Balsam Woolly Aphid Infestation of Fraser Fir in the Great Smoky Mountains

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Ronald L. Hay, Major Professor

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John Rennie, Hal DeSelm, Charles Pless

Accepted for the Council:

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BALSAM WOOLLY APHID INFESTATION OF FRASER FIR
IN THE GREAT SMOKY MOUNTAINS

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

Kristine D. Johnson
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ABSTRACT

The balsam woolly aphid (Adelges piceae (Ratz.)) has within the last decade become a serious pest on Fraser fir (Abies fraseri (Pursh.) Poir.) in the Great Smoky Mountains National Park, causing concern for the scenic and scientific resources of the spruce-fir forests. In order to determine and anticipate the nature and impact of the balsam woolly aphid in this area, a research project was designed to investigate some of the relevant biotic factors.

Objectives of this study were: (1) to determine relationships between levels of infestation, as indicated by aphid population and damage on individual trees, and the respective size, crown position, age, growth rate, and bark characteristics of these trees, and (2) to determine relationships between levels of infestation and selected site characteristics including slope, elevation, aspect, and ground vegetation.

Permanent plots were located throughout the Park in areas of varying levels of infestation, as determined from aerial photographs. Data were collected on individual trees and sites during the summer of 1976.

Individual tree characteristics were important in determining levels of aphid population on a tree and the amount of damage sustained. The most significant characteristic was tree size: large trees supported the heaviest populations while the smallest trees sustained more severe and/or rapid damage.
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I. INTRODUCTION AND REVIEW OF LITERATURE

The balsam woolly aphid (*Adelges piceae* (Ratz.)) has become a serious pest on Fraser fir (*Abies fraseri* (Pursh.) Poir.) in the Southern Appalachians, including the Great Smoky Mountains National Park within the last decade. Fraser fir is a major component of the spruce-fir forest type, which is limited in this region to mountain peaks above 4,500 feet elevation; severe damage to these trees is altering the scenic and scientific resources of the area and threatens the very existence of the Fraser fir.

In order to determine and anticipate the impact of the balsam woolly aphid, patterns of infestation must be examined. An understanding of why and how individual trees and stands differ in susceptibility and severity of attack is preliminary to damage forecasting and preventive control, and will be useful in resource management planning. If levels of infestation and damage are equal on all trees, then mortality will probably progress evenly as the insect becomes more widely dispersed; if differences in site and/or individual tree characteristics are associated with different levels of infestation and damage, then a more staggered or cyclic pattern may be expected.

An evaluation of some of the biotic factors relevant to the balsam woolly aphid infestation of Fraser fir in the Great Smoky Mountains National Park was designed to include the following objectives: (1) to determine relationships between levels of infestation, as indicated by aphid population and damage on individual trees, and the respective size,
crown position, age, growth rate, and bark characteristics of these trees, and (2) to determine relationships between levels of infestation and selected site characteristics including slope, elevation, aspect, and ground vegetation.

Because this research project was made possible in part by a grant from the National Park Service, the study area was confined to selected portions of the spruce-fir forests within the Great Smoky Mountains National Park. Field work was done during the summer of 1976.

A. REVIEW OF BALSAM WOOLLY APHID BIOLOGY

History and Distribution of the Balsam Woolly Aphid

**Adelges piceae** belongs to the insect order **Homoptera** (Hemiptera), family **Phylloxeridae** (Chermidae, Psyllidae, or Jumping plant-lice), superfamily **Aphidoidea** and sub-family **Adelginae**. The adelgids infest only conifers. Of the eleven species known to attack the true firs (Abies), all are holarctic in origin and they appear to have evolved into an ecological balance with their native hosts, becoming problematic only when they are introduced outside their natural ranges.

**Adelges piceae** originated in Europe, probably as a derivative of the closely related **A. nusslini** (Borner), where it was a relatively innocuous pest on European silver fir (Abies alba (L.) Mill). Its history on the North American continent is similar to that of several other disasterous plant pests: introduced accidentally on nursery stock, the woolly aphid thrived and spread so rapidly that it was already well established on balsam fir (Abies balsamea (L.) Mill) in Maine and Maritime Canada before official identification was made in 1908. Damage to
This commercially important fir has been extensive and occasionally severe all over the northeast.

A separate introduction from Europe put the woolly aphid into the Western United States, where it first appeared around 1930 on noble fir (Abies procera Rehd.) and grand fir (Abies grandis (Doug.) Lind.) near San Francisco. Damage is now widespread over the Pacific Northwest on Pacific silver fir (Abies amabilis (Doug.) Forbes) and subalpine fir (Abies lasiocarpa (Hook.) Nutt.). (See Appendix, Table 2) The last fir region to become infested was the Southern Appalachian mountains. In 1957 the balsam woolly aphid was identified on Fraser fir on Mt. Mitchell, North Carolina, and soon spread south to Mt. Sterling and into the Great Smoky Mountains National Park. (See Figure 1) At present, Mt. Rogers in Virginia is the only major area of host type that is uninfested.

**Life Cycle and Morphological Development**

The Adelginae subfamily is particularly noted for an unusually complex life cycle, frequently including alternation of hosts. As an impressive example of the evolutionary flexibility of these insects, Adelges piceae probably evolved as an asexual form of A. nusslini in the Caucasus with Picea orientalis as the primary host. It then lost its capacity for asexual reproduction on alternate hosts when it was moved to Europe.

Adelges piceae is an exule form capable of maturing and reproducing parthenogenetically, thus maintaining its population solely on the secondary host. The functional life cycle of the balsam woolly aphid consists of an egg stage, three larval instars and the adult:
Figure 1. Bark characteristics.

A. Balsam woolly aphids congregating about bark irregularities.
B. Example of trunk with smooth bark and no epiphytes.
C. Example of very rough bark.
D. Example of heavy epiphyte cover.
(1) Eggs laid by the stationary adult are attached to the bark by a silken thread. Initially light amber-colored, the egg becomes orange-brown as the embryo develops. The incubation period is about 12 days, but varies greatly with environmental conditions. Young larvae emerge head first from the end opposite the thread attachment, leaving the empty shell behind.

(2) Motile larvae or "crawlers" are light purple in color with a flattened, oval body between .35mm. and .47mm. long. This is the **first instar**, or neosistens stage. After inserting the stylect (a slender, thread-like mouthpart used for feeding) into the host, the insect becomes dark purple-black with a fringe of white waxy threads, and the legs and antennae begin to atrophy. A dormant period of variable length occurs before the first moult. When this diapause occurs during the winter the neosistens is known as "heimosistens," while the corresponding phase of summer generations is called an "aestivosistens." The heimosistens begins to feed when the sap rises in spring, while the aestivosistens is dormant for three to eight weeks. The insects remain stationary during the following three larval moults.

(3) The **second instar** develops after the first moult; it has a longer (.45mm. to .55mm.) and more broad body than the first instar, with longer, curling waxy threads.

(4) The **third instar** is similar to the second, except that it is .60mm. to .86mm. long.

(5) **Adults** are .70mm. to 1.0mm. long, hemispherically shaped and covered with long, curling wax threads of "wool." Since the insects tend to congregate, the wool forms a dense protective covering, making
infestations more readily visible. All adults are female and reproduce by thelytokus parthenogenesis, beginning with oviposition a few days after maturation (Balch, 1952). See Figure 2.

**Seasonal Chronology**

Metamorphosis of the balsam woolly aphid is influenced by such environmental factors as temperature, moisture and light. Temperature is particularly critical: under controlled laboratory conditions, neosistens reared from the final adult generation of the season developed best with fluctuating temperatures. Progeny of the following spring developed with both constant and fluctuating temperatures and displayed a developmental variability that could provide a basis for distinct ecological races (Atkins, 1972).

Such developmental variability allows the balsam woolly aphid to infest hosts over a wide range of climatic zones and to adjust to local weather extremes; a portion of the population can break dormancy early if conditions are favorable, thereby increasing the number of generations per year. If early development should occur during unfavorable conditions, the slower developing portion of the population can maintain the infestation.

The number of generations per year is variable. Balch (1952) found two generations in Maritime Canada. Even in the less extreme climate of North Carolina, the balsam woolly aphid can overwinter only as a dormant neosistens. The heimosistens begin to break dormancy in mid-March, as elsewhere, but development is generally faster throughout the season and continues into the early fall. Amman (1962) found that three
1. Glue bead was placed in each grooved slot, the increment core was sandwiched between slots and the entire piece was clamped firm until dry.

2. Parallel blades of table saw were used to cut cross-sections.

3. Mounted cross-section of increment core.

Figure 2. Increment core mounting procedure.
and sometimes four generations could reach maturity.

Intraregional variations in seasonal biology are greatest in the Pacific Northwest, due to the wide range of elevation and differences among host species. At the higher elevations, where the balsam woolly aphid is found on Pacific silver fir and subalpine fir, only two generations were observed. At intermediate elevations there were usually three generations annually, and woolly aphids on grand fir in the lowland valleys can have as many as four generations (Mitchell, Johnson and Rudinsky, 1961).

