4).

			R^2	n	S.E.E.
1.	(U All)	Y4 = 2.84 - 0.21X2	.18	46	0.46
2.	(I All)	Y4 = 1.81 - 0.33X7 + 0.20X2	.33	58	0.61
3.	(U > 6)	Y4 = 11.53 - 0.19X2 - 0.001X1	.46	19	0.38
4.	(I > 6)	Y4 = -12.61 - 0.30X7 + 0.002X1	.60	27	0.43
5.	(U < 6)	Y4 = 2.67 - 0.12X2	.06	27	0.48
6.	(I < 6)	Y4 = 18.01 - 0.003X1 + 0.20X2	.44	31	0.56

Total overstory basal area in uninfested stands was influenced most by aspect (X2); basal area decreased toward more southerly and westerly exposures.

In infested stands, total basal area was predicted most by time since aphid disturbance (X7), aspect (X2) and elevation (X1). As expected, basal area decreased with increased time since aphid disturbance (X7); more death occurred on the more stressed south aspects. The weak positive (equation 4) and negative (equation 3) relation of elevation (X1) to basal area is not understood.

The second procedure used to analyze data from these stands tested the predictability of 10 independent variables:

elevation (X1), aspect (X2), slope angle (X3), slope position (X4), slope form (X5), surface rock cover (X6), time since balsam woolly aphid disturbance (X7), canopy closure (X8), total overstory density (X9) and total overstory basal area (X10), on the density of sapling fir (Y5) and total sapling density (Y6). The results of this analysis follow.

<u>Density of sapling fir (Y5).</u>

			R^2	n	S.E.E.
1.	(U All)	Y5 = 24.29 - 0.16X3 - 3.43X5	.13	46	8.77
2.	(I All)	Y5 = -69.68 + 0.01X1 + 0.13X8	.16	58	10.69
3.	(U > 6)	Y5 = -167.16 + 0.03X1 - 3.54X5 + 0.27X8 - 6.18X10	.66	19	4.68
4.	(I > 6)	Y5 = -451.16 + 0.07X1 - 5.14X2	.20	27	13.33
5.	(U < 6)	Y5 = 12.55 - 0.30X3 + 7.96X10 - 4.77X4	.39	27	8.19
6.	(I < 6)	Y5 = 3.78 - 6.24X5 + 0.20X3 + 1.77X2	.36	31	5.55

The density of sapling fir displayed distinctive trends. In uninfested stands, density increased with a decrease in slope angle (X3), possibly due to elevation, and toward convex-shaped slope form (X5), possibly also an elevational effect. Sites with increased elevation (X1) and canopy closure (X8) showed increased densities of sapling fir. The effect of total overstory basal area (X10) (negative in equation 3, positive in equation 5) is not understood.

Infested stands showed similar relationships although sapling fir density increased with an increase in slope angle (X3) in lower elevation infested stands (equation 6) for unknown reasons.

<u>Total sapling density (Y6)</u>.

			R^2	n	S.E.E.
1.	(U All)	Y6 = 31.09 - 4.32X5 - 0.17X3	.13	46	10.58
2.	(I All)	Y6 = 27.19 - 8.56X5 + 0.18X8	.16	58	13.78
3.	(U > 6)	Y6 = -179.36 - 6.94X5 + 0.03X1 + 0.24X8	.52	19	6.35
4.	(I > 6)	Y6 = 22.67 - 0.28X3	.08	27	14.95
5.	(U < 6)	Y6 = 14.82 - 0.38X3 + 7.31X10	.26	27	10.74
6.	(I < 6)	Y6 = 15.21 + 1.09X9 + 0.15X6 - 8.38X5	.49	31	10.74

Among the equations, canopy closure (X8), overstory basal area (X10) and overstory density (X9) are positively related to total sapling density which apparently has not yet responded to the newly created openings. In the uninfested stands, sapling density is also predicted by convex slope form (X5), shallow slope angle (X3) and increased elevation (X1). Infested stands showed similar trends though at low elevations (equation 6), density is also related to surface rock cover (X6).

The third procedure used to analyze data from these stands tested the predictability of 12 independent variables: the same 10 as used previously and density of sapling fir

(X11) and total sapling density (X12), on the density of subsapling fir (Y7), total subsapling density (Y8), density of _Rubus_ (Y9), density of _Viburnum alnifolium_ (Y10) and density of _Vaccinium erythrocarpum_ (Y11). The results of this analysis follow.

Density of subsapling fir (Y7).

