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Distribution and Characteristics of Balsam Woolly Aphid Infestations in the Great Smoky Mountains

C. Christopher Eagar
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by C. Christopher Eagar entitled "Distribution and Characteristics of Balsam Woolly Aphid Infestations in the Great Smoky Mountains." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Ronald L. Hay, Major Professor

We have read this thesis and recommend its acceptance:

Edward E. C. Clebsch, John C. 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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Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

DISTRIBUTION AND CHARACTERISTICS OF BALSAM WOOLLY APHID INFESTATIONS IN THE GREAT SMOKY MOUNTAINS

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

C. Christopher Eagar

August 1978

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ABSTRACT

The balsam woolly aphid was inadvertently introduced into North America in Maine around 1900 and has subsequently spread throughout the eastern spruce-fir forests. Within the past 20 years the aphid has become a serious pest of Fraser fir in the Southern Appalachians, causing concern for the scenic and scientific resources of the spruce-fir forests. Fraser fir is highly susceptible to attack by the aphid with mortality occurring within 2 to 5 years following colonization. This rapid mortality in combination with the phenomenal reproductive potential of the aphid threatens the existence of Fraser fir. Investigations were conducted within the Great Smoky Mountains National Park to determine the history, current distribution, and level of damage of balsam woolly aphid investations. The relationship of levels of infestations with selected community structure and environmental factors was also investigated.

The balsam woolly aphid arrived in the Great Smoky Mountains around 1960. The initial infestation was on Mt. Sterling, located on the eastern boundary of the spruce-fir distribution within the Park. Analysis of the aerial infrared transparencies revealed that the aphid is distributed throughout the entire spruce-fir forest type. Infestation intensity, as determined by the extent of fir mortality and the size of the infestation, was highest in the eastern portion of the spruce-fir distribution, lower in the middle portion, and lowest in the western portion. Detailed information of the location and size of infestations was recorded on 1:24000 topographic maps.

Permanent plots were located throughout the spruce-fir forests in the Park in areas of varying infestation levels. Sampling was proportional

to the area involved in each level. Low levels of balsam woolly activity were associated with dense, pure, young, even-aged stands of Fraser fir growing on eastern and northeastern aspects at the higher elevations of the spruce-fir distribution within the Park. High levels of aphid activity were more common in less dense, mixed, mature, uneven-aged stands located on western and southwestern aspects at the lower elevational limits of Fraser fir's distribution. Initial infestations occurred at the northern hardwood-fir ecotone and gradually expanded upslope.

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CHAPTER I

INTRODUCTION

Migration of the balsam woolly aphid (*Adelges piceae* Ratz.) into the Southern Appalachian spruce-fir forests has concerned scientists, resource managers, and recreationalists. This pest is a tiny, sucking insect that feeds on the bark of true firs (*Abies* spp.) causing mortality much out of proportion to its size. Fraser fir (*Abies fraseri* (Pursh) Poir.) is easily killed by the balsam wooly aphid, with the time from initial infestation being as little as three years (Amman, 1962). The intensity of the host reaction combined with the phenomenal reproductive potential of the aphid has already created significant changes in the species composition and structure of the Southern Appalachian spruce-fir forests. The existence of Fraser fir is now threatened.

I. SOUTHERN APPALACHIAN SPRUCE-FIR

The Southern Appalachian spruce-fir forests are found at elevations above 1280 meters in a disjunct pattern throughout southwestern Virginia, eastern Tennessee, and western North Carolina (Figure 1-1). Red spruce (*Picea rubens* Sarg.) attains larger size and lives longer than Fraser fir, but Fraser fir grows more rapidly and produces more prolific seed crops. Fraser firs seldom live longer than 150 years and attain a maximum height of 25 meters and diameter of 50 centimeters. Oosting and Billings (1951) found five times as many Fraser fir as red spruce seedlings per 100 square meters. Both species are extremely shade tolerant, and they are capable of resuming normal growth after 50 years of suppression.

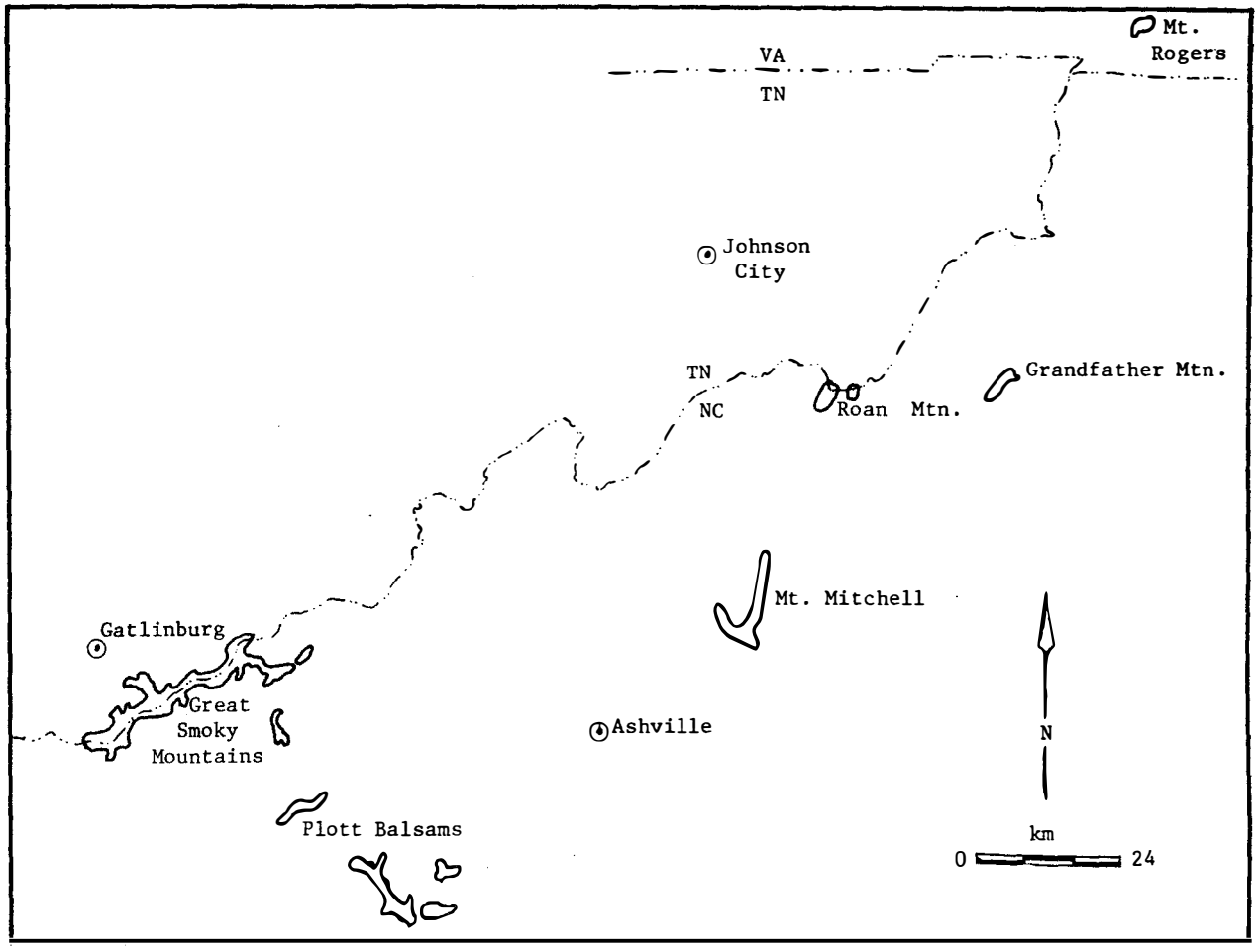

Figure 1-1. Spruce-fir forest type in the Southern Appalachians.

Legend: Spruce-fir type

Fraser fir serves a dual role in the regeneration of the forests at elevations above 1700 meters. First due to its capabilities as a highly shade tolerant species, Fraser fir seedlings and saplings often form a second generation under the existing canopy. When an opening is created in the canopy fir reproduction will respond and grow into the canopy. The second role involves Fraser fir as a pioneer species. When openings are created in the overstory and advanced regeneration is not present, Fraser fir will eventually occupy these openings with dense, vigorous reproduction.

In mature communities red spruce is dominant in the canopy at elevations between 1280 meters and 1700 meters, with fir restricted to intermediate and occasionally codominant crown class status. Between 1700 meters and 1830 meters the mixture of spruce and fir is more uniform, but red spruce decreases in importance in size and stem frequency toward the upper limits of this elevational segment. Above 1830 meters Fraser fir occurs in virtually pure stands (Whittaker, 1956).

II. THE APHID IN NORTH AMERICA

The balsam woolly asphid originated in Europe and was first identified in North America in 1908 on balsam fir (*Abies balsamea* (L.) Mill.) in Maine (Kotinsky, 1916). The insect probably arrived in North America prior to 1900 on imported nursery stock with separate introductions in southern Nova Scotia and Maine (Balch, 1952). Having spread throughout the Maritime Provinces and New England the aphid has caused damage and mortality to balsam fir over thousands of hectares.

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

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

The asphid was discovered within the Great Smoky Mountains National Park in 1963 (Ciesla et al., 1963). The initial infestation was located on Mt. Sterling, 64.4 kilometers, S85° W of Mt. Mitchell in the extreme northeastern end of the spruce-fir type within the Park.

III. STUDY OBJECTIVES

The Great Smoky Mountains National Park encompasses the last, large mountain wilderness in the eastern United States and is especially noted for the great diversity and abundance of plant and animal life found within its boundaries. The spruce-fir forests are unique and contribute significantly to this diversity; they are highly regarded as a scenic and scientific resource.

The balsam woolly aphid is altering these forests in a manner that will have far reaching consequences on all flora and fauna found within the spruce-fir communities. Openings created by the death of Fraser fir will cause dramatic shifts in the species composition and abundance of herbaceous plants. Plants adapted to deep shade will perish; those adapted to direct sunlight will flourish. The added solar radiation will intensify evaporation, causing significant changes in the soil moisture balance, with possible detrimental reperoussions among the living trees and herbaceous plants. Birds and small mammals which feed and nest in the firs will have to undergo major adaptations or perish.