Variations in number of generations per year also occur within localized areas as a result of stand conditions. Insects on open-grown or stand-edge trees develop faster, perhaps by a full month, than those on trees in the stand interior. In dense stands those insects located near the base of the tree may have fewer generations than those higher on the stem because of slower development (Mitchell, et al. 1961).

**Dispersal**

The passive dissemination of insects is primarily determined by the availability of a mobile stage, plus the direction and velocity of the wind. Dispersal of the balsam woolly aphid occurs during the egg and crawler stages and is mainly passive. Once dislodged from the tree, they can be carried more than 300 feet by surface winds and several miles by vertical air currents (Balch, 1952).

Whether the synchronous dispersal and arrival of many aphid crawlers on the host facilitates establishment and survival is unknown. In laboratory experiments, groups of insects settled more rapidly than
isolated individuals (Atkins, 1972). In the forest, adjacent heavily infested and uninfested trees are common. Since the matted wool masses are protective, groups would be better able to become established and survive, at least up to the point where overcrowding occurs. Infestation spread would be affected by the number of generations per year and perhaps also by the synchrony of crawler development and dispersal, both of which are influenced by environmental factors (Atkins, 1972).

**Population Dynamics**

Factors that limit the distribution and abundance of the balsam woolly aphid are varied and include intraspecific (seasonal development, habits and population behavior), host characteristics, biotic, abiotic and applied factors.

**Abiotic factors.** Mortality due to climatic factors may be high occasionally, but it does not provide an effective limit to population growth (Balch, 1952). Of the various climatic factors, winter temperatures appear to be particularly important: the lethal minimum temperature for overwintering neosistens is around -30 F and around 0 F for all other stages. Low temperatures during the summer months increase incubation time.

High temperatures appear to have little effect on aphid survival except in combination with low relative humidity; dessication is a frequent cause of mortality on exposed bark areas and during the late summer. Heavy rains may mat the wool and lead to subsequent dessication, or wash eggs away, but neither rain nor heavy fog will "drown" aphids. Protection from the weather is afforded by the wool itself, the shade of
the tree crown, and by the insect's habit of congregating on the under-sides of twigs, branches, mosses and lichens and in bark crevices and lenticels.

Balch (1952) observed that climatic factors are important in influencing the rate at which the population reaches outbreak proportions and disperses. Winter temperatures can produce irregular, periodic fluctuations in the population over large areas. However, it is doubtful that the moderate climate and weather conditions are significant control mechanisms in the Southern Appalachians.

**Applied factors.** At present, applied control is impractical in the forest. Lindane is effective in killing the balsam woolly aphid, but it must be applied until run-off occurs along the entire bole and branches. To further compound the difficulty of this procedure, spraying must be done from the ground. Silvicultural control has involved complete removal of the host species.

**Biotic factors.** Since reproduction is not limited by the necessity of mating, the biotic potential of the balsam woolly aphid is quite high. The average number of eggs laid by one adult of the heimo-sistens generation is 100, although as many as 250 have been observed. The less fecund aestivosistens generations average 50 eggs. Thus the potential annual multiplication approximates a magnitude of 5000, and under optimal environmental conditions, survival to the adult stage is about 60% (Balch, 1952).

A greater proportion of the winter generation survive environmental stresses than of the summer. Amman (1970) observed that during
the initial period of outbreak in a stand, increased insect population density appeared to result in increased fertility. Later there was a strong inverse relation between adult density and fertility, probably due to competition for food at peak densities. Thus survival and reproduction was best on trees with less than extremely dense populations of aphids.

The balsam woolly aphid is apparently not bothered by parasites or disease, and the reproductive potential is so high that predators cannot reduce the populations before the host trees die. Amman (1970) recorded ten native and one introduced predators in North Carolina, most of which were mites feeding on the egg stage. Predators introduced as possible means of controlling aphid populations have either failed to become established or have otherwise been ineffective.

In the absence of other biotic factors capable of effective control, the upper limit of the population must be determined by intra-specific competition and starvation. In the case of the balsam woolly aphid, this is accomplished by severe injury to the host, usually followed by its death. Thus the host tree itself becomes the most significant factor in determining levels of aphid populations. Balch (1952) recorded the following population density sequence on stands of balsam fir in Maritime Canada:

(1) Insects become established on individual scattered trees (often the larger trees with rough bark) and then spread to neighboring trees.

(2) The population increases steadily (unless depleted by severe winter temperatures) and reaches a peak when a large proportion of trees
within a stand are heavily infested.

(3) Populations decline as susceptible trees are eliminated, and remain at lower but continually fluctuating levels with recovery, re-infestation and occasional new infestations occurring simultaneously.

Characteristics of fir stands and individual trees that are most relevant in the course of an infestation were a major portion of this investigation.

Activity

Balsam woolly aphids in the crawler stage are active and usually move about for several hours before inserting their stylets. If suitable feeding sites are available most will settle near their parent, but they are capable of moving 100 feet or more under their own power; they can survive for at least 8 days without feeding (Balch, 1952). However, larval mobility is more important for movement on the host tree than for dispersal. Distribution on a given host depends upon available light, gravity, and accessibility of young, tender parenchyma at wounds, lenticels and crevices, and feeding areas stimulated by other larvae.

The initial locus of infestation by wind-transported aphids would seem to be a matter of chance primarily, although Amman (1970) observed that it usually began near mid-height. This varies with tree height and age; on older trees with rough bark the infestation starts higher in the tree, but on younger trees infestation usually begins at the base.

Woolly aphids migrate both upward and downward after initial attack. The selection of a certain height on the bole is probably a result of the crawler's tendency to settle in moderately intense light (Balch, 1952),
but bark thickness and texture also seem to be important. In any case, crawlers appear capable of locating preferred feeding sites.

The feeding process begins when the stylet is inserted intercellularly (aided by a dissolving action of the saliva on the middle lamella), passing through the epidermis into the cortical parenchyma. During feeding the stylet is partially withdrawn and reinserted several times in new directions, while the insect itself remains stationary. Saliva flows into adjoining tissues in the tree. Nerves at the base of the stylet provide a tactile sense; obstructions can be felt, absence of satisfactory food detected, and relocation of stylets prompted. Spring feeding usually begins first on more vigorous trees with earlier sap flow; inception of feeding may vary among individual insects on a given tree by as much as 20 days (Balch, 1952).

B. THE HOST: FRASER FIR

The genus Abies is represented in eastern North America by two closely related species: balsam fir and Fraser fir. The latter was once considered a variety of balsam fir, Abies balsamea var. fraseri, and there remains some doubt concerning the validity of its recognition as a separate taxa on basis of differences in geographical distribution and certain morphological characteristics (Thor and Barnett, 1974).

The range of balsam fir extends from Newfoundland west to Manitoba and North Dakota, north into the Canadian tundra and south along the Appalachian mountain range into Virginia. The intermediate form known as bracted balsam fir (Abies balsamea var. phanerolepis Fernald) is found in the mountains of Virginia and West Virginia. Fraser fir has a
limited, disjunct distribution in the highest peaks of the Southern Appalachians, growing at elevations above 4,000 feet from Southwestern Virginia to Eastern Tennessee and Western North Carolina.

The spruce-fir forest type of the Southern Appalachians is characterized by the dominance of red spruce (*Picea rubens* Sarg.) and Fraser fir. Where the two grow together either may be dominant, depending usually upon stand history and site characteristics. Although fir grows more rapidly, it attains a smaller size and is much shorter-lived than spruce. At the highest elevations, usually above 6,000 feet, nearly pure stands of Fraser fir are found.

The stem of Fraser fir is composed of a series of internodes produced in successive growing seasons. On healthy young trees the bark surface is smooth along internodes and roughened at nodes by bark folds. Internodal bark surface is interrupted by lenticels, needle scars and numerous small swellings or "blisters" which contain clear liquid resin. Bark fissures and scales develop on the lowest portion of the stem and become more widespread as the tree ages or is unthrifty. Bark on mature trees is seldom thicker than 0.3 inch near the top and 0.7 inch near the stump (Bryant, 1976). The stem surface is sometimes covered by mosses and/or lichens; site moisture and stand density seem to influence the abundance of these epiphytes.

C. HOST: PEST INTERACTIONS

The balsam woolly aphid is an obligate parasite on Fraser fir, obtaining food and shelter in amounts dependent upon the host's capacity to provide them. There is considerable evidence that some trees are
more favorable to the multiplication of the insect than others. The ability of the woolly aphid to become established and reproduce is affected by external conditions of the tree, e.g. bark characteristics, form, size, and by feeding conditions within the bark. Such qualities can be influenced by genetics, modified by the environment, and/or related to the age, size and physiological condition of the tree (Balch, 1952).

With continued infestation development, host trees display characteristic reaction patterns. These help to explain how the insect injures the tree and they also provide an index of the amount of damage already sustained. For the purposes of discussion here, tree reactions have been divided into microscopic symptoms that concern cell and tissue changes, and macroscopic symptoms that are readily observed in the tree.

