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I am submitting herewith a thesis written by George F. Smith entitled "Southern Appalachian Fir and Fir-Spruce Forest Community Changes Following Balsam Woolly Adelgid Infestation." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Niki S. Nicholas, Major Professor

We have read this thesis
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Accepted for the Council:

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Southern Appalachian Fir and Fir-Spruce Forest Community Changes Following Balsam Woolly Adelgid Infestation

A Thesis

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Abstract

The southern Appalachian fir and fir-spruce forests are unique glacial relict communities that occupy 26,600 ha at the highest elevations of only seven mountain areas. Over the last three and a half decades an exotic insect, the balsam woolly adelgid (*Adelges piceae* Ratz.), has caused catastrophic mortality to populations of the endemic Fraser fir (*Abies fraseri* (Pursh) Poir.) throughout its entire native range. In 1990 and 1991, a set of temporary and permanent plots were established at the summits of five mountains in the Great Smoky Mountains to study processes of community change in overstory and understory composition and fir size and age distributions. Nearly 70% of standing fir basal area is dead over the entire study area. Patterns of overstory dominance are determined primarily by elevation and time since the major wave of mortality. Overstory fir mortality and the resulting increases in canopy openness have led to decreases in densities of 0 - 10 yr old fir seedlings and bryophyte cover. Herbaceous vegetation cover, densities of red spruce (*Picea rubens* Sarg.) seedlings, and small shrub densities have increased in some stands. Understory fir are growing and maturing more rapidly with greater insolation. Understory fir recruitment and selective mortality of larger fir are causing overstory size and age classes to become more skewed towards smaller and younger individuals. Future rates and spatial patterns of infestation and mortality will be determined by rates of fir recovery in patches subject to different biotic and abiotic stressors. Poorly reproducing fir may be eliminated in lower elevation mixed stands.

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Chapter I

Introduction and Objectives

1.1 Introduction

The southern Appalachian fir and spruce-fir forests are physiognomically and floristically unique ecosystems found only in an island-like distribution at the peaks of the seven highest mountain areas in North Carolina, Tennessee, and southwestern Virginia (Oosting and Billings 1951; Ramseur 1960). These communities are the remains of a once continuous band of coniferous forest extending south along the Appalachians during the Pleistocene that migrated upslope following climate warming (Oosting and Billings 1951; Delcourt and Delcourt 1984). The endemic Fraser fir (*Abies fraseri* (Pursh) Poir.) is a forest canopy species that is codominant with red spruce (*Picea rubens* Sarg.) at elevations of about 1675-1850 m; fir is the sole dominant at elevations over about 1850 m elevation (Whittaker 1956; Crandall 1958; Busing et al. 1993).

In 1957, an exotic insect, the balsam woolly adelgid (*Adelges piceae* Ratz., Homoptera: Adelgidae) was detected in the southern Appalachians (Speers 1958) and has since spread throughout the spruce-fir forests, killing enormous numbers of Fraser fir. Dull et al. (1988) calculated that mortality by volume of fir greater than 12 cm dbh ranges from 44% on Roan Mountain to 91% in the Great Smokies. With such severe mortality, it is possible that Fraser fir may be lost from its native range.

The loss of fir from the high elevations of the southern Appalachians would have several consequences in addition to the extirpation of an endemic species. Since fir is the most

important tree species at the highest elevations, its demise is having and will continue to have a profound impact on the spruce-fir forest community, including vascular plants, bryophytes, invertebrates, amphibians, and birds (Boner 1979; DeSelm and Boner 1984; Matthews and Echternacht 1984; Smith 1984; Hall 1989; Nicholas et al. 1992a; USDI Fish and Wildlife Service 1995). Changes in species abundances and long term increases in carbon and nitrogen inputs from decaying fir boles will affect nutrient cycling. Since fir and spruce-fir forests are found at the heads of several major southern Appalachian watersheds (Pyle 1984), the effects of fir death will propagate to communities downstream.