Research on the effect of the environmental and community characteristics on the location and development of balsam woolly aphid infestations can perhaps provide resource managers with the necessary information to slow the damaging impact of this pest. Identification of those characteristics most conducive to aphid attack and those least conducive to attack would be useful in determining how, when, and where to allocate manpower and equipment in an effort to preserve Fraser fir as a component of the Southern Appalachian forests. Accordingly the following study objectives were developed:

(1) Determine the location, developmental pattern, and intensity of balsam wooly aphid infestations in the Great Smoky Mountains National Park (reference 1976 and 1977).

(2) Determine which of the many stand species composition, stand structure, and environmental factors were associated with different levels of balsam woolly aphid infestations.

(3) Establish permanent plots for future analysis of changes within the spruce-fir type of the Great Smoky Mountains National Park.

CHAPTER II

LITERATURE REVIEW

I. BIOLOGY AND ECOLOGY OF THE APHID

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

Life Cycle and Development of Adelges Piceae

The fir adelgids exhibit complex polymorphic life cycles which often include alternation of hosts, with spruce (*Picea* spp.) being the primary host and the true firs (*Abies* spp.) being the secondary host. Sexual reproduction is associated with the primary host and parthenogensis with the secondary host. Throughout its range the balsam woolly aphid

has evolved the capacity to produce successive generations on the secondary host and is not found in the sexual or migrant form in North America.

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

Eggs are oval, light purplish-brown, about 0.4 millimeters long, and are attached behind the stationary parent by a silken thread. As the egg matures the color changes to orange-brown. Emergence occurs at the opposite end of attachment with the larvae emerging head first.

The first instar (neosisten) is the only form capable of initiating movement. This "crawler" is about 0.4 millimeters long with an oval, ventrally flattened body. Upon emerging from the egg, its color is light purplish-brown. Once a suitable feeding site is located the stylet is inserted into the bark and feeding begins. This developing instar becomes purplish-black and small tuffs of wax threads appear on its sides. The insect remains at this location for the rest of its life.

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

The third instar is about 0.65 millimeters long with all other characteristics similar to the second instar.

Adults have a hemispherical body that is slightly longer than it is wide. The color is still purplish-black and the aphid is about 0.8

millimeters long. By this time the wax threads have reached their maximum development and provide easy recognition.

Seasonal Development

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

Hiemosistens. All life-stages from eggs to adults have been observed in late fall; however, only the first instar larvae that have inserted their stylets and become dormant survive the winter. Insect activity begins when the host tree starts its annual growth cycle, but not all aphids begin feeding at the same time. Balch (1952) reported 20 days variation between individuals in the time that aphids broke dormancy on the same tree. Vigorous trees are the first to initiate growth in the spring; therefore, these are the first to show signs of aphid feeding. This is indicated by swelling of the body and the formation of a small, clear drop of honey dew at the anus. In the Southern Appalachians, Amman (1962) found that dormant first instars began feeding as early as April 10 and as late as May 15 during the 1960 growing season.

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

Aestivosistens. Within a few hours of hatching the first instar of the aestivosistens usually finds a suitable feeding site close to the parent. Two or 3 days after the stylet is inserted into the bark, the aphid enters diapause for a duration of 3 to 8 weeks. Fluctuating temperatures are required to break diapause and complete metamorphosis (Atkins, 1972). The adult aestivosistens are less fecund than the adult hiemosistens and produce only about half as many offspring.

Seasonal history. In eastern Canada the balsam woolly aphid has two generations per year (Balch, 1952). However, Bryant (1971) reported that a third generation was completed in crown infestations in Newfoundland, Canada. This generation was comprised of the offspring of progredientes, a usually rare, non-diapause form which develops from the first eggs of the hiemosistentes. Progredientes are not an important factor in the population dynamics of the aphid in other regions of North America.

The greatest intraregional variation in seasonal development is encountered in the Pacific Northwest due to the wide range of elevations and environmental conditions. Four generations were reported for infestations located in the lowlands, three generations were found in the intermediate elevations, and only two generations occurred at the highest elevations (Mitchell, et al., 1961).

In the Southern Appalachians the balsam woolly aphid may have as many as three generations per year but two generations are more common (Amman, 1962).

Factors affecting development. Temperature and humidity are the principle factors that affect the developmental rate of the balsam woolly

Nymphal development can occur between 7° C and 25° C, with a regime of fluctuating temperature in the middle segment of this range being most beneficial for development (Atkins, 1972; Greenbank, 1970). Amman (1970) found that cool temperature and low humidity have an adverse affect on the hatching and subsequent nymphal development. When exposed to these conditions eggs suffer from desiccation. Low temperatures reduce crawler vigor, affecting their ability to locate suitable feeding sites (Atkins and Hall, 1969). Greenbank (1970) found that the duration of oviposition varied inversely with temperature, and low temperature produced the highest fecundities. Other factors such as the physiological condition of the host also affect the reproduction potential of individual aphids.

Reproductive potential. Balsam woolly aphid reproductive rates are influenced by the weather conditions throughout the entire life cycle of the insect, the vigor of the host tree, the amount of protection provided at the feeding site, and the individual aphid. Balch (1952) reported that the hiemosistens averaged about 100 eggs per adult with a maximum of 248 and that the aestivosistens averaged about 50 eggs per adult with a maximum of 105 eggs. With 60 percent survival for both generations the annual population increase approximates 5000.

Behavior of the Aphid

Dispersal. Being wingless and except for the first instar incapable of active travel, the balsam woolly aphid is dependent on passive forms of movement. The principal dispersal vector for the balsam woolly aphid is air currents. Crawlers, and occasionally eggs, are readily transported by wind. Balch (1952) found that they were transported more than 90

meters by surface winds and several kilometers by vertical air currents in eastern Canada. In the mountainous Southern Appalachians, wind has been responsible for the movement of the aphid of distances up to 68 kilometers (Amman, 1966). A more specific evaluation of the role that wind plays in the dispersal and infestation patterns within the Great Smoky Mountains National Park will be presented later.

Atkins and Hall (1969) found that crawlers located on trees around the perimeter of a stand were responsible for the majority of the long distance dispersal of the aphid. Within a stand that has a relatively closed canopy the movement of aphid crawlers is from crown-to-crown or from crown-to-stem, but rarely from stem-to-stem (Greenbank, 1970).

Gravity is an important means by which infestations spread within a stand. It is also the primary manner by which fir seedlings and saplings become infested.

Humans were responsible for the initial introduction of the insect into North America. It is possible that they have also contributed to the further spread of the aphid by movement of nursery stock and Christmas trees. Some may have unknowingly transported crawlers or eggs on clothes or vehicles.

Woods and Atkins (1967) determined that small animals are occasionally responsible for the movement of aphids; however phorsey is not a common method of dispersal.

Activity. Upon hatching aphid crawlers experience a period of wandering the length of which is variable. Tests conducted to determine if this movement is influenced by light or gravity yielded negative results. This wandering period is apparently only a random search for a suitable feeding site (Atkins and Hall, 1969).

Crawlers are capable of moving distances of 100 feet and they can remain active for as long as 8 days. However, they usually settle close to their sedentary parent within 2 or 3 hours of hatching. Temperature influences the length of crawler activity with high temperatures shortening the time that crawlers actively move. Crawlers tend to drop from trees at a higher rate during periods of high temperatures.

Atkins (1972) reported that in laboratory tests groups of crawlers tended to settle more quickly than isolated individuals. Therefore, the spreading process of the aphid may be facilitated by the synchronous dispersal and arrival of aphids. The occurrence of numerous crawlers at the same time is dependent on environmental conditions during the incubation period.

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

The first instar nymph enters diapause following the insertion of the stylet. Prior to diapause a salivary substance secreted from the tip of the maxillae forms a sheath around the stylet. This salivary substance is also secreted during feeding; its probable purpose is the modification of the feeding site in a manner that facilitates the uptake of needed nutrients (Balch et al., 1964).

Ecology and Population Dynamics of the Aphid

Environmental factors. High ambient air temperatures are not fatal to the balsam woolly aphid (Balch, 1952). In fact, consistently

warmer than normal temperatures within a region would benefit the population, because the increased developmental rate induced by the warmer temperature could increase the number of generations per year which would greatly add to the growth of the population. However, high temperatures at the bark surface, caused by direct sunlight on a darkened object, are fatal to the adult and all nymphal stages. The cause of death is desiccation. The second and third instars as well as the adult are afforded some protection from solar radiation by the wool that covers their bodies. Death of aphids due to exposure to direct sunlight is insignificant in terms of overall population dynamics.

Rain can dislodge and wash away eggs. It also mats down the wool and occasionally completely washes it away, increasing the probability of death from desiccation. Aphids are protected from drowning when immersed in water by their wax secretions (Balch, 1952).

Extremely cold temperatures limit population growth in the more northerly lattitudes but is not a factor in the Southern Appalachians. All aphid stages except the overwintering first instar are killed by prolonged exposure to temperatures below 0° C and instantly by temperatures below -20° C (Balch, 1952; Greenbank, 1970). Overwintering first instars require a period of gradual exposure to colder temperatures in order to develop cold-hardiness before they can withstand extremely low temperatures of -25° C to -34° C (Greenbank, 1970). The minimum lethal temperature for the overwintering first instar is -34.4° C. Amman (1967) reported that an overnight temperature of -34° C on Mt. Mitchell, North Carolina caused higher than normal mortality, but there was no indication that significant control of aphid populations would result from these

rare low temperatures in the Southern Appalachians. Under normal weather conditions all aphid stages have adaptations which enhance their survival.

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

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

Applied factors. Lindane will control the balsam woolly aphid; however, it is of little practical use in forest conditions since the bole of the tree must be sprayed from the ground to the point of saturation. Researchers in British Columbia found that Baygon applied as a systemic to the roots along with urea increased mortality by 30 to 50 percent, but only a single generation was affected (Carrow et al., 1977).

Silvicultural treatments used to control aphid populations have included complete removal of host trees and species conversion to something other than fir. Lambert and Ciesla (1967a) determined that cutting

infested trees increased the spread of aphids. This increase was due to the agitation within the stand which caused the release of more aphids than normal into wind currents. The removal of spot infestations is ineffective in slowing aphid spread.