**Microscopic Changes**

Microscopic tissue changes are quite similar in all *Abies*; the differences exist mainly in the rate and degree of change. Damage develops from both physical injury by insertion of stylets and also chemically-induced injury produced by salivary secretions. The latter is by far the more important because the secretions either directly or indirectly change the balance of growth hormones and inhibitors in the host, causing abnormal development of wood and bark tissues (Balch, et al., 1964). Individual feeding of such minute insects would hardly interfere with normal host functioning, but their enormous capacity to reproduce and rapidly spread disastrously multiplies the effects of the balsam woolly aphid.
Balch (1952) made the first comprehensive histological studies of the balsam woolly aphid's feeding process and its effects on host tissue. He observed that the stylets are inserted intercellularly and seldom, if ever, penetrate the cell wall. They pass through the epidermis or phellem into the cortex or phelloderm and feeding takes place only in the parenchyma. In young shoots, however, the phloem is sometimes slightly penetrated. The insertion of stylets is accompanied by ejection of a salivary substance which occasionally flows into adjoining intercellular spaces.

A substance contained in the saliva, or produced in the cortical tissue by action of the saliva, diffuses from the point of insertion and causes parenchyma cells contiguous to the stylet tracks to increase in number and size. This is accompanied by an enlargement of the nuclei and thickening of cell walls; giant cells six or seven times larger than normal are produced. This additional volume disrupts phloem channels, resulting in a girdling effect.

By the following season, neighboring cells proliferate and form a secondary phellogen or periderm surrounding the pockets of abnormal tissue. This represents the initial stage in the wound-healing process. European firs are able to complete this process rapidly enough to isolate affected tissues; some North American firs, notably white fir (Abies concolor Gord. and Glend1.) and noble fir exhibit this resistance while others apparently do not. Tree vigor may cause some differences in individual resistance (Bryant, 1974).

The salivary secretion also affects the xylem: cell division is stimulated in the cambium, resulting in production of tracheids with
thickened, irregularly shaped cell walls and dark, hard, brittle cellu­lose. These tracheids resemble those of compression wood: secondary walls are marked with checks, the number of rays and parenchyma cells increase, cells are highly lignified, short, and thick-walled with a small lumen. This abnormal wood is called "rotholz" or "redwood" because of its reddish color (Doerkson and Mitchell, 1965).

The reaction of the cambium is dependent upon the vigor of the tree and intensity of infestation: the greatest amount of abnormal wood is produced in fast-growing stems that are moderately infested (Balch, 1952). Presence of redwood can be useful in dating infestations, but its absence does not necessarily indicate that an attack has not occurred. It is only found in certain areas of affected wood; even a heavy attack will not always produce redwood and it is not uniform around a growth ring or along the stem vertically.

The bark of trees with increasing levels of infestation have higher amounts of protein, while those with declining aphid populations have reduced protein content. Aphid damage apparently modifies the bark so that a greater proportion of insects can survive per unit area of bark. Growth rate influences bark formation and thus may be relevant to aphid survival: Amman (1970) suggested that the bark of more vigorous trees should logically provide the most food for aphids and hence support the largest populations. He proposed that the aphid population which trees could ultimately support could perhaps be predicted on the basis of growth rate.

Death of the host is caused by a combination of factors:

(1) Production of abnormal cells and resultant interference
with translocation of fluids through the xylem.

(2) Killing of the outer tissues of the bark by the toxic effect of the saliva in heavy infestations.

(3) Production of secondary periderm in sufficient quantities to interfere with respiration in underlying tissues (Balch, 1952).

**Macroscopic Changes**

Effects of aphid attack that are outwardly apparent are more variable among host species than microscopic tissue changes. Infestations are usually classed as stem attack or crown attack, depending on where the aphid population is concentrated. Greenbank (1970) suggested that the type of attack is influenced more by climate than by species characteristics: stem attack is more common in continental climatic zones and crown attack is more common in maritime zones. Either or both may prevail in transitional zone forests. The bracted balsam fir of Virginia usually suffers crown attack; stem attack is the most frequent on Fraser fir, although small suppressed trees and reproduction can develop crown gouting as aphids drop onto them from the overstory (Amman and Talerico, 1967).

Crown infestations produce a swelling at the nodes, then a deformation of shoots and internodes followed by down-curling branches, tip inhibition and die-back. Appreciable mortality does not occur until after 10 to 20 years, and recovery is possible (Bryant, 1970).

Stem infestations cause death quite rapidly, often within a few years of initial attack, because of the direct translocation impairment.
This type of attack is evidenced by wool spots on the stem and change of foliage color from the normal healthy green to a faded yellow-green, then bright rusty red and finally dead-brown. The speed of these changes seems to reflect the severity of attack and/or the tree resistance. Amman (1970) observed the following infestation pattern, regardless of host characteristics:

1. increased diameter growth at the time of initial attack,
2. increased aphid survival as the bark is changed by aphid feeding,
3. peak aphid population, with aphid survival closely related to tree condition,
4. decline in aphid survival and also tree growth,
5. disappearance of aphids, and
6. death of host.

Other detrimental effects of infestation include increased susceptibility to Armillaria root rot and impairment of reproductive functions. Hudak and Wells (1974) found that damage caused by woolly aphids was the factor primarily responsible for the high incidence of Armillaria root rot in aphid-damaged stands, regardless of site quality. Fedde (1973) found that cone production decreased rapidly and was restricted to the upper third of the crown in infested Fraser fir trees. In addition, cones were shorter by 25%, more brittle, and less impregnated by gum-like substances. Seeds were smaller than normal, frequently lacked megagametophyte, and were likely to be infested by seed chalcids.
II. METHODS

A. SAMPLING PROCEDURE

Selection of Stand Units

Color infrared transparencies covering areas of potential infestation were provided by the U. S. Forest Service in cooperation with the National Park Service in May, 1976. Analysis with magnification and a light table included:

1. location of frame center on 1:24000 topographic map to determine flight lines and exact aerial coverage,
2. delineation of spruce-fir distribution on the maps,
3. location of balsam woolly aphid infestations on basis of crown color, and
4. estimation of infestation intensity in each affected area.

The spruce-fir forests were grouped into 11 geographic units and further subdivided into 224 "stand units" on basis of topography, accessibility, and infestation intensity. For example, there were 26 stand units in the Mt. LeConte geographic unit, 12 units with varying levels of infestation and 14 with none. Each stand unit was numbered according to geographic unit and level of aphid infestation. The infestation classifications follow:

I. Active - fir dead and dying from apparent balsam woolly 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 and a large total area.

II. Dead - high fir mortality with no "hot" trees (trees just beginning to decline showed light yellow-green, while dead trees were grey).

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.

III. None - no evidence of infestation.

Sample selection was made from each infestation category in proportion to the total possible number of stand units. A total of 30 stand units was selected at random, with alternates to accommodate field adjustments in classification. Of the selected stand units, 17 were sampled during the summer of 1976 (102 plots) and it was subsequently decided that the three "dead" stands on Mt. Sterling should be treated separately in another study. (See Table 1)

Location of plots

Six plots were established in each stand unit. Potential plot sites were located in advance on the topographic maps in order to distribute them throughout the unit over a representative range of slope, aspect and infestation intensity. These locations were sometimes modified in the field to avoid excessively dense rhododendron thickets or steep terrain, and also because of occasional discrepancies between
### TABLE 1

**INFESTATION RATING AND GEOGRAPHIC AREA OF SAMPLING UNITS**

<table>
<thead>
<tr>
<th>UNIT NAME</th>
<th>GEOGRAPHIC AREA</th>
<th>INFESTATION (from aerial photos)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ice Water Springs</td>
<td>Mt. Kephart</td>
<td>Hot - Medium</td>
</tr>
<tr>
<td>Mt. Ambler</td>
<td>Mt. Kephart</td>
<td>None</td>
</tr>
<tr>
<td>Snake Den</td>
<td>Mt. Guyot</td>
<td>Hot - Heavy</td>
</tr>
<tr>
<td>Tricorner Knob</td>
<td>Mt. Guyot</td>
<td>Hot - Light</td>
</tr>
<tr>
<td>Guyot Spur</td>
<td>Mt. Guyot</td>
<td>Hot - Medium</td>
</tr>
<tr>
<td>Laurel Top</td>
<td>Laurel Top</td>
<td>None</td>
</tr>
<tr>
<td>Mt. Collins</td>
<td>Clingman's Dome</td>
<td>Hot - Light</td>
</tr>
<tr>
<td>Big Slick</td>
<td>Clingman's Dome</td>
<td>Hot - Medium</td>
</tr>
<tr>
<td>Forney Ridge</td>
<td>Clingman's Dome</td>
<td>None</td>
</tr>
<tr>
<td>Nolan Divide</td>
<td>Clingman's Dome</td>
<td>Hot - Light</td>
</tr>
<tr>
<td>Mt. LeConte</td>
<td>Mt. LeConte</td>
<td>Hot - Light</td>
</tr>
<tr>
<td>Trillium Gap</td>
<td>Mt. LeConte</td>
<td>Hot - Medium</td>
</tr>
<tr>
<td>Peck's Corner</td>
<td>Hughes Ridge</td>
<td>Hot - Medium</td>
</tr>
<tr>
<td>Mt. Sequoyah</td>
<td>Mt. Sequoyah</td>
<td>None</td>
</tr>
</tbody>
</table>
aerial photography interpretation and ground reconnaissance. The actual plot locations were noted on topographic maps for future reference, and four trees in each plot were marked permanently with metal tags.