			R^2	n	S.E.E.
1.	(U All)	Y7 = -6.26 + 8.68X5	.05	46	22.48
2.	(I All)	Y7 = -18.87 + 5.52X7 + 0.16X6	.23	58	16.78
3.	(U > 6)	Y7 = 47.09 - 18.99X2 + 0.61X6 - 0.74X3 + 17.02X4	.64	19	15.22
4.	(I > 6)	Y7 = -620.79 + 24.59X5 - 0.44X8 + 0.38X6 + 0.09X1	.52	27	16.57
5.	(U < 6)	Y7 = 33.72 + 0.23X6 - 0.98X9	.11	27	21.15
6.	(I < 6)	Y7 = 378.38 - 0.07X1 + 7.02X7 - 0.27X3 - 5.67X4	.61	31	7.10

Several variables apparently affected the density of subsapling fir. When considering uninfested stands, subsapling fir density increased toward concave slopes (X5) and did so also in high elevation infested stands. Surface rock cover (X6) appeared to contribute significantly to increases in the density of subsapling fir as increased exposed rock surface (X6) provided more open space for establishment of these small stems. The density of subsapling fir also increased with an increased loss of overstory fir due to balsam woolly aphid disturbance (X7) and with a decrease in canopy closure (X8) demonstrating the positive response of fir reproduction to the increased light availability. Increased densities of subsapling fir accompanied both decreases in slope angle (X3) (elevation effect) and in total overstory density (X9) in certain stands. The influence of slope position (X4) is contradictory.

In infested stands, subsapling fir density was positively related to elevation (X1) in high stands (equation 4) and negatively so in lower stands (equation 6) for reasons unknown.

The very low R-square achieved in half of the equations strongly suggests the periodic seeding and survival of this layer in years prior to sampling.

<u>Total subsapling density (Y8)</u>.

			R^2	n	S.E.E.
1.	(U All)	Y8 = 22.16 - 1.53X9 + 30.86X10	.31	46	30.49
2.	(I All)	Y8 = 245.61 - 40.55X2 - 3.62X9	.40	58	63.50
3.	(U > 6)	Y8 = 62.07 - 20.95X2 + 20.88X4 + 0.43X6 - 0.60X3	.51	19	20.58
4.	(I > 6)	Y8 = 236.38 - 111.79X10 - 2.67X3 - 27.71X2 + 51.73X5	.59	27	66.64
5.	(U < 6)	Y8 = 77.69 - 3.76X9 + 23.67X10 + 0.76X3	.49	27	25.21
6.	(I < 6)	Y8 = 176.37 - 30.51X2 - 0.44X6	.38	31	44.66

Many factors affected the total subsapling density. In uninfested stands, this density increased with an increase in total overstory basal area (X10), toward downslope positions (X4) and with an increase in surface rock (X6). Slope angle (X3) displayed contrasting relationships here for reasons unknown. In certain uninfested stands and those infested stands of all elevations (equation 2), total subsapling density increased with decrease in total overstory density (X9), apparently due to increased light intensities. In infested stands, total subsapling density consistently increased toward the south and west aspects (X2). This apparently is caused by the increased density of Rubus stems which occurred on drier, more exposed sites (see later). Other variables appeared to have less influence on the total subsapling density.

Density of Rubus (Y9).

			R^2	n	S.E.E.
1.	(U All)	Y9 = 46.56 - 0.01X1 - 0.07X6	.13	46	9.97
2.	(I All)	Y9 = 72.45 + 25.96X7 - 1.191X3 - 26.61X2	.40	58	56.12
3.	(U > 6)	Y9 = 9.25 - 0.001X1 - 0.02X8 - 0.01X3 - 0.32X4	.42	19	0.36
4.	(I > 6)	Y9 = 2241.79 - 72.75X10 - 3.08X3 - 0.31X1	.56	27	64.88
5.	(U < 6)	Y9 = 29.80 - 13.36X4 - 0.25X6 - 0.32X11 + 0.33X3	.37	27	10.55
6.	(I < 6)	Y9 = 67.39 - 29.32X10 + 2.84X9 - 0.72X11 - 10.18X2	.51	31	22.96

In uninfested stands, elevation (X1) and surface rock (X6) were the best determinants of the density of Rubus--it increased with decreased elevation (X1) and surface rock (X6). Rubus density also increased on upper slopes (X4) and with a decrease in sapling density (X11) presumably due to increased light availability. The role of slope angle (X3) is contradictory.