II. REACTION OF THE HOST

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

Microscopic symptoms. Damage to cells is primarily due to chemically-induced injury resulting from salivary secretions by the aphid prior to and during feeding. The saliva produces abnormal cell development around the stylet through either an enzymatic or synergistic action with growth hormones and inhibitors already present in the host tree (Balch et al., 1964). Cortical parenchyma cells are enlarged six or seven times normal, cell walls are thickened, and the cell nuclei become larger. This process is closely followed by hyperplasia in the surrounding parenchyma and the formation of a secondary phellogen, which is the initial stage in the wound-healing process. Not all *Abies* in North America are able to complete this process, whereas European firs, which have evolved with the aphid, are able to effectively seal-off the feeding area before the tree suffers irreversible damage.

The xylem is also affected, even though the stylet usually does not penetrate that far into the tree. The cellular characteristics displayed by the xylem are similar to those of compression wood: short, thick, highly lignified, reddish tracheids; an increase in the number of rays;

checks in the secondary cell walls at a larger angle to the longitudinal axis than normal; a large reduction in the lumen; and the occlusion of pit membranes (Balch, 1952; Doerksen and Mitchell, 1965). *Abies alba* in Scotland did not exhibit these symptoms within the xylem (Varty, 1956).

For North American firs, the combination of the feeding effects on the bark and sylem diminishes the translocation of fluids within the tree. This is the probable cause of tree death.

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

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

Macroscopic symptoms of stem infestations are not outwardly apparent prior to the death of the tree. Characteristics of stem infestations include a brief period of increased diameter growth followed by 1 or 2 years of reduced diameter growth. The tree dies rapidly as manifested by the gradual change in foliage color from healthy blue-green,

to a faded yellow-green, to a bright rusty-red, and finally to dead-brown. The aphid population crashes prior to the completion of change in foliage color (Amman, 1970).

Reactions of North American Abies. Balsam fir suffers both types of attack, with crown infestations occurring in the maritime zones and stem infestations occurring further inland. This variation is apparently due to differences in climatic factors as opposed to insect or host tree factors (Greenbank, 1970).

Bracted balsam fir (*Abies balsamea* var. *phanerolepis* Fern.), indigenous to Virginia, usually experiences crown infestations; whereas stem infestations are associated with Fraser fir in the Southern Appalachians (Amman and Talierico, 1967).

In the Pacific Northwest, firs exhibit marked differences in their reaction to aphid attack. Grand fir (*Abies grandis* (Dougl.) Lindl.) is the most resistant species to attack and can survive stem infestations for 15 years or more. Crown infestations are more common on Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), but stem infestations may also occur. The degree of susceptibility exhibited by Pacific silver fir is related to site quality; trees on poor sites are more tolerant to aphid attack than trees growing on good sites. Subalpine fir (*Abies lasiocarpa* (hook.) Nutt.) is the most susceptible species in the Pacific Northwest, with stem infestations being responsible for tree mortality. Other species of *Abies* native to the Pacific Northwest have not been attacked by the balsam woolly aphid within their natural ranges (Mitchell, 1966).

In all regions of North America young saplings and seedlings exhibit signs of gouting common to crown infestations. Appreciable mortality

occurs only under heavy overstory infestations and recovery of young trees is more common than among mature individuals (Schooley, 1976).

CHAPTER III

METHODS AND PROCEDURES

I. METHODS AND PROCEDURES--1976

Selection of Stand Units

Color infrared aerial transparencies covering areas of potential balsam woolly aphid infestations were provided by the U. S. Forest Service, Forest Insect and Disease Management Division, State and Private Forestry, Asheville, North Carolina in cooperation with the National Park Service in May, 1976. Analysis and procedural organization included:

(1) photo centers were located on 1:24000 T.V.A. topographic quadrangle maps to serve as a reference when transferring features from the transparencies to various maps;

(2) spruce-fir vegetation type was identified and mapped on a separate set of 1:24000 topographic maps;

(3) balsam woolly aphid infestations were located and classified as currently active (hot) or old with most fir trees killed (dead);

(4) the spruce-fir type was partitioned into 11 geographic areas which were subdivided into 224 stand units.

The use of geographic areas permitted the grouping of areas which had experienced similar levels of aphid damage in regards to length of time infested, the size of the infestation, and the degree of damage.

Stand units were used as the bases for sample selection. They were not always defined as distinct biological communities, but they were

determined by topography and accessibility. For example, stand units frequently corresponded to small watersheds containing spruce-fir or followed the spruce-fir distribution onto spur ridges. It was not an objective to provide a cover-type map based exclusively upon community characteristics of species composition and age structure.

Sampling Strategy

The size and intensity of aphid infestations within each stand unit were determined from the aerial photographs and each stand unit was assigned to one of the following infestation classes.

(1) *Active:* fir dead and dying from apparent balsam wooly aphid attack.
   (a) Light: small infested area or scattered affected trees.
   (b) Medium: well-developed infestation with some dead trees in the center.
   (c) Heavy: severe, well-developed infestation with many dead trees in a large total area.

(2) *Dead:* high fir mortality with no "hot" trees (trees just beginning to decline showed bright yellow-green, while dead trees were gray).
   (a) Light: scattered small patches of dead trees, perhaps not caused by balsam woolly aphid attack.
   (b) Medium: larger patches of dead trees.
   (c) Heavy: complete mortality over large areas.

(3) *None:* no evidence of balsam woolly aphid infestation.

Sample selection of stand units was made at random from each infestation category proportional to the total possible stand units.

Plot Location

Six plots were established in each stand unit. The location of each plot was determined before entering the field by analysis of the aerial transparencies and topographic maps; plots were selected to represent the various topographic, vegetational, and balsam woolly aphid infestation conditions. Plot locations were indicated on topographic maps for the purpose of relocation of the plots for future analysis.

In the field, four witness trees were marked with numbered aluminum tags, positioned about 1 meter above ground facing plot center. The bearing and distance from plot center to each witness tree were recorded. Descriptive photographs of each plot were taken. When applicable photographs were taken of distinctive features on the trail or in the stand to define plot location.

Plot Evaluation

Plot size was 10 meters square with plot diagonals aligned north-south and east-west. The following characteristics were evaluated on each plot.

(1) *Species composition and diameter frequency:* frequency of all trees greater than 1 centimeter at 1.37 meters above ground was recorded by 1 centimeter diameter class. A metric diameter tape was used.

(2) *Slope:* percent slope was measured with an Abney level.

(3) *Aspect:* compass bearings at right angles to the contour were made from plot center.

(4) *Elevation:* contour lines on a 1:24000 topographic map were used to estimate plot elevation.

(5) *Aphid infestation rating:* each fir tree was classified as to aphid infested, uninfested, plus healthy, dying, or dead. Aphid presence was determined at 1.37 meters above ground. Health evaluations were based upon crown color.

(6) *Occurrence of past disturbance:* the type and extent of past distrubances, predominantly man-oriented, were recorded. Types included logging, fire, multiple-tree blowdown, or other means of initiating secondary succession within the community. Plots were classified as either disturbed or not disturbed.

(7) *Seedling counts:* Counts were made on 4, 1 meter square subplots located in the corners of the plot for descriptive purposes only.

(8) *General description:* each plot and its surrounding area were described subjectively to typify the Fraser fir community. Information included a subjective estimate of balsam woolly aphid activity and damage, general stand structure and species composition, and the dominant ground cover.

II. METHODS AND PROCEDURES--1977

Observations made during the 1976 field season indicated that balsam woolly aphid infestations occurred first at the northern hardwood-fir ecotone and spread toward the summit. To investigate this relationship,

changes in sample selection and plot location were implemented during the 1977 field season; plots were located along elevational transects at right angles to the contours.

Sample Selection

Sample selection was restricted to selected mountains that offered the greatest elevational change within the distribution of Fraser fir. In addition to insuring an adequate range of species composition and stand age structures, mountains were selected throughout the spruce-fir zone in the Great Smoky Mountains National Park to obtain a representative sample of length of infestation time. Mountains sampled were Big Cataloochee, Mount Guyot, Mount LeConte, Mount Mingus, and Clingmans Dome.

Big Cataloochee has been exposed to balsam woolly aphid infestations for the maximum time, while Clingmans Dome has only recently been infested at the lower elevations of fir. Therefore, this selection of mountains provided for the study a aphid infestations over their entire developmental sequence.

Transect and approximate plot locations were drawn on the topographic maps prior to field sampling. Each mountain was sampled as representatively as possible: aspect, slope steepness, stand species structure, and spur ridge location were all considered.

Plots were located at 60 meters elevational intervals along the transects, being measured on topographic maps and in the field. A pocket altimeter was used to substantiate the elevation of each plot.

Plot Evaluation

Plot evaluation was accomplished as in 1976 with the exception of the following modifications.

Aphid population levels. Results of studies conducted on Mount Mitchell, North Carolina by Amman (1969) determined that measurement of aphid population levels at breast height (1.37 meters) adequately represented the variation in infestation intensities between individual trees. An adaptation of the method used by Amman was utilized for the study. Levels were assigned to each fir tree on each plot based on the maximum density of aphid observed within a 2.54 X 2.54 centimeter square at breast height. Each tree was placed into one of five aphid population categories:

(1) no aphids,

(2) less than four wool masses per square,

(3) four masses per square to 25 percent covered,

(4) more than 25 percent covered, or

(5) death of the host from aphid attack (aphids were no longer present).

Seedling counts. During the 1977 field season, seedling counts were made on a 1 meter wide randomly located strip across the plot. Strip alignment was consistent on each plot. Seedling heights, by species, were categorized as follows: less than 15 centimeters, 50 centimeters, 100 centimeters, 150 centimeters, 200 centimeters, or 250 centimeters.

III. DATA ANALYSES

Adjustments to the Data Sets

Prior to analysis two adjustments in the data were necessary. Aphid population level estimates made during 1976 and 1977 were made consistent in order to compare analyses. The second data adjustment concerned how aphid population levels were to be expressed in the analyses. Aphid population levels were assigned to individual trees in the field, but analysis was based on the plot as the observation unit. To accomplish this transition the sum of diameters within each aphid population level on a per plot basis was used. That is, for each plot the diameters of all trees within the first aphid population level, representing uninfested trees, were added together and this total, along with the totals for the other four categories, gave a quantitative expression of the degree of aphid activity on that plot. Diameter was used instead of number of stems or basal area because diameter, being directly related to circumference, better represented the surface area available to the aphid for feeding.