**Description of Plot Measurements**

After the plot center was established, ten meters square were delineated using measured north-south and east-west diagonals.

All fir trees in the plot were tagged with sequential numbers. On a random subsample of three trees, data were taken to describe:

(1) individual tree characteristics that might be related to aphid attack, and

(2) indications of aphid attack intensity.

These data are listed and described below. In addition to characteristics of the individual subsample trees, data were also recorded to describe the plot for site quality analysis. This information included vegetation site type, slope, elevation and aspect; details of these data also follow below.

**Height.** Balch (1952) suggested tree height as a possible factor in the susceptibility of balsam fir to balsam woolly aphid attack, perhaps because taller trees were more likely to intercept the airborne eggs and crawlers.

Total height was measured with an Abney level.

**Diameter.** Balch (1952), Amman (1970) and Greenback (1970) thought diameter was at least indirectly relevant; Greenback correlated bark characteristics with diameter.

A metric diameter tape was used and all sample trees were measured
at breast height.

Crown class. Shooley and Oldford (1974), Balch (1952), and Johnson et al. (1963) attempted to correlate crown class with aphid attack. Site and host species variations are important in these relationships. Crown classes were defined according to the Society of American Foresters' Forestry Terminology as suppressed, intermediate, codominant and dominant.

Bark texture. Irregularities in bark texture provide shelter and feeding sites for the balsam woolly aphid (Balch, 1952), and may also reflect tree age, vigour, and stand density. Each tree was placed into one of four bark texture categories on basis of subjective inspection,

1. very smooth
2. some cracks, crevices and other irregularities,
3. more cracks, crevices and other irregularities,
4. Very convoluted, many irregularities.

See Figure 1, page 4.

Bark epiphytes. Moss and lichen cover are more abundant in stands that are stagnated or on very moist sites (Crandall, 1957). Bark epiphytes may protect trees by prohibiting woolly aphid feeding; conversely, aphids might use the epiphytes for protection. Previous studies have not examined this relationship.

Each tree was placed into one of four bark epiphyte categories,

1. none - clean bole, no epiphytes
2. sparse epiphyte cover
3. light but uniform or fairly heavy in patches
(4) uniformly thick moss and lichen cover
See Figure 1, page 4.

Bark thickness. Since the woolly aphid stylet must penetrate through the outer bark, bark thickness could be related to aphid attack. Bark thickness was measured directly from the increment core with a millimeter scale.

Increment cores. Increment cores were needed to determine age and growth rate. The cores were taken at breast height along north-south axes; when possible the entire diameter was sampled, but for larger trees two cores were obtained at 180 degrees. This procedure provided two pith-to-bark sections of each tree, which were averaged to calculate growth rate.

In preparation for analysis, the increment cores were glued between grooved slates of redwood and cut with parallel saw blades to produce a stable mounted cross section. See Figure 2, page 7. Cores were then examined under an 80X binocular microscope. Total age was obtained by counting annual rings from cambium to pith. Annual increment was recorded to the nearest .01 inch for each year from 1976 to 1967, and also for the years 1962 and 1957.

Aphid population on bole. Indications of aphid attack intensity were necessarily subjective. Estimates of aphid population were made with an emphasis on consistency and guided by the Amman (1969) method: he used an 8 x 8 cm. plastic grid placed on the tree trunk at breast height to supplement an overall subjective appraisal. The grid method alone was not sufficient because woolly aphids sometimes congregate on one side or at various locations along the vertical axis of the bole.
On the basis of overall inspection and use of the grid, each tree in the subsample was placed into one of four aphid population categories,

(1) none
(2) light - less than four wool masses per grid square,
(3) moderate - four masses per grid square to 25% covered, or
(4) severe - more than 25% covered with wool masses

_Crown color._ Foliage color was used as a symptomatic criterion for determining aphid infestation severity. Each subsample tree was rated according to the crown color categories

(1) green - no discoloration of needles
(2) light-fading - yellowing or reddening of some needles or branches
(3) red-dying - bright red needles throughout the crown
(4) brown-dead - dark red to brown needles throughout the crown.

_Vegetation site type._ Crandall (1957) proposed and described vegetation site types based on understory plant communities for the spruce-fir forests of the Great Smoky Mountains National Park. Each plot was classified according to her site types as follows:

(1) **Oxalis - Hylocomium** - most commonly found on north facing slopes at the highest elevations. The forest floor is usually wet with seeping water and the substratum is loose slate. Fir trees are closely spaced and even-aged.

(2) **Oxalis - Dryopteris** - usually occurs on moderate slopes with greywacke substratum. Firs are relatively branchy and
(3) **Senecio** - most common on the drier southwest or northwest facing slopes; firs are usually of relatively small diameter.

(4) **Viburnum - Vaccinium - Dryopteris** - frequently occurs on the lower portion of northerly, steep slopes with a bouldery greywacke substratum.

(5) **Rhododendron** - fir trees growing through the dense under-story of rhododendron are relatively large, and the soil is acidic.

**Slope.** Percent slope was measured with an Abney level.

**Aspect.** Compass bearings at right angles to the slope were made from plot center.

**Elevation.** Contour lines on an 1:24000 topographic map were used to estimate plot elevation.

**Percent infestation.** After field work was completed, an estimate of the infestation level in each plot was calculated to use in determining the relationship between infestation and other site characteristics. Each fir tree in every plot was recorded as "infested" or "uninfested" on basis of apparent aphid attack (e.g. crown color or presence of aphids). The percent infestation was a ratio of the number of infested trees compared to the total number of firs in the plot.
B. DATA ANALYSIS

Data were analyzed on the IBM Model 360/65 computer using Statistical Analysis Systems programs (Barr, Goodnight, Sall and Helwig, 1976). Continuous variable data (bark thickness, diameter, height, age, growth rate, slope and elevation) were sorted according to categories of aphid population and crown color; the means, frequencies and variance of each were calculated. Aspect and vegetation site type were sorted similarly. The Scheffe multiple range test (Chew, 1976) was used to compare means for each variable by aphid population and crown color categories. Differences between the mean percent infestation for each vegetation site type and aspect were also tested using the Scheffe procedure.

Ranked data included bark epiphytes, bark texture, crown color, aphid population and crown class. The following pairs of tree characteristics were analyzed using chi square contingency tests:

1. crown color X aphid population
2. crown class X aphid population
3. crown class X crown color
4. bark epiphytes X aphid population
5. bark epiphytes X crown color
6. bark texture X aphid population
7. bark texture X crown color

The same analyses were done with the data grouped by geographic units. This was done to provide a means of comparing relationships in areas where the balsam woolly aphid had been present for different lengths of time.
III. RESULTS

A. CROWN COLOR AND APHID POPULATION

Results are summarized in Appendix, Tables A-1 - A-8.

A significant relationship was found between crown color and aphid population (chi sq. = 87.57, with probability of greater value under $H_0 = 0.0001$). Trends were as follows:

(1) A majority (85.7%) of the trees with green crowns was infested; conversely a majority (76.3%) of the un-infested trees had green crowns. Some of the "un-infested" trees were those that had already reached such advanced stages of decline that the aphids were no longer present.

(2) Of the trees supporting the heaviest aphid population, 40% were green and 53% were light-fading.

(3) Light-fading trees usually had intermediate levels of aphid population.

(4) By the time trees had reached the later stages of decline, the aphid population was reduced: 63.2% of the red-dying trees and 72.4% of the brown-dead trees had no aphids.

B. TREE HEIGHT

Mean height did not differ significantly among trees having different levels of aphid population on the bole. Mean height was greatest (46.9 feet) for the severely infested trees and least (33.8 feet) for
those moderately infested. Trees infested slightly or not at all were of intermediate height. When the data were grouped by geographic units, this trend was most pronounced in the Mt. Kephart and Clingman's Dome areas; elsewhere heights varied by only a few feet.

**Height and crown color**

The comparison of mean height among the four crown color categories revealed significant differences between the following pairs:

1. mean height of green and mean height of brown dead
2. mean height of green and mean height of red-dying
3. mean height of light-fading and mean height of brown-dead
4. mean height of light-fading and mean height of red-dying
5. mean height of red-dying and mean height of brown-dead

Green and light-fading crowns had the same mean height.

Mean height was greatest for red-dying trees (44.8 feet) and least for the brown-dead ones (33.7 feet). Trees with green or light-fading foliage were of intermediate height (39.0 feet).