In infested stands, Rubus density displayed an increase with increased overstory fir death due to balsam woolly aphid disturbance (X7), a demonstration of the probably high light requirements of Rubus spp. In these stands, Rubus density increased toward south and west exposures (X2), increased as slope angle (X3) decreased, increased as total overstory basal area (X10) decreased and increased as total sapling density (X11) decreased. All these relationships demonstrate that drier, more exposed and open areas are required for dense Rubus growth. This has been previously reported (Brown, 1941; Crandall, 1958).

Density of Viburnum alnifolium (Y10).

			R^2	n	S.E.E.
1.	(U All)	Y10 = 21.56 - 0.44X9 - 0.19X6 + 0.33X3	.30	46	12.51
2.	(I All)	Y10 = 41.40 - 6.67X7 - 0.63X9	.27	58	11.61
3.	(U > 6)	Y10 = 11.37 - 0.13X6	.32	19	6.69
4.	(I > 6)	Y10 = 43.16 - 0.01X1 - 0.02X6 - 0.03X9	.43	27	0.96

5.	(U < 6)	$Y10 = -122.78 - 1.18X9 + 0.03X1 + 5.82X5$	.43	27	12.43
6.	(I < 6)	$Y10 = 309.77 - 18.88X7 - 1.31X9 - 0.04X1$	.51	31	12.55

The density of *Viburnum alnifolium* was greatest where exposed surface rock (X6) was the least and where total overstory density (X9) was low. Increased densities of *Viburnum alnifolium* also occurred toward concave slopes (X5) and usually decreased elevation (X1). *Viburnum* density decreased with an increase in overstory fir death due to aphid disturbance (X7), a negative response to increased light intensities.

Density of *Vaccinium erythrocarpum* (Y11).

			R^2	n	S.E.E.
1.	(U All)	$Y11 = 4.75 + 14.58X10 + 0.44X11 - 0.32X8 - 3.09X2 - 0.25X9$	.56	46	8.74
2.	(I All)	$Y11 = 10.90 + 11.47X10 - 0.64X9 - 3.44X2$	.27	58	10.23
3.	(U > 6)	$Y11 = -14.89 + 12.46X10 - 0.13X9 + 0.28X11 - 0.18X8 + 2.34X4$	.59	19	3.17
4.	(I > 6)	$Y11 = -1.51 + 1.03X4 + 0.02X3$	.48	27	0.79
5.	(U < 6)	$Y11 = -19.21 + 22.32X10 - 0.85X9$	.44	27	12.50
6.	(I < 6)	$Y11 = 41.23 + 0.72X3 - 14.58X7 - 0.33X11$	.36	31	12.63

Density of Vaccinium erythrocarpum in uninfested plots was positively related to overstory basal area (X10), negatively related to overstory density (X9) and positively on sapling density (X11), all indicating mature stands. That there are openings even in these stands is suggested by the negative canopy closure (X8) relationship.

Infested plots were also positive on basal area (X10) and negative on overstory density (X9), sapling density (X11) and time since aphid attack (X7).

The fourth analytical procedure used tested the ability of 12 independent variables: elevation (X1), aspect (X2), slope angle (X3), slope position (X4), slope form (X5), surface rock (X6), time since balsam woolly aphid disturbance (X7), canopy closure (X8), total overstory density (X9), total overstory basal area (X10), total sapling density (X11) and total subsapling density (X12), to predict total moss cover (Y12), Oxalis acetosella cover (Y13) and total pteriodophyte cover (Y14).

Moss cover (Y12).

			R^2	n	S.E.E.
1.	(U All)	Y12 = 133.92 + 0.26X6 - 0.02X1 - 7.12X5	.38	46	12.32
2.	(I All)	Y12 = 96.74 - 0.01X1	.22	58	10.27
3.	(U > 6)	Y12 = 176.83 + 10.25X2 - 0.03X1 + 0.21X8	.71	19	6.57
4.	(I > 6)	Y12 = 8.80 + 0.18X8	.15	27	8.48

			R^2	n	S.E.
5.	(U < 6)	Y12 = 15.78 + 0.30X6	.35	27	14.02
6.	(I < 6)	Y12 = -7.00 + 0.12X12 + 0.60X3	.53	31	8.00

The relationships between moss cover and other variables are instructive. Moss cover decreased distinctly with an increase in elevation (X1), in contrast to previous reports that moss cover in fir and spruce-fir forests of the Southern Appalachians strongly increase along an increasing elevational gradient (Whittaker, 1956; Crandall, 1958). Moss cover increased toward north aspects (X2) (see also Whittaker, 1956) and increased with an increase in canopy closure (X8). The shade tolerance of these bryophytes is well known (Sharp, 1939). Sites with greater amounts of exposed rock surface (X6) displayed greater moss cover suggesting the epilithic growth habit common among the mosses. The role of steep slopes (X3) is probably a function of rock cover (Table 15, page 65). The relationship to convex form (X5) is not understood.