Statistical Methods

Variables used in analyses were grouped into those representing the environmental factors and those representing the community factors. The environmental factors included:

(1) elevation,

(2) slope,

(3) aspect (coded: 1-N, 2-NE, 3-E, 4-SE, 5-S, 6-SW, 7-W, 8-NW),

(4) presence or absence of disturbance (coded: 1-not disturbed and 2-disturbed), and

(5) geographic area (coded with 1 in the northeast and 11 in the southwest).

The community factors included:

(1) the percentage of Fraser fir and the percentage of red spruce, based on sum of diameters, as expressions of species composition,

(2) the mean diameter of Fraser fir, red spruce, and all trees as expressions of size and relative age class, and

(3) stand density as measured by the total sum of diameters of all trees on each plot.

Canonical correlation analyses were used to determine which community and environmental factors were associated with the various aphid population levels and stages of infestation development. Canonical correlation is a form of multivariate analysis that enabled determination of the degree of relationship between two groups of variables. This was accomplished through two linear combinations of coefficients (weights), such that the Pearson product-moment correlation between the two groups of variables was as large as possible. Additional combinations of coefficients were calculated as long as the new combination was uncorrelated with previous combinations. There can be as many linear combinations as the minimum variables in either group. However, each subsequent linear combination accounted for less variation between the two groups of variables. These linear combinations were called "canonical variables."

Two primary statistics were calculated through canonical correlation analysis. The first statistic consisted of a between group correlation coefficient (canonical-R) showing the overall strength of the relationships

found for that grouping of linear combinations (canonical variables). The canonical-R for each new linear combination of the variables was lower than the preceding one. These correlation coefficients were tested for significance with Chi-square at the probability of 1 percent. The second statistic was the within group correlation coefficient which expressed the degree of relationship between the variables within the two groups. These coefficients also represented how the variables in the first group were related to the variables in the second group. (Harris, 1975).

For this study one group of variables was composed of the aphid population levels expressed as the sum of diameters within each category and the other group consisted of the community and environmental factors. The aphid population levels were compared with the community and the environmental factors combined and with them independent of each other. Separate analyses were performed to reduce the random variability when all factors were grouped together, thereby identifying realistic relationships between the aphid and its host.

Separate analyses were accomplished with the following data:

(1) the 1976 data--84 plots total,

(2) the 1977 data--47 plots total,

(3) the 1976 and 1977 combined data--131 plots total, and

(4) the combined 1976 and 1977 data from the western geographic area--81 plots total.

The western portion of the spruce-fir type, i.e., the Clingmans Dome area, the Mt. LeConte area, and the Mt. Kephart area, represented the most recently infested portion of the Park. Separate analyses of these areas provided a determination of the factors associated with the

earliest stages of balsam woolly aphid infestation activity. Therefore, a total of 12 canonical correlation analyses were accomplished; three groupings of the community-environmental factors within each of four groupings by year and location.

Canonical correlation analyses were not solely sufficient to identify the relationships between aphid infestation levels and the community and environmental factors. For example, was the correlation between a particular aphid infestation level and the percentage of fir in that community real or was it due to the correlation of the community structure at that elevation and the aphid population level? These interrelationships were tested using standard correlation analyses to produce a correlation matrix of the community and environmental factors.

Data were summarized by species and aphid population level categories on a WANG 720 C calculator. Canonical correlation analyses and standard correlations were performed on an IBM 360/65 computer using Statistical Analysis Systems programs (Barr et al., 1972; Barr et al., 1976).

CHAPTER IV

RESULTS

I. DISTRIBUTION OF THE BALSAM WOOLLY APHID IN THE GREAT SMOKIES

The balsam woolly aphid was distributed throughout the spruce-fir vegetation type in the Great Smoky Mountains National Park. Plate 4-1 in the attached map pocket presents the aphid distribution as of July, 1977. The earliest infestations were on Mt. Sterling and from that locus the insect has spread throughout the available host range. Fraser fir mortality was most severe in the eastern portion of the Park with varying amounts of mortality occurring throughout the remaining host distribution. That the aphid was intermediate in its chronological development and range expansion within the Great Smoky Mountains provided an excellent opportunity to study those factors associated with aphid infestations in Fraser fir.

Mt. Sterling Gergraphic Area

The Mt. Sterling Geographic Area extended from Mt. Sterling southwest along Mt. Sterling Ridge to Big Butt. Nearly 100 percent of the fir within the canopy had been killed by the aphid. Along Mt. Sterling Ridge near the junction with Mt. Sherling Gap Trail, there were two living, infested firs that probably owed their continued presence to their open-grown habit; full, broad crowns extending nearly to the ground provided added vigor which extended their lives. A dense, even-aged patch of small, pole-sided fir located on top of Big Butt showed no mortality, but ground checks confirmed aphid presence on some trees.

Big Catloochee Geographic Area

Being contiguous with the Mt. Sterling Area on the east, the Big Cataloochee Geographic Area extended along the Balsam Mountains northwest to Tricorner Knob and south to near Beech Gap. Fir mortality was near maximum along the lower slopes of the Balsam Mountains; however some individuals remained alive and infested along the ridge-line. Balsam woolly aphid development on Mt. Hardison was apparent from the summit of Mt. Guyot.

Heintooga Geographic Area

The Heintooga Geographic Area was not contiguous with the Cataloochee Area, extending further south along the Balsam Mountains from Spruce Mountain to Polls Gap. Fir mortality was extremely heavy in the Spruce Mountain portion of the area, and balsam woolly aphids have infested most of the fir stands at the lower elevations throughout the entire area.

Mt. Guyot Geographic Area

The Mt. Guyot Area was bounded on the northeast by Camel Hump Knob, and on the southeast by Tricorner Knob; Greebrier Pinnacle and Guyot Spur on the Tennessee side of the State-Line Ridge were included. Fir mortality was observed throughout the lower elevations with the heaviest damage on the Tennessee side of Old Black, Inadu Knob, and Snake Den Mountain. Heavy mortality was observed in the Ramsey Prong Drainage during the 1977 field season, although very little mortality or indication of aphid presence was observed there either on the aerial photographs or during ground checks in 1976. Mt. Guyot at 2018 meters elevation is the

most prominent peak in the area, and it was ringed with balsam woolly aphid infestations on all sides to about 1950 meters elevation. Aphids were observed on a single fir located at the very summit of Mt. Guyot but careful checks surrounding it failed to locate additional infested trees.

One plot at 1950 meters on the west slope of Mt. Guyot contained two suppressed trees that had an isolated balsam woolly aphid on each stem. These trees were growing subordinate to a large dominant which had probably intercepted aphids moving on upslope winds.

Dashoga-Hyatt Ridge Geographic Area

This area extended from Mt. Hardison near Tricorner Knob south along Dashoga and Hyatt Ridges, the two prominent ridges in the area, to approximately Hyatt Bald at 1571 meters elevation. With high aphid populations, fir mortality was most severe in the southern portion of this area, i. e., around Breakneck Ridge. Mortality was most prominent at the lower elevations throughout the entire area.

Mt. Sequoyah Georgraphic Area

The Mt. Sequoyah area extended along the State-Line Ridge from Tricorner Knob to Eagle Rocks. The size of the infestations in this area was smaller than in previous areas and fir mortality was less pronounced. The largest infestations were located south of the State-Line Ridge between Mt. Sequoyah and Mt. Chapman. The aphid was distributed throughout the lower portion of the fir range in this location, but had not yet reached the top of the ridge. Mortality was restricted to the lower elevations of the State-Line Ridge; balsam woolly aphid infestations were widely scattered along the hardwood-fir ecotone.

Hughes Ridge Geographic Area

The Hughes Ridge Geographic Area was entirely within North Carolina, extending from Pecks Corner on the State-Line Ridge south encompassing the entire range of Fraser fir in that locality. Due to the prevalent lower elevations (generally less than 1676 meters), there were few pure stands of Fraser fir. Interpretations of aerial transparencies were more difficult. However, ground checks revealed that most of the fir located along the hardwood-fir ecotone had already been killed by the aphid. There were many small infestations scattered throughout, with one large infestation on Katalsta and Bulldie Ridges.

Laurel Top Geographic Area

The Laurel Top Geographic Area extended southwest along the State-Line Ridge from Pecks Corner to Charlies Bunion. Pure fir stands were infrequent in this area, being found only on the summit of Laurel Top and Porters Mountain. The southern portion of this area had only two small infestations, located about 800 meters east of Laurel Top and just below the State-Line Ridge. The northern portion of the area had many small, scattered infestations just above the hardwood-fir ecotone that contained dead fir trees. A ridge north of Laurel Top, known as Woolly Tops Mountain, contained the heaviest aphid infestations in this area.

Mt. Kephart Geographic Area

This area was bounded by Charlies Bunion on the northeast and Newfound Gap on the southwest, crossing the Boulevard between Anakeesta Knob and the Jumpoff. Heavy infestations of moderate size were located

south of Masa Knob and along the ridge south and east of Icewater Springs. There was some fir mortality in these infestations and they were confined to the lower edges (less than 1646 meters) of the spruce-fir type. Numerous and smaller infestations were distributed on both the north and south sides of the State-Line Ridge between Mt. Ambler and Newfound Gap. These infestations were mostly restricted to the hardwood-fir ecotone. The aphid was observed along the State-Line Ridge during the 1977 field season; some trees at Newfound Gap were heavily infested.

Mt. LeConte Geographic Area

Because of its unique geographic placement and stage of aphid infestation development, Mt. LeConte provided excellent study opportunities; the entire mountain is located north of and connected to the State-Line Ridge by the Boulevard which provided a continuous band of Fraser fir between Mt. Kephart and Mt. LeConte.

Mt. LeConte was completely encircled by isolated infestations of varying sizes. The largest infestations were located on the north side of the mountain. These infestations were no longer restricted to the lower elevations where most of the fir had already been killed, but they were found as high as 1829 meters. Infestations south and east of the summit were small and widely scattered, with only a few dead firs.