When the data were grouped by geographic units, these trends were most pronounced in the Mt. Kephart and Clingman's Dome areas.

**C. DIAMETER**

**Diameter and aphid population**

The Scheffe procedure showed a significant difference in one of the comparisons of mean diameter among the different aphid population levels: severely infested and moderately infested. The most severely infested trees had the largest mean diameter (19.7 cm.), while those moderately infested had the smallest (15.0 cm.). When the data were
grouped by geographic units, this trend was most pronounced in the Clingman’s Dome area.

**Diameter and crown color**

The brown-dead trees had the smallest mean diameter (15.8 cm.), while the red-dying ones had the largest (22.5 cm.). None of the other paired comparisons of mean diameter among the crown color categories were significantly different. Trees with green and light-fading crowns were of intermediate diameter. These trends were most pronounced in the Hughes Ridge, Clingman's Dome and Mt. Kephart areas.

**D. CROWN CLASS**

**Crown class and aphid population**

No significant relationship existed between aphid population and crown class (chi sq. = 87.57, probability of a greater value under H₀ = 0.2209). The following trends were observed, however:

1. Crown class distribution was fairly even among the un-infested trees.
2. A majority (40%) of the lightly infested trees were intermediates.
3. A majority (38.5%) of the moderately infested trees were suppressed.
4. Among the severely infested trees, none were suppressed and there was an equal percentage (33.3%) of dominants, co-dominants and intermediates.

**Crown class and crown color**

The chi square contingency test showed that the relationship
between crown class and crown color was not statistically significant (chi sq. = 3.813, probability of a greater value under $H_0 = 0.9866$). The following trends were observed, however:

(1) Crown class distribution was fairly uniform among trees with green crowns.

(2) Of the trees in the most advanced stage of decline (those with brown-dead crowns), 37.9% were suppressed and 13.8% were dominants.

E. AGE

Age of the sample trees ranged from 15 to 166 years; there was no significant difference in mean age among trees in the various aphid population and crown color categories.

F. BARK CHARACTERISTICS

Bark thickness

Differences in mean bark thickness among trees having different levels of aphid population and crown color were not significant. Bark thickness ranged from 1mm to 14mm.

Bark texture

Bark texture had no significant relationship with either aphid population or crown color (respectively: chi sq. = 7.70, probability of greater value under $H_0 = 0.5645$, and chi sq. = 6.62, probability of greater value under $H_0 = 0.676$).

Bark epiphytes

Bark epiphytes were correlated with both aphid population and
crown color (respectively: chi sq. = 19.05, probability of greater value under H₀ = 0.0248, and chi sq. = 21.05, probability of greater value under H₀ = 0.0124). The trend was for higher aphid population where bark epiphyte cover was light to moderate. Aphid damage as indicated by crown color was heaviest among trees with light epiphyte cover.

G. GROWTH RATE

Growth rate and aphid population

Growth rates did not differ significantly among trees having different levels of aphid population. The following trends were observed, however:

(1) In 1976, the greatest annual radial increment was found among trees with no aphids (0.03 inch/year), followed by trees with moderate infestations (0.02 inch/year).

(2) When average growth rate was computed for the past 5, 10, 15 and 20 years, the most rapid growth was found in the uninfested trees, while those with the heaviest populations had the slowest growth.

Growth rate and crown color

Radial growth rates among trees having different crown color were not significantly different for any of the time periods computed. However, the following trends were observed:

(1) Radial growth rates for 1976 were greatest among the light-fading and green trees (0.03 inch/year) and least for the red-fading and brown-dead ones (0.02 inch/year).

(2) Radial growth rates for the last 5, 10, 15 and 20 years were
generally most rapid for the green trees.

H. SITE QUALITY INDICATORS

Percent infestation and vegetation site type

Comparison of mean percent balsam woolly aphid infestation was not significantly different among plots in the various vegetation site types. Highest infestation levels were associated with Oxalis-Dryopteris (mean infestation 49%) and Oxalis-Hylocomium (46%). The lowest mean percent infestation (24.5%) was found on sites where Viburnum-Vaccinium-Senecio predominated.

Percent infestation and aspect

Mean percent infestation differed significantly between plots facing west (17.2%) and those facing southwest (77.7%).

Slope and aphid population

Slope ranged from 6% to 79%, but when mean slope was computed for the sites of trees having different aphid population levels, mean slope differed only slightly. Mean slope of heavily infested trees was 40.5%, compared with 47.8% for those with moderate infestations.

Elevation and aphid population

Elevation ranged from 4840 feet to 6500 feet. Mean site elevation of trees having different aphid population levels did not differ significantly: trees with moderate infestations had a mean elevation of 5646 feet, while those with heavy infestations averaged 5534 feet.

Elevation and crown color

Trees with green crowns had a mean elevation of 5549 feet while
the light-fading ones averaged 5656 feet. These differences were not significant.
IV. DISCUSSION

A. APHID POPULATION AND CROWN COLOR

When trees decline under balsam woolly aphid attack, crown color first becomes light green with some leaves or occasionally entire branches of foliage turning yellow to red, usually proceeding gradually from the bottom of the crown upward. Bright red foliage throughout the crown follows and the foliage turns dark reddish-brown as the tree dies. A severe bole attack can bring about the complete color change sequence in a single season.

Trees with green crowns can be uninfested; there was a time lag between aphid attack and crown color change. The most heavily infested trees still had green or light fading crowns. The interval between initial infestation and subsequent color change varies with the duration and severity of the infestation, and there may also be individual differences in resistance due to genetic or environmental circumstances that hasten or delay the process of decline (Balch, 1952). Crown color was thus an indication of the amount of accumulated damage sustained by a tree.

By the time the foliage has turned red throughout the crown, the aphid population was gone. These dying trees were no longer able to perform the normal processes of photosynthesis and trans-location and became unsuitable hosts. Amman (1970) also observed this relationship between tree condition and aphid survival.

A peculiarity of our system of aphid population classification
was that the categorized levels of aphid population did not reflect the amount of damage to a tree. A tree with no aphids may have been healthy and never infested, having escaped or developed resistance, or it may have been dead or dying from aphid attack and thus unable to sustain a population. The aphid population classification did, however, indicate the ability of a tree to provide an environment conducive to woolly aphid establishment, survival, and reproduction. Some trees with heavy aphid populations may have been infested longer than others, thus allowing additional time for populations to build up; in any case, all trees with many aphids were considered to be good hosts.

The strong relationship between aphid population and crown color permits their use as complimentary indicators of balsam woolly aphid infestation.

B. TREE SIZE AND APHID INFESTATION

Tree size was the most important factor in determining suitability as a host to the woolly aphid and the amount of damage it is likely to sustain. There was a consistent relationship between size characteristics, e.g. height, diameter, and crown class, and the infestation indices of aphid population and crown color. Since both indices provide different information, they will be considered separately here.

Aphid population

Trees presently supporting the heaviest aphid populations were the dominants and co-dominants with the largest mean height and diameter. This relationship between size and aphid population was more distinct for height and diameter than for crown class, but by definition dominants
and co-dominants have the largest diameter and height. Explanations for this trend include the following:

(1) Larger size of these trees increased the probability of intercepting air-borne aphids, thereby causing them to be the first in the stand to become infested. This additional time could permit the development of populations larger than those on the smaller trees.

(2) Vigorous, large trees provided a favorable habitat for aphid population build-up.

Balch (1952) and Johnson, et al. (1963) observed that in newly infested areas, the insect first became numerous on the larger trees. Balch also found that in his sample, the larger trees were also those with the most rapid growth, and suggested that tree vigor favors the multiplication of the insect. After an infestation had been active for several years, the balsam woolly aphid became more generally distributed throughout the stand, although there was still considerable variation between trees. There was no way to accurately date any of the infestations in our sample area, but analyses were grouped into geographic units on the assumption that stands in the same unit had been subjected to aphid attack for approximately the same amount of time and they could be compared with stands in other units that had different durations of aphid contact.

The trend for large trees to have heavy aphid populations was most pronounced in the Mt. Kephart and Clingman's Dome areas. Both were regions of relatively recent infestation; as the insects multiplied and spread, most trees were attacked and the effects of individual differences such as height and diameter were masked. In other geographic
units, there was no apparent relationship between size and aphid population.

Trees with slight to moderate infestations were in the suppressed and intermediate crown classes with small stem diameters. However, this trend can provide little information about infestation patterns since there is no way to determine whether the population is increasing or decreasing. The most probable explanation is that intermediates have moderate but increasing populations while suppressed trees have moderate but decreasing populations. This is likely because crown color and tree size comparisons indicated the most advanced decline among the smallest trees. The largest trees became infested first, and the aphid populations, though comparatively less on the intermediates, were still increasing. The small, suppressed trees became infested about the same time as the intermediates, but they succumbed rapidly after attack. The aphid population was decreasing in these dying trees. Their relatively light aphid populations suggest that these small trees may be poor hosts; however, a large population would not be necessary to kill a tree that is already under stress.