Oxalis acetosella cover (Y13).

			R^2	n	S.E.
1.	(U All)	Y13 = 15.85 + 14.22X10 - 0.41X3	.27	46	15.59
2.	(I All)	Y13 = 160.31 - 0.02X1 - 6.29X7	.47	58	13.84
3.	(U > 6)	Y13 = 404.22 - 0.06X1 - 7.13X2 + 0.40X8	.56	19	14.04
4.	(I > 6)	Y13 = 3.28 + 0.33X8	.76	27	3.68

5. (U < 6)	Y13 = -76.12 + 0.63X11 + 0.02X1	.28	27	13.81
6. (I < 6)	Y13 = 125.50 - 0.16X12 -15.18X7 - 10.93X5	.49	31	13.98

In this study, Oxalis cover decreases (equations 2 and 3) and increases (equation 5) with increased elevation (X1). Oxalis cover has been previously reported to increase with an increase in elevation (Crandall, 1958). The relative shade tolerance of Oxalis was demonstrated by its increase with increased canopy closure (X8) and with decreased overstory fir death due to aphid disturbance (X7). Increased coverage of Oxalis accompanied decreases in slope angle (X3), and toward south and west exposures (X2). In uninfested stands, cover of the shade tolerant Oxalis increased with increases in total overstory basal area (X10), increased canopy closure (X8) and total sapling density (X11). However, apparently Oxalis requires more light than was available in the infested stands that had been invaded by subsaplings since Oxalis cover decreased with an increase in total subsapling density (X12).

In lower elevation infested stands (equation 6), Oxalis cover increased toward convex slopes (X5) for unknown reasons.

Pteridophyte cover (Y14).

		Equation	R^2	n	S.E.E.
1.	(U All)	Y14 = 73.17 - 19.77X10 - 0.31X6 + 7.77X5	.34	46	17.60
2.	(I All)	Y14 = -5.48 + 15.20X2 - 0.66X3 + 9.79X4	.47	58	16.32
3.	(U > 6)	Y14 = 33.56 - 0.48X6 - 0.88X9 + 23.32X4 - 0.38X12 + 14.22X5	.78	19	13.23
4.	(I > 6)	Y14 = -1.94 + 20.48X4 - 0.70X3 + 10.14X2	.64	27	13.49
5.	(U < 6)	Y14 = -51.15 - 11.47X10 - 0.72X9 + 0.02X1 + 6.37X5	.38	27	13.00
6.	(I < 6)	Y14 = -758.70 + 14.78X2 + 0.13X1	.57	31	15.15

Pteridophyte cover in uninfested plots (equations 1, 3 and 5) was higher in low overstory basal area (X10) and density (X9) stands, with less rock cover (X6), concave slope shapes (X5), lower slope positions (X4), higher elevations (X1) and fewer subsaplings (X12). Pteridophyte cover in infested plots (equations 2, 4 and 6) was related to north and east aspects (X2), low slope angles (X3), lower slope positions (X4) and higher elevations (X1).

V. CONCLUSIONS

Distinct trends were apparent in the population dynamics of the Southern Appalachian boreal forest ecosystem due to the death of Fraser fir as a result of balsam woolly aphid attack. As expected, overstory density and basal area totals decreased drastically following aphid kill of overstory fir from the 280.4 and 354.7 stems per acre and 205.6 and 232 square feet per acre in uninfested stands above and below 6000 feet elevation, respectively. Sixteen to 20 years after initial fir death due to aphid attack, these boreal forests averaged only 59.3 stems per acre and 33.8 square feet per acre. Correlation and regression analyses on this same data set demonstrated this effect that aphid-caused fir death had on the overstory.

Most apparent changes in the populations of these high elevation forests were in the understory and ground cover strata. As shown by simple vegetation analysis and by correlation and regression results, the common understory taxa in these forests, mountain cranberry (*Vaccinium erythrocarpum*) and hobblebush (*Viburnum alnifolium*), decreased in density due to opening of the canopy upon fir death. Densities of mountain cranberry and hobblebush decreased from 257.6 and 454.0 in uninfested stands to 19.0 and 42.5 stems per acre respectively in stands 16-20 years after initial fir death. Thornless blackberry (*Rubus canadensis*) showed a significant increase in density as aphid attack caused increased openings in the canopy. It averaged 199.8 stems per acre in uninfested stands and increased to 1938 in the most infested and oldest stands sampled.