Several of the large Fraser firs landscaping the Mt. LeConte Lodge were found to be infested in July 1977. Careful ground checks at that time did not reveal additional infestations; however, by November more aphids were on the previously infested trees plus numerous other trees surrounding the Lodge were found to support isolated but frequent aphids. This area was situated at the head of a long, deep valley which serves to

funnel air currents toward the summit, thereby providing a ready invasion mechanism for balsam woolly aphids to the summit of Mt. LeConte.

Clingman Dome Geographic Area

At the time of aerial photography, this area showed little indication of balsam woolly aphid activity. Consequently it was designated from Newfound Gap to Silers Bald including the various spur ridges from Mt. Collins and Clingmans Dome.

Aerial transparencies showed several small scattered infestations along some of the spur ridges; e.g., Forney Ridge off Clingmans Dome and Loggy Ridge from Mt. Buckley. Extensive ground checks revealed numerous and large infestations in these areas. In most cases, known infestations in the Clingmans Dome area were at the hardwood-fir ecotone; however some infestations have spread almost to the State-Line Ridge along Mingus Lead and along Big Slick Ridge. A large infestation with severe fir mortality was located on Noland Divide. This infestation was still below 1768 meters in the 1977 field season. Balsam woolly aphids were not found on the summit of the Dome during November 1977.

II. CHARACTERISTICS OF APHID INFESTATIONS

Canonical correlation analyses results are presented in Tables 4-1 through 4-4. The standard correlation analysis used to clarify the interrelationships identified by the canonical correlation analysis is presented in Table 4-5. Due to the analysis techniques utilized in these experiments the results will be presented and discussed in terms of "typical" communities. These typical communities represent a composite,

Table 4-1. Canonical Correlation Coefficients for Balsam Woolly Aphid Populations (1976 and 1977) Throughout the Spruce-fir Type in the Great Smoky Mountains (131 plots).

CANONICAL VARIABLE	ALL FACTORS #1	ALL FACTORS #2	ENVIRONMENTAL FACTORS ONLY #1	ENVIRONMENTAL FACTORS ONLY #2	COMMUNITY FACTORS ONLY #1
CANONICAL R	.970	.581	.656	.512	.966
Aphid Population Levels					
APOP 1	.565	-.757	.893	-.302	.579
APOP 2	.400	.411	.118	.483	.391
APOP 3	.226	.520	-.129	.430	.224
APOP 4	.124	.039	-.041	-.135	.132
APOP 5	.116	.825	-.341	.769	.096
Environmental Factors					
Elevation	.588	-.490	.979	.122	
Slope	-.183	-.016	-.223	-.184	
Aspect	-.035	.328	-.201	.293	
Disturbance	-.201	.301	-.129	-.532	
Geo. Area	-.212	-.652	.018	-.863	
Community Factors					
Percent Fir	.708	-.137			.713
Percent Spruce	-.509	.199			-.513
Stand Density	.631	.119			.631
Mean DBH Fir	-.128	.255			-.132
Mean DBH Spruce	-.204	.072			-.204
Mean DBH All	-.241	.224			-.245

Table 4-2. Canonical Correlation Coefficients for Balsam Woolly Aphid Populations (1976) Throughout the Spruce-fir Type in the Great Smoky Mountains (84 plots).

CANONICAL VARIABLE	ALL FACTORS #1	ALL FACTORS #2	ENVIRONMENTAL FACTORS ONLY #1	ENVIRONMENTAL FACTORS ONLY #2	COMMUNITY FACTORS ONLY #1
CANONICAL R	.974	.619	.639	.439	.869
Aphid Population Levels					
APOP 1	.658	-.618	.912	.140	.653
APOP 2	.371	.348	.065	.364	.411
APOP 3	.202	.104	.007	-.080	.208
APOP 5	-.132	.912	-.765	.579	-.157
Environmental Factors					
Elevation	.507	-.558	.941	.226	
Slope	-.025	.110	-.107	.146	
Aspect	.115	.295	-.094	.503	
Disturbance	-.184	-.199	-.077	-.582	
Geo. Area	-.004	-.541	.354	-.466	
Community Factors					
Percent Fir	.628	-.242			.669
Percent Spruce	-.357	.376			-.469
Stand Density	.684	.265			.751
Mean DBH Fir	-.225	.105			-.252
Mean DBH Spruce	-.055	-.079			-.064
Mean DBH All	-.330	.060			-.365

Table 4-3. Canonical Correlation Coefficients for Balsam Woolly Aphid Populations (1977) Throughout the Spruce-fir Type in the Great Smoky Mountains (47 plots).

CANONICAL VARIABLE	ALL FACTORS #1	ALL FACTORS #2	ENVIRONMENTAL FACTORS ONLY #1	ENVIRONMENTAL FACTORS ONLY #2	COMMUNITY FACTORS ONLY #1
CANONICAL R	.979	.680	.704	.660	.971
Aphid Population Levels					
APOP 1	.382	.858	.771	-.536	.471
APOP 2	.420	-.538	-.011	.451	.343
APOP 3	.328	-.697	-.055	.725	.262
APOP 4	.172	-.237	-.278	-.036	.141
APOP 5	.377	-.644	.039	.707	.321
Environmental Factors					
Elevation	.529	.577	.962	-.114	
Slope	-.265	.002	-.422	-.279	
Aspect	-.263	-.484	-.431	.415	
Disturbance	-.363	.542	-.321	-.830	
Geo. Area	-.451	.448	-.447	-.759	
Community Factors					
Percent Fir	.710	.229			.730
Percent Spruce	-.599	-.186			-.616
Stand Density	.627	-.115			.620
Mean DBH Fir	-.019	-.299			-.033
Mean DBH Spruce	-.310	-.216			-.330
Mean DBH All	-.192	-.273			-.204

Table 4-4. Canonical Correlation Coefficients for Balsam Woolly Aphid Population Levels (1976 and 1977) in the Western Geographic Areas of the Great Smoky Mountains (81 plots).

CANONICAL VARIABLE	ALL FACTORS #1	ALL FACTORS #2	ENVIRONMENTAL FACTORS ONLY #1	ENVIRONMENTAL FACTORS ONLY #2	COMMUNITY FACTORS ONLY #1
CANONICAL R	.959	.683	.729		.956
Aphid Population Levels					
APOP 1	.687	-.704	.981		.688
APOP 2	.127	.679	-.396		.123
APOP 3	.025	.638	-.462		.015
APOP 4	.218	.285	-.082		.218
APOP 5	-.001	.709	-.537		.004
Environmental Factors					
Elevation	.495	-.769	.972		
Slope	-.205	.231	-.348		
Aspect	-.188	.345	-.411		
Disturbance			.012		
Community Factors					
Percent Fir	.624	-.154			.626
Percent Spruce	-.395	.282			-.397
Stand Density	.577	.168			.579
Mean DBH Fir	-.156	.288			-.156
Mean DBH Spruce	-.091	.188			-.092
Mean DBH All	-.247	.271			-.247

Table 4-5. Correlation Matrix of Environmental/Community Factors

	Elev.	Slope	Aspect	Distur.	Geo. Area	% Fir	% Spruce	Mean DBH Fir	Mean DBH Spruce	Mean DBH All	Stand Density
Elevation	1.00	-0.29*	-0.18	-0.06	-0.15	0.61*	-0.43*	0.03	-0.10	-0.02	0.15
Slope		1.00	-0.03	0.09	0.08	-0.22	0.16	-0.08	0.10	0.01	-0.10
Aspect			1.00	0.00	0.07	-0.04	0.09	0.16	0.19	0.23*	0.00
Occurrence of Disturbance				1.00	0.21	0.05	0.09	-0.10	0.11	0.02	-0.26*
Geographic Area					1.00	-0.10	0.07	-0.16	0.05	-0.16	-0.13
Percent Fir						1.00	-0.77*	0.18	-0.33*	-0.04	-0.09
Percent Spruce							1.00	-0.26*	0.51*	0.01	0.13
Mean DBH Fir								1.00	-0.07	0.73*	-0.35*
Mean DBH Spruce									1.00	0.28*	0.06
Mean DBH All										1.00	-0.29*
Stand Density											1.00

*Significant at $\alpha = 0.01$.

as determined by analysis, according to the various balsam woolly aphid population levels and community-environmetnal factors. Cognizance must be taken that a specific community is not being described, rather a typical community as defined by analyses.

Aphid population levels (APOP) as coded in the field were used in analysis to define "typical stands" as follows.

(1) The typical uninfested stand was based on a very strong positive APOP-1 correclation with the other APOP levels very weakly and/or negatively correlated.

(2) The typical slightly infested stand was based on a medium to strong positive APOP-1 correlation coefficient with the other APOP levels moderately to weakly, directly correlated.

(3) The typical moderately infested stand was based on either a strong positive APOP-2 or APOP-3 correlation coefficient in association with weak APOP-5 and APOP-1 correlation coefficients.

(4) The typical heavily infested stand was based on very strong positive APOP-5 correlation coefficient with APOP-2, APOP-3, and APOP-4 directly correlated and APOP-1 strongly negatively correlated.

Similar trends occurred in all analyses comparing aphid population levels and community-environmental factors. Therefore "typical" communities are described with confidence in their reality, although no such community existed. The most significant characteristic is presented first followed in decreasing order to the least significant.

Typical Uninfested Stand

The typical uninfested stand was identified in 6 of 12 analyses and it was best characterized according to these community-environmental factors.

Elevation. Uninfested stands were strongly correlated with the higher elevations of spruce-fir type within the Great Smoky Mountains (above 1768 meters).

Percent Fraser fir. Uninfested stands were associated with communities containing at least 60 percent Fraser fir.

Stand density. Communities with a high stand density were associated with uninfested stands. Fraser fir is capable of growing in very dense communities.

Aspect. Eastern aspects (NE, E, and SE) were more likely to support uninfested stands than other aspects.

Geographic area. Uninfested stands were moderately correlated with the western portion of the spruce-fir type in the Park. There were no uninfested stands in the eastern portion of the Park, characterized by the Balsam Mountains and Mt. Guyot areas. There were some uninfested stands on Mt. LeConte, Mt. Kephart, Porters Mountain, and Clingmans Dome.