Crown color

Suppressed trees have suffered the heaviest damage, as indicated by crown color changes, and were the first to succumb to aphid attack. These trees were apparently less able to withstand insect infestation because they were already under stress from competition and were not vigorous enough to resist by building up secondary periderm cells which protect the parenchyma. Bryant (1974) noted that this wound-healing process is often delayed because of a reduction in tree vigor, and this
would be more critical in suppressed trees.

Red-dying trees had the largest height and diameter, and the green and light fading trees were intermediate in size. The larger trees had suffered more severe damage than the intermediates, since their crown color showed a more advanced stage of decline. These trees may have been infested longer than the others; their greater vigor permitted them to survive longer than other trees after attack, but it also provided such a favorable habitat that the aphid population increased rapidly and eventually killed the tree. Bryant (1974) observed that the wound-healing response is usually overcome during a continued heavy attack.

The tendency of short trees to be the most heavily damaged was more pronounced in areas of relatively recent infestation. The effects of tree size differences and aphid preferences were masked as damage became more widespread in the stands: for instance, the larger trees that were red in recent infestations would soon become brown and increase the mean size of the dead group. This was apparent on Mt. Guyot where infestations were older. In a study of balsam woolly aphid infestations of silver fir in Washington, Johnson, et al. (1963) found damage most severe on larger trees; this work was done in areas where the insect had been established for some time.

In another study relating crown class to aphid damage, Schooley and Oldford (1974) found that in young stands of balsam fir in Canada, trees in the various crown classes had the same probability of having aphid damage, but that suppressed trees were most likely to recover. We found damage heaviest on the smaller trees. However, mortality was rare in young balsam fir stands, and infestations were in the crown
instead of on the bole as is the case with Fraser fir. In addition, their small trees were growing in even-aged plantations, while in our study the small trees were likely to be relatively old but growing very slowly underneath the canopy. Thus the differences between their results and ours are attributable to differences in host species, stand structure and perhaps climate.

C. GROWTH RATE AND APHID INFESTATION

Previous studies have shown inter-relationships between aphid infestation and growth rate of the host trees; Balch (1952) and Amman (1970) suggested that vigorous, rapidly growing trees provided the most food for the woolly aphids and therefore supported the largest populations. Both also observed a marked increase in the annual increment during the first one to two years of infestation. According to Balch, et al. (1964), maximum stimulation of growth occurred in vigorous trees with moderate infestations; heavy infestations tended to inhibit growth. They suggested that some substance in the aphid saliva was toxic in high concentrations and growth responses depended upon interaction with some factor in the tree that varied with its vigor. As infestations progressed, the host's physiological processes were impaired and growth rate slowed as the tree died.

Aphid population

Amman (1970) found that when the maximum number of aphids observed was compared to growth of trees in the year just prior to infestation, the fastest growing trees supported the densest aphid populations. Our study indicated that for 1976, growth rate was most rapid
in the moderately infested trees and slowest in those heavily infested. The rapid growth that we observed probably reflected the growth spurt associated with initial infestation, while the heavily infested trees had begun to die and their growth had slowed. Since we could not accurately date the infestations, there was no way to determine the relationship between current aphid population level and growth rate prior to infestation. Average growth rates for the past 5, 10, 15, and 20 years showed high variability due to differences in site, age, and crown class. In addition, the rapidly growing "uninfested" category combined both healthy trees and those which had experienced the growth spurt associated with initial infestation and then declined to the point where aphids were unable to survive. The increased growth of the latter during their initial period of infestation would inflate the average growth rate of the uninfested trees.

Crown color

In 1976, trees with the largest annual increment had light-fading foliage. This rapid growth rate could be in response to aphid attack, or a result of tree vigor, or a combination of these two factors. When average growth rates were computed for 5, 10, 15, and 20 years prior to 1976, the trees which had suffered the greatest damage were growing relatively rapidly during those periods. This suggests that the rapidly growing trees became infested first, supported the heaviest aphid populations, and experienced the growth spurt that accompanied initial attack. The growth rate differences were not statistically significant. Our results agree with Balch's (1952) conclusions that the effect of aphid infestation on tree growth varies considerably, according to the
type and degree of infestation that the resistance of the tree and the action of the other control factors permit.

D. OTHER FACTORS

**Age and bark characteristics**

Neither of these characteristics was found to influence aphid population levels or the amount of damage sustained by a tree.

Age was not a determinant characteristic for Fraser fir, as a tolerant species growing in uneven-aged stands. Age did not correlate directly with size; a small, suppressed tree may be older than a dominant. Tree age would thus have little discernable effect on woolly aphid success in establishment and proliferation.

Balch (1952) found that resistance by formation of secondary periderm below affected tissues most often occurred in areas where the bark was thick. He noted, however, that the ability of the tree to provide itself with this protection depended upon its vigor and the portion of the tree that was heavily infested. The bole infestations of Fraser fir were generally more serious than the crown infestations of the balsam fir in Balch's study; this may explain why we did not find significant differences in bark thickness among the various aphid population and crown color categories. Woolly aphid stylets were long enough that outer bark within the normal range of thickness was not an important obstacle to penetration, and total bark thickness was not a determining factor.

Greenbank (1970) and Amman (1970) found that infestations were more severe on rough-barked trees than on those with smooth bark, and suggested that crevices and lenticels provided protection for the
insects. However, smooth bark might afford easier access to the tender parenchyma. We found no statistically significant relationship between bark texture and aphid infestation. Bark texture was also related to growth rate, tree vigor and stand density; the high variability in our sample with respect to these factors may have masked any significant relationship.

Bark epiphytes (mosses and lichens) can provide protection from the weather for the aphids; they may also protect the tree from aphids although insects were sometimes found beneath moss and lichen cover. The motile larvae were able to crawl between the bark and epiphytes. Our results indicate that the aphids were better able to become established and survive on trees with a moderate cover of moss and lichen: those with no epiphytes provide little protection and a heavy mat prevents penetration.

E. SITE QUALITY INDICATORS

Previous studies have noted differences in aphid damage associated with environment, and they have found relationships between infestation levels and site quality. Site characteristics may affect aphid populations directly by determining accessibility (aspect and elevation may be important in the distribution of the air-borne insects) and micro-climate, or indirectly by influencing the growth rate and overall vigor of host trees.

Johnson, et al. (1963) found that aphid populations were usually high on sites with high site index for silver fir; understory vegetation types were also correlated with site index. Brower (1942) found
that in Maine the infestations on balsam fir were most severe on those
trees growing on poor sites with low-lying, poorly drained soils. Balch
(1952) could find no conclusive relationship between forest type, site
quality and degree of infestation or damage on balsam fir in eastern
Canada. Bryant (1974) reported that damage was more severe on dry
sites than on moist sites in Newfoundland.

The most widely accepted method of evaluating site quality is
standard site index, i.e. the average height of sample canopy trees at
a selected age. This method, however, is designed for use in even-aged
stands, a condition not consistently found in natural Fraser fir forests.
Site index curves have not been developed for Fraser fir under any con-
ditions, and it is unlikely that curves developed for balsam fir in the
northeast would be valid here. Because a thorough site index study
was beyond the scope of this project, secondary site quality indicators
were used: slope, elevation, aspect and vegetation site type were
recorded for each plot.

**Vegetation site type**

The presence and abundance of plant species have been used as
indicators of site quality on the assumption that plant communities re-
fect the interaction of the various environmental factors that char-
acterize a site. The method has a successful history in Scandinavia
and has been adapted for use in some regions of North America. Site
index is determined by the standard height/age method for each vegeta-
tion type, so that the occurrence of that type in another area serves
as a secondary indicator of site quality. Vegetation site types must
be fairly consistent, simple and readily identifiable; spruce-fir is
one of the few forest types in the United States where these necessary conditions exist (Carman, 1971).

Crandall's (1958) vegetation site types developed for the Great Smoky Mountains National Park represent only a nominal classification since no attempt has been made to correlate them with site index. The classification of plots by vegetation site type may be useful in identifying the environmental conditions associated with various levels of balsam woolly aphid infestation. Johnson, et al. (1963) were able to designate areas of high aphid potential by correlating aphid population with vegetation site types, which were in turn related to site index. Since site index data were not available for Fraser fir, Johnson's second step was not possible here.

The major limitation of the plant indicator method, whether used descriptively or as a measure of site quality, is that since it was developed for use in fully stocked, undisturbed stands, it is not totally applicable to seriously disturbed or open stands. In some areas sampled in this study, the effects of balsam woolly aphid attack - e.g. increased sunlight, deposition of dead needles and falling trees, and decomposition of organic matter - could have altered the composition of understory plant communities.

Johnson, et al. (1963) found that Oxalis was associated with severe infestation areas and Vaccinium with those having the least damage. In our study, the two vegetation site types associated with the highest percent infestation both contained Oxalis as a major component; a separate study on Mt. Sterling showed that these same types were most frequent in areas where all the fir had been dead for several years. It
may be that these species (Oxalis, Hylocomium, and Dryopteris) respond most favorably to the opening of the canopy, soil chemistry changes, or other factors associated with heavy aphid damage. Another possibility is that the presence of these species reflects a combination of environmental conditions (e.g. aspect, moisture in the soil and air, soil type, etc.) more favorable to aphid infestation, either affecting the insects directly, or indirectly through the host tree response.