Total ground cover remained rather constant as aphid-caused fir death increased. However, composition of this stratum changed. *Oxalis acetosella* decreased from a coverage of 32% in uninfested stands to 6% in stands with the oldest and most severe aphid damage. Total moss cover decreased from 19.5% in uninfested stands to 10.5% in stands with initial fir death 16-20 years prior.

Several important relationships were demonstrated by correlation and regression analyses. Total overstory tree basal increased as elevation decreased. Densities of thornless blackberry, mountain cranberry and hobblebush and moss cover all increased downslope. Pteridophyte cover was positively related to elevation.

Oxalis acetosella cover and thornless blackberry density increased toward drier sites. Pteridophyte cover increased toward mesic sites.

Thornless blackberry and mountain cranberry densities and *Oxalis* and pteridophyte cover increased where there was less exposed surface rock.

Decreased density and basal area of overstory Fraser fir due to attack by the balsam woolly aphid were good predictors of increased thornless blackberry density. Decreased density and basal area of overstory fir were negatively related to coverage of mosses and pteridophytes and to densities of mountain cranberry and hobblebush. Subsapling fir densities increased with increased time since fir death due to aphid attack.

Site relationships that were demonstrated included elevation negatively related to slope angle and concave slope form. This suggests rounded summits and less dissection of the mountains at high elevations in the Southern Appalachians. Increased exposure of surface rock on north slopes and greater slope angles indicated greater rock exposure on steeper slopes.

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APPENDIX

APPENDIX

TABLE 18

INDEPENDENT VARIABLES USED IN CORRELATION AND REGRESSION ANALYSES

Variable	Code
X1 - Elevation	Recorded to nearest 10 feet
X2 - Aspect	Recorded to nearest degree then coded
202.5°-247.5°	1
157.5°-202.5°	2
247.5°-292.5°	2
112.5°-157.5°	3
292.5°-337.5°	3
67.5°-112.5°	4
337.5°- 22.5°	4
22.5°- 67.5°	5
X3 - Slope angle	Recorded to nearest percent
X4 - Local slope position	
Upper slope to ridge	1
Middle slope	2
Lower slope to draw	3
X5 - Slope form	
Convex	1
Flat	2
Concave	3
X6 - Surface rock	Recorded to nearest 5%
X7 - Balsam woolly aphid disturbance	Recorded to number of years since time of death of fir then coded
0 years (uninfested)	1
0 years (infested, fir not dead)	2
5-6 years	3
7-10 years	4
11-15 years	5
16-20 years	6

TABLE 18 (Continued)

Variable	Code
X8 - Canopy closure	Recorded to nearest 5%
X9 - Total density of overstory	Recorded by absolute number of stems
X10 - Total basal area of overstory	Recorded by absolute basal area of stems
X11 - Total density of saplings	Recorded by absolute number of stems
X12 - Total density of sub-saplings	Recorded by absolute number of stems

TABLE 19

DEPENDENT VARIABLES USED IN CORRELATION AND REGRESSION ANALYSES

Variable Symbol	Variable
Y1	Density of overstory fir
Y2	Total density of overstory
Y3	Basal area of overstory fir
Y4	Total basal area of overstory
Y5	Density of fir saplings
Y6	Total density of saplings
Y7	Density of fir subsaplings
Y8	Total density of subsaplings
Y9	Density of *Rubus*
Y10	Density of *Viburnum alnifolium*
Y11	Density of *Vaccinium erythrocarpum*
Y12	Moss cover (percent)
Y13	*Oxalis acetosella* cover (percent)
Y14	Pteridophyte cover (percent)

VITA

Rex Randall Boner was born September 30, 1950, in Franklin, Indiana. He attended Greenwood Public Schools in Greenwood, Indiana and graduated from Greenwood High School in June 1968. He enrolled at Wabash College, Crawfordsville, Indiana in September 1968 and graduated from that same institution in June 1972 with a Bachelor of Arts degree, biology major.

He entered the Graduate School of The University of Tennessee, Knoxville, in September 1973 as a student in the Ecology Program. While a graduate student, he was a graduate teaching assistant and assisted the Tennessee Valley Authority in environmental assessment and continuous forest inventory research. He has worked for the Tennessee Heritage Program, Tennessee Department of Conservation. He currently is Regional Director of Land Stewardship for The Nature Conservancy. He is a member of the Tennessee Academy of Science, the Association of Southeastern Biologists and the Tennessee Native Plant Society.

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