Percent red spruce. Uninfested stands did not contain more than 25 percent red spruce.

Slope. Slopes below 35 percent grade were more likely to support uninfested stands than steeper slopes.

Mean diameter all trees. Regardless of species composition, uninfested stands were more likely to be comprised of trees less than 15 centimeters in diameter than larger trees.

Fraser fir diameter. Fir communities comprised of trees less than 14 centimeters in diameter were more likely to be uninfested than infested. Stands composed of larger Fraser firs experienced higher aphid population levels.

Typical Slightly Infested Stand

Slightly infested stands were identified by 4 of the 12 canonical correlation analyses. The trends were similar to that previously discussed with uninfested stands.

Stand density. Slightly infested stands were strongly correlated with high stand density, as expressed by the sum of diameters for all trees on each plot. Values ranged from 59 to 621 total centimeters of diameter; the mean was 287 centimeters per plot. Stands of high density were characterized by more than 300 total centimeters of diameter per 100 square meters of ground surface.

Percent Fraser fir. Slightly infested stands, in addition to being dense, were comprised of greater than 60 percent Fraser fir.

Elevation. Slightly infested stands were only moderately correlated with the high elevations (greater than 1768 meters) in the spruce-fir type. Progressively lower elevations revealed higher percentages of balsam woolly aphids.

Percent red spruce. There was some indication that slightly infested stands were comprised of less than 25 percent red spruce. This trend was not strongly developed, however.

Diameter of all trees. There was only a weak correlation between slightly infested stands and those containing trees less than 15 centimeters in diameter, regardless of species composition.

Fraser fir diameter. In contrast to uninfested stands, there was only a weak correlation between slightly infested stands and Fraser fir communities comprised of fir less than 15 centimeters in diameter.

Typical Moderately Infested Stand

Combinations of aphid population levels and community-environmental factors that would identify typical moderately infested stands were not statistically significant in any of the canonical correlation analyses. Our system of field coding individual trees and plots probably made this category difficult to isolate in the analysis. Aphid behaviour and aphid/host interaction are such that a moderately infested stand is short lived in the field.

Typical Heavily Infested Stand

Typical heavily infested stands were identified by six analyses. The following characteristics were associated with these stands.

Geographic area. Heavily infested stands were strongly correlated with geographic area. Communities located within the eastern geographic areas: Mt. Sterling, Big Cataloochee, and Mt. Guyot were heavily infested and predominately comprised of dead fir and a few live spruce. Those stands located in the western portion of the Park were not heavily infested. Those patterns were described previously.

Elevation. Heavily infested stands were strongly correlated with elevations less than 1768 meters. Only in those geographic areas exposed to the aphid for the longest periods were stands heavily infested at high elevations. Undoubtedly this reflects future trends in the remaining stands, however.

Aspect. Heavily infested stands were more likely to be found on the western to northern aspects than on any other. Uninfested stands were on eastern and southeastern aspects.

Occurrence of disturbance. Heavily infested stands were moderately correlated with areas that had had some form of disturbance, predominantly by logging, fire, or extensive windfall.

Fraser fir diameter. Those communities containing large fir trees (greater than 15 centimeters) were slightly correlated with heavily infested stands. These results substantiate those found in a related study (Johnson, 1977).

Diameter of all trees. Regardless of species composition heavily infested stands were more likely to contain large trees (larger than 15 centimeters diameter) than uninfested stands. Large trees are excellent interceptors of air-borne aphids.

Percent red spruce. Heavily infested stands were weakly correlated with communities containing a high percentage of spruce (greater than 40 percent).

Slope. Slopes greater than 50 percent were weakly correlated with heavily infested stands. Uninfested stands occurred on lesser slopes and at higher elevations, i.e., along ridges and summits.

Summary of Community-Environmental Factors

Several trends developed when the five balsam woolly aphid population levels were categorized by community-environmental factors. The important environmental relationships were elevation, aspect, and geographic area. The significant community factors were stand density, the proportion of Fraser fir in relation to red spruce, and tree size.

Environmental factors. The relationship between elevation and the level of balsam woolly aphid activity was important in all cases and was the strongest relationship found. Balsam woolly aphid infestations began at the hardwood-fir ecotone and progressed upslope. The most intense aphid populations were associated with the hardwood-fir ecotone and few aphids were found at the highest elevations. This pattern was most apparent on Mt. LeConte and along the State-Line Ridge from Newfound Gap to Clingmans Dome where light infestation levels existed.

All new infestations were located at the hardwood-fir ecotone. Older infestations that had progressed upslope had many more dead trees at the lower elevations than upslope. This pattern was also evident in older infestations found in the eastern portion of the Park. The aphid had killed most of the fir on Mt. Guyot and Big Cataloochee with the exception of some remnant Fraser fir stands at the highest elevations. The degree of fir deterioration was greatest at the hardwood-fir ecotone and less on the summit.

Aspect had an influence on aphid infestation patterns. Western aspects (NW, W, and SW) supported the heaviest infestations and eastern aspects (NE, E, and SE) had uninfested communities. This trend was most apparent in the Mt. LeConte and Clingmans Dome areas. The eastern portion of the Park did not exhibit this trend because the aphid had completely surrounded the mountains.

The correlation between aphid population and geographic area was related to the aphid history within the Park. The initial infestation within the Park was on the northwest slope of Mt. Sterling located on the eastern boundary of the spruce-fir distribution with in the Park.

During the following years the aphid gradually spread southwestward, becoming established throughout the entire spruce-fir type. This correlation was of a temporal nature and not because trees in the western geographic areas were less susceptible to the aphid than trees in the eastern areas.

Community factors. Community structure, as described by stand density, the amount of Fraser fir and red spruce, and the size of all trees influenced aphid infestations. Young, dense Fraser fir stands appeared less susceptible to balsam woolly aphid attack than older and more open stands. This condition was most noticeable on Big Cataloochee, which had a minimum of 15 years of aphid activity. On the summitt (1866 meters) there are three separate patches of Fraser fir, two of which are young and dense and the third consists of slightly older trees with less uniform structural characteristics. The young, dense patches were aphid free but the older patch was showing signs of aphid attack around the perimeter. The larger dominant and codominant Fraser firs in the surrounding stands had long been dead. Similar conditions were also found in the Heintooga Geographic Area, particularly on Cataloochee Balsam.

CHAPTER V

DISCUSSION

I. APHID CHRONOLOGY IN THE SOUTHERN APPALACHIANS

Balsam woolly aphids were first confirmed in the Southern Appalachians on Mt. Mitchell, North Carolina, in 1957 (McCambridge, 1958). The entire 3000 hectares of Fraser fir type were infested at the time of discovery (Nagel, 1959), indicating a long history of balsam woolly aphids on Mt. Mitchell.

Balsam woolly aphids could not have chosen to invade a better peak in order to further their population expansion. Mt. Mitchell, the tallest peak in the East, is centrally located to all Fraser fir in the Southern Appalachians. The Black Mountains, of which Mt. Mitchell is a part, have a north-south orientation in an otherwise southwest-northeast oriented chain. Therefor, Mt. Mitchell is a distinctively tall peak in a continuum of tall peaks. This geography when combined with wind movement for maximum geographic effect, insured abundant aphid dissemination throughout the region.

Balsam woolly aphids were detected in 1962 on Roan Mountain (Ciesla and Buchanan, 1962), which is located 32 kilometers N 15° E. of Mt. Mitchell. Grandfather Mountain was found to have aphids in 1963; it is 48 kilometers N 50° E from Mt. Mitchell. The same year, aphids were found on Mt. Sterling which is 72 kilometers S 85° W of Mt. Mitchell (Ciesla et al., 1963). In subsequent years balsam woolly aphids have been found in all Fraser fir associations except the one on Mt. Rogers in Virginia.

Wind was the probable vector of aphid dissemination from Mt. Mitchell to the other Fraser fir communities. Amman (1966) reported that, even though the prevailing winds were from the northwest in this region, there was enough variation in wind direction during the months when aphids were mobile to allow their dissemination in all directions. The combination of moderate to high wind speeds, the orographic and convectional uplifts encountered in mountainous regions, and the light weight of aphid eggs and crawlers enable the aphid to remain aloft sufficiently long to be carried the distances required. For example, weather records (Amman, 1966) showed at least one period with 56 kilometers per hour winds blowing from Mt. Mitchell toward Mt. Sterling during the suspected time of initial attack within the Great Smoky Mountains National Park.

Within the Park

The early years. The initial infestation within the Great Smoky Mountains National Park was on Mt. Sterling Ridge, about 1.6 kilometers north of the summit. When discovered, the infestation covered an area approximating 600 meters long by 150 meters wide. There were 45 trees already dead or dying (Ciesla et al., 1963). Rotholz analyses (Doerkson and Mitchell, 1965) of the dying trees revealed that the aphid had been present, albeit undetected, prior to 1958. The exact attack date could not be confirmed.

An attempt to contain the aphid within the original infestation was initiated by the National Park Service during September 1963 and continued the following summer. All fir trees in the infested area were cut; since

the aphid is an obligate parasite, death of the tree caused the death of the aphids. Ground checks in October 1964 showed that aphids had colonized an additional 16 hectares. These pests were either more widely distributed than originally thought or stem and crown agitation from cutting facilitated their spread. Containment efforts were discontinued when it was realized that failure was imminent.

During 1964, 7 separate, small infestations containing 50 trees with stem infestations were found south of Butt Mountain, which is a spur ridge leading southeast from Big Cataloochee (Ciesla et al., 1965). There were other stands of Fraser fir between Butt Mountain and Mt. Sterling, but their distribution was not contiguous. Fires and logging during the early twentieth century on both sides of Mt. Sterling created patchy patterns of Fraser fir in this area. It appeared that the aphid had jumped some of the Fraser fir stands near Pretty Hollow Gap between these two mountains. This was an early indication of how the insect was going to encircle much of the fir type before merging adjoining infestations. There was not the need to spread from one stand into another along a contimuum. These leapfrog dissemination patterns would speed aphid population expansion within the Great Smoky Mountains National Park.