Determining the exact relationship between vegetation site type and aphid infestation would require further research to analyze the successional effects, and these would certainly have to be considered in any attempt to correlate vegetation site type with more direct measures of site quality.

Slope, aspect and elevation

Topographic factors may be relevant to site quality through influence on temperature, soil properties, water balance and insolation. Since there is no direct measure of site quality to use in correlation, these factors can only be used as a descriptive classification.

Stands having the highest percentage of infestation were found on south-facing slopes; normally rainfall in the spruce-fir forest is abundant, but during the relatively dry recent summers the southern exposed sites have been dry. Since the woolly aphid impairs the tree's fluid translocation system, trees on these sites may have suffered more damage.

Differences between mean slope and elevation among the various levels of aphid populations were not statistically significant. General field observations indicated, however, that elevation may be an
important factor in the spread of aphid infestation. Further research is being conducted on this possibility.

F. INFESTATION PATTERNS

Previous research involving different geographical localities and host species indicated that susceptibility (probability of attack) and degree of infestation (severity of attack) varied among and within stands containing fir trees. Both of these ecological phenomena were determined primarily by the dispersal capacity of the insect, the physiological and morphological characteristics of individual trees, and their relationship to the stand and site. Climatic factors are most critical in determining the rate at which the insect population reaches outbreak proportions and spreads, as well as regional patterns of dispersal. The ultimate level of the population (and hence the degree of infestation and damage) is dependent upon biotic factors, particularly those properties of host trees relevant to their suitability as food and shelter for the woolly aphid (Balch, 1952, and Greenbank, 1970). Biotic factors of potential importance investigated in this study included characteristics of individual trees and the sites on which they occurred. On basis of the preceding analysis and interpretation of field research, the following inferences concerning patterns of infestation in the Great Smoky Mountains National Park were made.

As the wind-borne balsam woolly aphids were transported into the uneven-sized stands of fir typical of the Smokies, they were deposited on trees of various size and species. They became established immediately if that spot was suitable, or attempted to locate a suitable host
in so far as their limited mobility permitted. Large dominant and co-
dominant firs would logically be more likely to become infested because
of their size and prominence, but the insects could settle on trees of
any size, depending upon stand structure, species composition, air
current patterns, slope, and many other factors. As the woolly aphid
population increased on the trees initially infested, crawlers and eggs
spread to other trees in the stand.

Small, suppressed firs were probably the first to succumb to
aphid attack, completing the foliage color sequence of decline and turn-
ing brown before the larger trees. These small trees were already under
stress from competition and therefore less able to withstand the addi-
tional stress of insect damage. Trees showed a marked increase in
growth rate as the aphid saliva stimulated the cambium, but growth
slowed and then stopped altogether as the physiological processes were
impaired.

The larger, dominant trees were next in showing symptoms of
decline. Large trees can generally undergo a longer period of contin-
uous infestation before dying; their greater vigor has enabled them to
survive longer than the weaker suppressed trees. Aphid populations
frequently build rapidly on vigorous trees, however, and recovery is
seldom possible.

Trees of intermediate size may have become infested later than
the larger ones, and been better able to withstand attack than the
smaller suppressed trees. Thus they will probably be among the last in
the stand to succumb to aphid attack.

These patterns were more pronounced in early infestations; as the
insect became well established and spread throughout the stand, individual tree characteristics became less important in determining susceptibility and the amount of damage sustained. Our conclusions concur in general with those of Balch (1952) and Johnson, et al. (1963) who found (in Canada and Washington, respectively) that the larger firs were most susceptible to heavy infestation at the beginning of an outbreak.

Further studies in areas where the date of initial infestation is known would be necessary to determine the relationships between levels of infestation and both growth rate and site quality.
V. CONCLUSIONS

1. Some individual tree characteristics were associated with different levels of aphid population and damage. The most significant of these were height and diameter: the largest trees supported the heaviest populations of woolly aphids, while the smallest trees sustained more severe and/or rapid damage.

2. Foliage color was related to the level of aphid population. Trees were green to light-fading while heavily infested; as they succumbed to attack, the aphid population decreased and crown color changed to red and finally brown.

3. There was no apparent relationship between aphid infestation and either age or bark characteristics.

4. Annual increment for 1976 showed that trees in the initial stages of decline were growing rapidly. This may have been a result of the characteristic growth spurt response, or may indicate high susceptibility of vigorous trees.

5. Stratification of data analysis by geographic units suggests the following pattern of infestation: large, dominant trees become infested first and may maintain heavy aphid populations for several years before succumbing. The smaller trees may be infested later, but die relatively quickly.

6. Additional site index data and further study are needed to determine the relationships between aphid infestation and site quality.
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1952. Studies of the balsam woolly aphid, Adelges piceae (Ratz.) and its effects on balsam fir Abies balsamea (L.) Mill. Canada Department of Agriculture Publication 867, 76pp., illustrated.

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Bryant, D. G.

Bryant, D. G.

Carmean, W. H.
1975. Forest site quality evaluation in the United States. In


APPENDIX
TABLE 3
APHID POPULATION LEVELS ON BOLE COMPARED WITH HEIGHT, DIAMETER, CROWN CLASS AND CROWN COLOR

<table>
<thead>
<tr>
<th></th>
<th>None</th>
<th>Standard Error</th>
<th>Light</th>
<th>Standard Error</th>
<th>Moderate</th>
<th>Standard Error</th>
<th>Heavy</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Trees</td>
<td>173</td>
<td>35</td>
<td>16.8</td>
<td>1.719</td>
<td>15.0</td>
<td>1.790</td>
<td>19.7</td>
<td>2.298</td>
</tr>
<tr>
<td>Average DBH (cm)</td>
<td>17.23</td>
<td>0.718</td>
<td>1.719</td>
<td>15.0</td>
<td>1.790</td>
<td>19.7</td>
<td>2.298</td>
<td></td>
</tr>
<tr>
<td>Average Height (ft)</td>
<td>40.00</td>
<td>1.405</td>
<td>3.467</td>
<td>33.8</td>
<td>4.068</td>
<td>46.9</td>
<td>4.300</td>
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<td>Crown Class:&lt;sup&gt;a&lt;/sup&gt;</td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>% Dominant</td>
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<td></td>
<td>33.3</td>
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<tr>
<td>% Co-dominant</td>
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<tr>
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<td>33.3</td>
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<tr>
<td>% Suppressed</td>
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<tr>
<td>Crown Color:&lt;sup&gt;b&lt;/sup&gt;</td>
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<td></td>
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<tr>
<td>% Green</td>
<td>76.3</td>
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<td>23.08</td>
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<tr>
<td>% Light-fading</td>
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<td>42.86</td>
<td></td>
<td>61.54</td>
<td></td>
<td>53.33</td>
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<td></td>
</tr>
<tr>
<td>% Red-dying</td>
<td>6.94</td>
<td>14.29</td>
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<td>7.69</td>
<td></td>
<td>0</td>
<td></td>
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<tr>
<td>% Brown-dead</td>
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<td>14.29</td>
<td></td>
<td>7.69</td>
<td></td>
<td>6.67</td>
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<td></td>
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</tbody>
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<sup>a</sup>Chi Square = 15.387, 12 d.f.; probability of greater value under H<sub>0</sub> = 0.2209.

<sup>b</sup>Chi Square = 87.57, 9 d.f.; probability of greater value under H<sub>0</sub> = 0.0001.
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<th>Green</th>
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<th>Light-fading</th>
<th>Standard Error</th>
<th>Red-dying</th>
<th>Standard Error</th>
<th>Brown-dead</th>
<th>Standard Error</th>
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<td>47</td>
<td>19</td>
<td>29</td>
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<td>Average DBH (cm)</td>
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<td>0.732</td>
<td>17.7</td>
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<td>22.5</td>
<td>2.550</td>
<td>15.8</td>
<td>1.623</td>
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<td>Average Height (ft)</td>
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<td>44.8</td>
<td>3.574</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Dominant</td>
<td>18.8</td>
<td>17.2</td>
<td>15.8</td>
<td>13.8</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>% Co-dominant</td>
<td>26.6</td>
<td>29.8</td>
<td>26.3</td>
<td>17.2</td>
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<td></td>
<td></td>
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<tr>
<td>% Intermediate</td>
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<td>27.7</td>
<td>31.6</td>
<td>31.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Suppressed</td>
<td>29.2</td>
<td>25.5</td>
<td>26.3</td>
<td>37.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aphid Population:&lt;b&gt;</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% None</td>
<td>85.71</td>
<td>17.02</td>
<td>63.16</td>
<td>72.41</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Light</td>
<td>6.49</td>
<td>31.91</td>
<td>26.32</td>
<td>17.24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Moderate</td>
<td>3.90</td>
<td>34.04</td>
<td>10.52</td>
<td>6.90</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>% Heavy</td>
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<td>0</td>
<td>3.45</td>
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<a>Chi Square = 3.813, 12 d.f.; probability of greater value under $H_0 = .9866$.