By 1965, balsam woolly aphids had colonized the entire northwest slope of Mt. Sterline and some had reached the summit (1780 meters elevation). It would take several years to kill all the fir on the summit. New mortality was not detected within the Butt Mountain infestations, but the number of living, infested trees increased. During 1965 no new areas of infestation were observed (Lambert and Ciesla, 1966).

Aphids were detected on the southeastern slopes of Mt. Guyot, at the headwaters of Big Creek in 1966. This first Mt. Guyot infestation was located at the northern hardwood-fir ecotone, an occurrence that was to be repeated many times throughout the Park. Also during 1966 the entire Mt. Sterling Ridge became infested when separate infestations merged around Big Cataloochee and Mt. Sterling (Lambert and Ciesla, 1967). Three patches of fir on the summit of Big Cataloochee remained aphid free, a condition which still existed in 1977.

During the next several years, the aphid continued to expand its population. Although 1967 was an uneventful year (Lambert and Rauschenberger, 1968), during 1968 the aphid colonized the northern portion of the disjunct spruce-fir type in the Heintooga area. When dying trees were first spotted in the Heintooga Geographic Area, approximately 80 hectares on Spruce Mountain were already infested. Now the Balsam Mountains were infested all the way from Big Cataloochee to Polls Gap. The aphid was also occurring in the northern Balsam Mountains where a new infestation was found on a ridge leading north from Luftee Knob.

During 1969 mortality on Mt. Sterling was far more severe than at any time or place in the history of the aphid in the Park; the upper slopes and the summit of Mt. Sterling were completely covered with thousands of red-fading Fraser firs. After encircling the summit during the preceding 11 years, the balsam woolly aphid population exploded bringing complete destruction to fir on Mt. Sterling.

The only new infestation detected during 1969 was on the southeastern slope of Luftee Knob at the headwaters of Dans Creek, a tributary of Straight Fork.

Activity during the Seventies. Aerial detection within the National Park was not maintained regularly by the U. S. Forest Service after 1970. Aphid population expansion was not chronicled as thoroughly as it might have been. National Park Service personnel were not maintaining control programs because there were none available, and except for the color display on Mt. Sterling the infestations were too scattered and small to attract much attention from backcountry visitors.

During the early seventies just a few new infestations were located. Existing hotspots grew larger and mortality occurred, sometimes alarmingly. During 1972 the northern section of the Balsam Mountains between Big Cataloochee and Tricorner Knob experienced severe mortality at the lower elevations of fir. Fir trees on the summit of Luftee Knob and along the main ridge of the Balsam Mountains were not killed at that time. Severe fir mortality was also found in several sections of the Heintooga Geographic Area, especially around Spruce Mountain and Cataloochee Balsam.

Due to the two to five year time delay between colonization and the appearance of red-crowned trees necessary for aerial detection, ground checks were devised during 1969 by personnel from the U. S. Forest Service (Rauschenberger and Lambert, 1970). Microscope slides coated with sticky material were mounted on tree stems so that wind transported aphids would be trapped. This method would allow for earlier detection than that provided by aerial reconnaissance. Traps were located in critical protection areas along the Clingmans Dome Road and the Heintooga Overlook Road.

During 1970 aphids were found at five of the eight trapping stations along the Heintooga Overlook Road. Light infestations were found near the road, but severe infestations were found near the hardwood-fir ecotone west (below) the road. Aphids were not detected along the Clingmans Dome Road (Flavell and Lambert, 1971).

One aphid crawler was found on a trap located at Newfound Gap during 1972; however, no aphids were found on any of the fir trees in the surrounding area (Ward et al., 1973). Monitoring of the traps was discontinued after 1972 because a control program suitable for use within the "natural" ecosystem of the National Park was not available.

Analysis of current infestations located southeast of the Clingmans Dome Road revealed that aphids were active there at least three or four years prior to 1972. Why then was the aphid not detected by the traps located along the road? Research into the development of the balsam woolly aphid in the Southern Appalachians in conjunction with our field work has shown that the initial location of new balsam woolly aphid infestations was near the northern hardwood-fir ecotone. The U. S. Forest Service trapping system did not include sites near the ecotones because this would have entailed considerable off-trail logistics. The traps were placed at high elevations due to the ease of access afforded by these locations. Only by 1977 had the aphids come close to the State-Line Ridge in some locations west of Tricorner Knob.

Analysis of the current distribution and levels of infestation development indicated that the aphid moved directly from Tricorner Knob and Mt. Guyot into the Mt. LeConte and Clingmans Dome areas. Infestations between Tricorner Knob and Mt. Kephart were not as well developed as those

located in the eastern portions of the spruce-fir distribution. The lower elevation of the State-Line Ridge from Mt. Sequoyah to Mt. Kephart would enable the windblown aphids to pass without being intercepted. Those that landed would find fewer Fraser fir to attack in this area . Stands on Charlies Bunion and Porters Mountain are still recovering from past fires and hardwoods have replaced spruce-fir in many areas.

Summary. Balsam woolly aphids were present throughout the entire spruce-fir distribution in the Great Smoky Mountains National Park. Initial infestations were located at the extreme eastern portion of the spruce-fir type, and damage to fir communities located east of Tricorner Knob was severe. Aphid infestations west of Tricorner Knob were small, isolated, and more prevelant at the hardwood-fir ecotone than at higher elevations. Damage will intensify when these infestations merge as they approach the State-Line Ridge.

II. ENVIRONMENTAL CHARACTERISTICS

The steep and highly dissected topography of the Great Smoky Mountains offers significant variation in the environmental characteristics associated with the various combinations of elevation, slope, and aspect. These environmental characteristics are important because of their effect on aphid development and the vigor and growth rate of the host tree--two factors of primary importance in the population dynamics of the aphid. Previous studies in Eastern Canada and the Pacific Northwest have identified certain environmental characteristics as influencing the level of susceptibility to attack and the probability of attack (Balch, 1952; Mitchell, 1966; Greenbank, 1970). Those of concern to the present project

were elevation, aspect, slope, geographic area, and occurrence of disturbance.

Elevation

Uninfested stands were growing at the highest elevations and heavily infested stands were found at the lowest elevations of the spruce-fir type. There was a definite gradient of aphid population level between these elevational extremes. Areas that had recently been infested offered the best example of this pattern. On Mt. LeConte and from Newfound Gap to Silers Bald, all heavy infestations were located at or just above the hardwood-fir ecotone (Plate 4-1). The heavily infested stands had many dead trees at the lower elevations and red-crowned trees above. Ground checks revealed that the firs above the red-crowned trees were infested but had not yet begun to change color. Characteristics of infestation development were due to dissemination patterns of the balsam woolly aphid by wind.

Wind Dissemination. As an air mass approaches a physical obstruction such as a mountain or large ridge the air is forced to rise toward the summit. The air mass above the mountain is essentially unaffected by the obstruction and maintains its original speed and direction vector. Thus, air that is forced up by the mountain is restricted to less space, forcing a major air speed increase as the mountain summit is passed. On the leeward side, air pressure is lower so the speed slows and the air mass falls through a series of eddies. The stronger the wind, the larger the eddy, and the more force within the eddy (Schroeder and Buck, 1970). During June and September these winds are laden with balsam woolly aphid

crawlers and occasionally eggs. The wind speed at the windward side and at the summit is too great for the deposition of crawlers within the forest canopy. If by chance they should encounter a tree crown, they probably would not survive the collision. However, on the leeward side of the mountain the aphid-laden air slows within the eddy, thereby providing a high probability of successful insect deposition. If the crawler lands in or near a Fraser fir, a new infestation has begun.

Elevational transects on Clingmans Dome and Mt. LeConte revealed similar patterns with respect to aphid population levels and degree of damage. Firs growing on the summit and upper slopes of these mountains were free of aphids. Only at elevations below 1770 meters were aphids detected. Between 1585 and 1770 meters various degrees of aphid damage were found depending on the length of time the stand had been infested. Below 1585 meters the aphid had killed most of the fir. If the wind had randomly deposited the aphid throughout Fraser fir stands on a mountain, aphid damage would have been observed along the entire transect.

In the Pacific Northwest, Mitchell (1966) noted that grand fir and subalpine fir growing at the lower elevational limits of their distribution were more susceptibile to aphid attack than those growing at the upper limits. Aphids were present at the upper limits, but either did not attack the firs growing at their upper elevational limits or, if infested, the trees were usually not seriously damaged. Grand fir has the lower elevational distribution and subalpine fir is found at the higher elevations of the mountains in that region. Grand firs growing among infested subalpine firs in the same stands were unaffected by the aphid and appeared immune to attack. No reason has been found for the apparent resistance.

Conditions differ in the Southern Appalachians. The aphid has already exhibited an ability to infest and kill trees growing on the summit of the highest peaks. The history of the aphid on Mt. Mitchell has shown that the aphid was not deterred by high elevation.

Method of infestation expansion. As infestations located at the hardwood-fir ecotone develop in size and severity of damage there are fewer suitable feeding sites available on the host tree. When this occurs crawlers drop from the host tree and can be transported upslope by convective winds during midday. Johnson (1977) found that the largest Fraser firs supported the highest aphid populations and from their tall crowns they provided optimum loci to spread infestation upslope.

Aspect

Heavily infested stands were more likely to be on western and southwestern aspects and uninfested stands were more common on eastern and northeastern aspects. These patterns were not apparent in areas that had been long infested because with continued development the aphid killed all mature firs regardless of their position on the mountain. Areas that had been infested less than seven years best demonstrated the effect of aspect, i.e., the most severe infestations on Mt. LeConte were approaching the summit from the west/northwest.

Greenbank (1970) and Atkins (1972) reported that high temperature increased the rate of aphid metamorphosis form egg to adult. Western and southwestern aspects, because of more solar radiation and the concomitant higher temperature of longer duration, enable established infestations to develop more rapidly. Consequently aphid populations in these areas were capable of producing an additional generation per year. This

resulted in heavily infested stands on the western and southwestern aspects.

Slope

There was a slight tendency for heavily infested stands to be associated with steep slopes and uninfested stands to be associated with gentle slopes. The analysis of the correlations among the environmental factors showed that steep slopes were highly correlated with lower elevations and gentle slopes with higher elevations. The strength of the relationship between aphid population levels and elevation was much greater than that between aphid population levels and slope. Consequently, the occurrence of a significant relationship between aphid population level and slope was a result of the inter-relationship between elevation and slope.

Geographic Area

The correlation between aphid population levels and geographic area was related to the chronological development of the balsam woolly aphid within the Park. Since the initial infestation occurred in the extreme eastern portion of the spruce-fir distribution, development of aphid population and damage was greatest in geographic areas located there. Similarly, the correlation between uninfested stands and those geographic areas in the western portion of the spruce-fir type was due to the lack of aphid development in these areas.

Occurrence of Distrubance

Heavily infested stands were moderately correlated with areas that had been disturbed. Most of the logging and subsequent fires within the

spruce-fir type in the Park occurred in the eastern portion of the spruce-fir distribution. The entire eastern portion of the Park was heavily infested, therefore, the relationship between aphid population levels and the occurrence of disturbance was not related to the distrubance but was coincidental to the history of the aphid within the Park.

III. COMMUNITY STRUCTURE CHARACTERISTICS

Community structure, indicated by stand density, species composition, and size category, had exerted a significant influence on the spread of aphids throughout the Great Smoky Mountains National Park. It was not the intention of this study to evaluate each component of community structure in detail within the spruce-fir type but only to determine on a broad scale which combination of stand density, species composition, and size distribution had the greatest impact on susceptibility to aphid attack.

Stand Density and Tree Size

Communities with high stand densities were strongly correlated with uninfested and slightly infested stands, as were those with small stem diameters. Small stem diameters and high stand density were strongly correlated with each other when the inter-relationships among the community characteristics were analyzed using basic correlation analysis (Table 4-5, page 40). Heavily infested stands were more common to communities composed of large diameter trees with wide spacing.

There are two primary reasons for aphids' not preferring dense stands. First, the top of the canopy of these stands was relatively

smooth and regular due to the closeness of the crown and the uniform stem heights. This makes it more difficult for windblown aphids to be screened from the air currents. Conversely, older stands composed of mature trees growing at wide spacing have differentiated into crown classes with the crowns of some trees extending well above the forest canopy. These dominant trees serve as prime interceptors of windblown apids.

Secondly, aphids finding their way into dense stands of small diameter trees have few feeding sites on the stem of the trees. Stands of this nature are comprised of young fir trees having tight, smooth bark with few of the cracks and crevices which are preferred feeding sites for aphids. Greenbank (1970) and Amman (1970) found that infestations were more severe on trees with rough bark than on those with smooth bark. Fraser firs growing under natural conditions do not develop roughened bark until they reach 18 to 20 centimeters in diameter. Few trees have attained this size within the young, dense stands that were identified by this study.

Stands on Mt. Sterling and Big Cataloochee provided an excellent example of the influence of density and tree size on the level of balsam woolly aphid damage. Both areas were extensively logged and red spruce, which was a major interest to loggers, is no longer an important component of the forest canopy. Stand structure on the summit and upper slopes of Mt. Sterling, with the exception of areas that were seriously burned after the logging operations, consisted of mature individuals of moderate to light densities with diameters between 20 and 30 centimeters. Virtually all of these firs have been killed by the aphid.

On Big Cataloochee aphid-caused mortality was similar to Mt. Sterling among the mature firs growing on the slopes and prominant spur ridges. However, on the summit there existed a dense, young stand of Fraser fir. A similar stand was located toward Big Butt. A third stand toward Balsam Corner was older and, although quite dense, most of the trees were larger than those in the other stands.

Aphid presence in the three stands on Big Cataloochee varied according to stand density and tree size. The summit stand was free of aphids. Aphids were found in the Big Butt stand well into the crowns of the larger trees. Aphid-caused mortality had not occurred in either of those two stands. Because of their larger size and lower density the trees in the Balsam Corner stand had aphids throughout and some crowns were fading.

The importance of stand density and tree size on the ability of the balsam woolly aphid to infest and kill Fraser fir was strengthened by the lack of correlation between stand density and elevation (Table 4-5, page 40). This indicated that regardless of elevation, young, dense, even-aged stands of Fraser fir were the least susceptible to aphid attack. Stand manipulation which would encourage the formation of dense patches of fir reproduction would slow the rate of aphid damage and insure the continued presence of Fraser fir within the Great Smoky Mountains National Park.

There are two methods which would aid in the establishment of fir reproduction. The first is the release of the existing fir understory. Fraser fir seedlings, which have developed roots within the mineral soil and not just in the humus layer, are capable of responding to release when the overstory is removed. Selection of stands based on understory

species composition, stage of development, and density would result in even-aged stands of fir following the removal of the overstory. If these released stands could attain seed-producing age before being killed by the aphid, the fir could be perpetuated.

The second method is to encourage seed production in Fraser fir stands that are approaching reproduction size and remain aphid-free; stands similar to those on Big Cataloochee which were not yet badly affected by the aphid. Encouragement of early seed production could be accomplished by thinning these stands. Crown release and subsequent increased growth of selected individuals would provide the necessary space and energy required for cone maturation. Thus, a layer of advanced reproduction could be secured before the aphid kills the overstory.

These procedures would not preserve Fraser fir as it exists today in mature old-growth stands, but they might afford the necessary time required to find some method of eliminating the balsam woolly aphid in the Southern Appalachians.

Species Composition

Uninfested and slightly infested stands were associated with a high percentage of Fraser fir and a corresponding low percentage of red spruce. Conversely, heavily infested stands consisted of more red spruce than Fraser fir.

Elevation greatly affects the species composition within the spruce-fir type, with red spruce reaching its maximum development at the low to middle elevations of the spruce-fir distribution and diminishing

in both size and numbers as elevation increases. At the higher elevations Fraser fir dominated, forming nearly pure stands.

Even though aphids do not attack red spruce, they plan an important role in the initiation and spread of balsam woolly aphid infestations. Tall, mature red spruces with their crown extending above the forest canopy, provided the necessary obstacle to intercept windblown aphids. If Fraser fir were growing subordinate or adjacent to the red spruce, the aphid could crawl or fall into its crown. Thus, the irregular canopy created by the large red spruce, in combination with the effects of wind dissemination of the elevational distribution of the aphid, facilitated the occurrence of heavy infestations in communities with a high percentage of red spruce.

Summary of Environmental and Community Characteristics

The correlation between high aphid population levels and not-so-dense, mixed, uneven-aged, mature stands of predominately red spruce located on western and southwestern aspects at low elevations resulted from an accumulation of indirect occurrences. Large trees with irregular height profiles screened sufficient aphids out of the wind to establish a new infestation. Characteristics of air mass movement determined where the initial colonization occurred. Once established, the larger fir trees provided the most favorable habitat for rapid population expansion.

Aphid populations were low in dense, pure, young, even-aged stands growing on eastern and northeastern aspects at the high elevations. This was primarily because the aphid had not arrived in sufficient numbers to

cause significant damage to fir stands with these environmental and community structure characteristics. A combination of physiological and morphological factors associated with small, young fir trees apparently restricted the biotic potential of the aphid and populations did not increase at their otherwise phenomenal rate. However, as aphid populations increase throughout the Park and as these young dense stands grow older and the trees larger, even these stands will eventually succumb to the aphid.

CHAPTER VI

CONCLUSIONS

Balsam Woolly Aphids have Colonized the Entire Spruce-Fir Type in the Great Smokey Mountains National Park

Fir mortality was greatest in the northeastern areas of the Park, but many Fraser fir were dying on all prominent mountains. Infestations were above 1950 meters on Mt. Guyot and Mt. LeConte and near 1829 meters on Clingmans Dome. Although infestation development is somewhat dependent on the environment, aphid populations should consume the fir on Mt. Guyot in 3 to 5 years, on Mt. LeConte in 5 to 10 years, and on Clingmans Dome in 10 to 15 years. Detailed work maps (1:24000 topographic) are on file with the National Park Service, Southeast Region, Chief Scientist, Atlanta and with Dr. Ronald L. Hay, Department of Forestry, Fisheries, and Wildlife, University of Tennessee, Knoxville.

Balsam Woolly Aphids Preferred Communities with Mature Fraser Fir and Red Spruce in Which to Initiate Infestations

Random, passive dissemination of aphids probably placed them into many communities, but those with maturing Fraser fir were most efficient in intercepting aphids and the large fir provided adequate attack sites plus abundant energy for developing large aphid populations. Dense, pure, even-aged Fraser fir stands at high elevations were nearly of aphids. However, there was limited reason to assume that they would remain healthy.

Balsam Woolly Aphid Infestations Appeared at the Northern Hardwood-Fir Ecotone and Spread Toward the Summit with Increasing Speed as the Aphid Population Expanded

Initial infestations found along the northern hardwood-fir ecotones were small, numerous, and scattered. As they expanded and merged, large infestations grew and provided aphids which convective winds moved upslope. Future analyses will indicate the speed of the aphid population development along elevation gradients.

Permanent Plots were Established Throughout the Project

A system of permanent plots was established throughout the spruce-fir type in the Great Smoky Mountains National Park. They were marked in the field, on aerial transparencies, on maps, and they were filed with National Park Service, Southeast Region, Chief Scientist, Atlanta.

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VITA

C. Christopher Eagar was born in Chattanooga, Tennessee on December 28, 1946. He attended elementary school in that city and was graduated from Notre Dame High School in June 1965. He entered Tennessee Technological University in Cookeville, Tennessee in September 1965 and transferred to the University of Tennessee, Knoxville in September 1967. He received a Bachelor of Science degree in Business Administration (Marketing) in December 1969.

Mr. Eagar was drafted into the United States Army in May 1970 and served until December 1971. After an extended period of traveling throughout the western United States, he was employed as a Department Manager for Montgomery Ward Company in Fort Collins, Colorado. He returned to the University of Tennessee, Knoxville in March 1975 and began the necessary prerequisite course work for admission into graduate school in Forestry. He was admitted to Graduate School in March 1976 and was awarded a Master of Science degree in Forestry in August 1978. Mr. Eagar intends to work toward a Doctor of Philosophy degree in Ecology.

He is married to the former Jane Tate of South Pittsburg, Tennessee.