<b>Chi Square = 87.57, 9 d.f.; probability of greater value under $H_0 = 0.0001$. 
<table>
<thead>
<tr>
<th>Bark Characteristics</th>
<th>Green</th>
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<th>Light-fading</th>
<th>Standard Error</th>
<th>Red-dying</th>
<th>Standard Error</th>
<th>Crown Color</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Bark Thickness (mm)</td>
<td>4.38</td>
<td>0.23</td>
<td>5.13</td>
<td>0.42</td>
<td>5.79</td>
<td>0.60</td>
<td>4.82</td>
</tr>
<tr>
<td>Bark Epiphytes: a (No. Trees)</td>
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<td></td>
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<tr>
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<td>27</td>
<td>8.44</td>
<td>10.64</td>
<td>5.26</td>
<td>27.59</td>
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</tr>
<tr>
<td>% Light</td>
<td>131</td>
<td>48.05</td>
<td>68.09</td>
<td>52.63</td>
<td>51.72</td>
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<td></td>
</tr>
<tr>
<td>% Moderate</td>
<td>70</td>
<td>31.82</td>
<td>19.15</td>
<td>31.58</td>
<td>20.69</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Heavy</td>
<td>21</td>
<td>11.69</td>
<td>2.13</td>
<td>10.53</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bark Texture: b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Smooth</td>
<td>138</td>
<td>57.14</td>
<td>57.45</td>
<td>42.11</td>
<td>51.72</td>
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<td></td>
</tr>
<tr>
<td>% Average-Smooth</td>
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<td>31.91</td>
<td>42.11</td>
<td>24.14</td>
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<tr>
<td>% Average-Rough</td>
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<td>9.09</td>
<td>6.38</td>
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<td>20.69</td>
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<td>Rough</td>
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<td>3.45</td>
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</table>

*a Chi Square = 21.05, 9 d.f.; probability of greater value under $H_0 = 0.0124$.

*b Chi Square = 6.625; 9 d.f.; probability of greater value under $H_0 = 0.6761$. 
TABLE 6
BARK CHARACTERISTICS (THICKNESS AND TEXTURE) COMPARED WITH APHID POPULATION

<table>
<thead>
<tr>
<th>Bark Characteristics</th>
<th>None</th>
<th>Standard Error</th>
<th>Light</th>
<th>Standard Error</th>
<th>Moderate</th>
<th>Standard Error</th>
<th>Heavy</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Bark Thickness (mm)</td>
<td>4.64</td>
<td>0.225</td>
<td>4.80</td>
<td>0.493</td>
<td>4.19</td>
<td>0.514</td>
<td>5.73</td>
<td>0.564</td>
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<tr>
<td>Bark Epiphytes:</td>
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<tr>
<td>% None</td>
<td>9.83</td>
<td>27</td>
<td>11.43</td>
<td></td>
<td>7.69</td>
<td></td>
<td>26.67</td>
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</tr>
<tr>
<td>% Light</td>
<td>47.98</td>
<td>131</td>
<td>48.57</td>
<td></td>
<td>80.77</td>
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<td>66.67</td>
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<tr>
<td>% Moderate</td>
<td>32.37</td>
<td>70</td>
<td>31.43</td>
<td></td>
<td>7.69</td>
<td></td>
<td>6.67</td>
<td></td>
</tr>
<tr>
<td>% Heavy</td>
<td>9.83</td>
<td>21</td>
<td>8.57</td>
<td></td>
<td>3.85</td>
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<td>0</td>
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<tr>
<td>Bark Texture:</td>
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<td></td>
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<tr>
<td>% Smooth</td>
<td>53.18</td>
<td>138</td>
<td>57.14</td>
<td></td>
<td>65.38</td>
<td></td>
<td>60.00</td>
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</tr>
<tr>
<td>% Average-Smooth</td>
<td>30.64</td>
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<td>31.43</td>
<td></td>
<td>34.62</td>
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<td>33.33</td>
<td></td>
</tr>
<tr>
<td>% Average-Rough</td>
<td>12.72</td>
<td>25</td>
<td>8.57</td>
<td></td>
<td>0</td>
<td></td>
<td>0</td>
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</tr>
<tr>
<td>% Rough</td>
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<td>2.86</td>
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\[a\text{Chi Square} = 19.05, 9\text{ d.f.; probability of greater value under } H_0 = 0.0248.\]

\[b\text{Chi Square} = 7.70, 9\text{ d.f.; probability of greater value under } H_0 = 0.5645.\]
**TABLE 7**

AGE AND GROWTH RATE\(^a\) (X 10\(^{+2}\)) COMPARED WITH APHID POPULATION

<table>
<thead>
<tr>
<th>Age</th>
<th>None</th>
<th>Standard Error</th>
<th>Light</th>
<th>Standard Error</th>
<th>Moderate</th>
<th>Standard Error</th>
<th>Heavy</th>
<th>Standard Error</th>
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</thead>
<tbody>
<tr>
<td>Mean, 1976 (.01 in)</td>
<td>2.6184</td>
<td>0.1852</td>
<td>2.3333</td>
<td>0.2843</td>
<td>2.4231</td>
<td>0.3097</td>
<td>2.0714</td>
<td>0.5078</td>
</tr>
<tr>
<td>Mean, 5 yrs (.01 in)</td>
<td>2.9607</td>
<td>1.0342</td>
<td>2.5091</td>
<td>1.7612</td>
<td>2.4615</td>
<td>2.0326</td>
<td>2.1571</td>
<td>2.3538</td>
</tr>
<tr>
<td>Mean, 10 yrs (.01 in)</td>
<td>3.3334</td>
<td>1.9900</td>
<td>2.6697</td>
<td>3.5493</td>
<td>2.7923</td>
<td>4.0398</td>
<td>2.3571</td>
<td>4.1479</td>
</tr>
<tr>
<td>Mean, 15 yrs (.01 in)</td>
<td>3.6493</td>
<td>2.9270</td>
<td>2.8141</td>
<td>4.9547</td>
<td>3.0872</td>
<td>5.7310</td>
<td>2.7190</td>
<td>5.8160</td>
</tr>
<tr>
<td>Mean, 20 yrs (.01 in)</td>
<td>4.0650</td>
<td>4.1209</td>
<td>3.0530</td>
<td>6.1819</td>
<td>3.6865</td>
<td>8.2791</td>
<td>3.2393</td>
<td>9.0652</td>
</tr>
</tbody>
</table>

\(^a\)Growth rate measured to the nearest .01 inch.
## TABLE 8

**AGE AND GROWTH RATE**\(^a\) (X 10\(^{-4}\)) **COMPARSED WITH CROWN COLOR**

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td>Age</td>
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<td>Mean, 1976 (.01 in)</td>
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<td>2.6889</td>
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<td>2.2105</td>
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<td>2.1071</td>
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<td>Mean, 5 yrs (.01 in)</td>
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<td>1.1253</td>
<td>2.7067</td>
<td>1.6176</td>
<td>2.4737</td>
<td>2.1497</td>
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<td>3.2773</td>
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<td>2.7844</td>
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<td>Mean, 15 yrs (.01 in)</td>
<td>3.6346</td>
<td>3.2172</td>
<td>2.9437</td>
<td>4.1407</td>
<td>2.8526</td>
<td>5.8871</td>
<td>3.4333</td>
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<td>Mean, 20 yrs (.01 in)</td>
<td>4.1227</td>
<td>4.5494</td>
<td>3.2600</td>
<td>5.0800</td>
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\(^a\)Growth rate measured to the nearest .01 inch.
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<th>Vegetation Site Type</th>
<th>Mean % of Plot Infested</th>
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<th>Number of Plots</th>
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<tr>
<td>Viburnum-Vaccinium-Senecio</td>
<td>24.75</td>
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<td>Rhododendron</td>
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<td>Senecio</td>
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<td>Viburnum-Vaccinium-Dryopteris</td>
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<td>Oxalis-Hylocomium</td>
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<td>Oxalis-Dryopteris</td>
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<table>
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<th>Aspect</th>
<th>Mean % of Plot Infested</th>
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<td>Northwest</td>
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<td>Northeast</td>
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<tr>
<td>North</td>
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<td>Southwest</td>
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<td>1.0449</td>
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</table>
VITA

Kristine D. Johnson was born in York, Pennsylvania in 1951 and moved to Tennessee in 1954. She attended Calhoun Elementary and graduated from McMinn County High School in 1969. She majored in philosophy at the University of Tennessee, Knoxville, and in 1973 received the Bachelor of Arts Degree, magna cum laude. She completed course requirements for the Master of Science Degree in Forestry at the University of Tennessee in 1977. Her parents are James and Alliene Johnson of Calhoun, Tennessee.