Adequate assessment of likely future trends in fir and spruce-fir forest dynamics requires understanding of several aspects of fir and spruce-fir community structure. More information about how overstory stand structure has changed following adelgid infestation would improve understanding about how current patterns of overstory abundance and conditions below the canopy are different from historical conditions. Trends in the densities and size and age distributions of live overstory fir have implications for future fir regeneration. More knowledge of what species can be expected to increase or decrease in the understories of former fir-dominated and mixed stands that have been impacted by the adelgid is needed. An assessment of competitive relationships between fir seedlings and other understory taxa under changing environmental conditions is necessary to identify potential threats to successful fir seedling germination and survival. Information about fir seedling growth and abundances under different canopy compositions is needed to determine whether or not decreases in fir reproduction are occurring.

1.2 Objectives

To address some of these gaps in understanding, this study will focus on three main questions. Following a comprehensive literature review, Chapters 3 - 5 will each discuss one of the below objectives and is written as a separate paper. Chapter 6 will summarize and integrate the results of the previous three chapters and explore the implications for Fraser fir viability.

1) **What is the current overstory composition and what factors determine species distributions?** In Chapter 3, differences in fir, spruce, and hardwood overstory basal area will be compared among a chronosequence of five mountains in the Great Smoky Mountains using a set of temporary plots. Distribution of overstory abundances in a set of permanent plots will be compared among the five mountains and four different stand types (defined by the proportions of live and dead overstory fir and other species). The effects of such site characteristics as elevation, aspect, and time since the major wave of adelgid-caused mortality on species distributions will be examined. The factors that control the proportion of dead fir stems as a function of total standing fir stems will be analyzed.

2) **What is the current composition of the understory, what factors influence species distributions, and what are the threats to fir regeneration?** In Chapter 4, differences in fir, spruce, hardwood, and shrub seedling and sapling densities among mountains, stand types, and differing site conditions will be determined. Correlations between different size classes of fir with other species will be identified. The

distribution of different ground cover types, such as leaf litter, bryophytes, and herbs, following changes in canopy composition will be investigated as well as the association between ground cover types and fir seedling abundances.

3) **How have mean fir age, overstory fir size and age class distributions, and understory fir age distributions changed, and what are the implications for fir regeneration?** In Chapter 5, mean ages of fir in several size classes and the mean sizes and ages of cone-producing fir will be calculated by mountain. Density-size and density-age distributions will be constructed to determine how they are changing. Density-age distributions for understory fir by mountain and stand type will be constructed and compared. Simple curvilinear models will be fitted to the distributions and compared.

Chapter II

Literature Review

2.1 The Southern Appalachian Spruce-Fir Forest Community

2.1.1 Paleoecology

The southern Appalachian spruce-fir forests occupy seven separate mountain areas with elevations greater than 1680m: Mount Rogers, VA; Grandfather Mountain, NC; Roan Mountain, TN; the Black Mountains, NC; the Balsam Mountains, NC; the Plott Balsam Mountains, NC; and the Great Smoky Mountains, TN and NC (Fig. 2.1) (Ramseur 1960). Other areas exist that have red spruce populations but do not support Fraser fir, including Whitetop, VA and Long Hope Mountain, NC.

To explain the disjunct distribution of spruce-fir forests in the southern Appalachians, Oosting and Billings (1951) suggested that during the Pleistocene glaciation, montane red spruce-fir forests extended south throughout the Appalachians in an unbroken chain. Later, when the climate warmed, these forests retreated northward and upward where the habitat was sufficiently cool and moist. A large distribution gap exists between roughly 38°N and 42°N latitude where the mountains are too low to support well-developed spruce and fir populations.

Whittaker (1956) noted that those peaks that seem suitable for spruce-fir forests, but are not occupied by them, are all under 1740 m elevation. He suggested that during the last hypsithermal period, which peaked about 4000 years ago, the spruce-fir type was restricted to elevations above 1740 m and populations on lower peaks became extinct. Supporting evidence

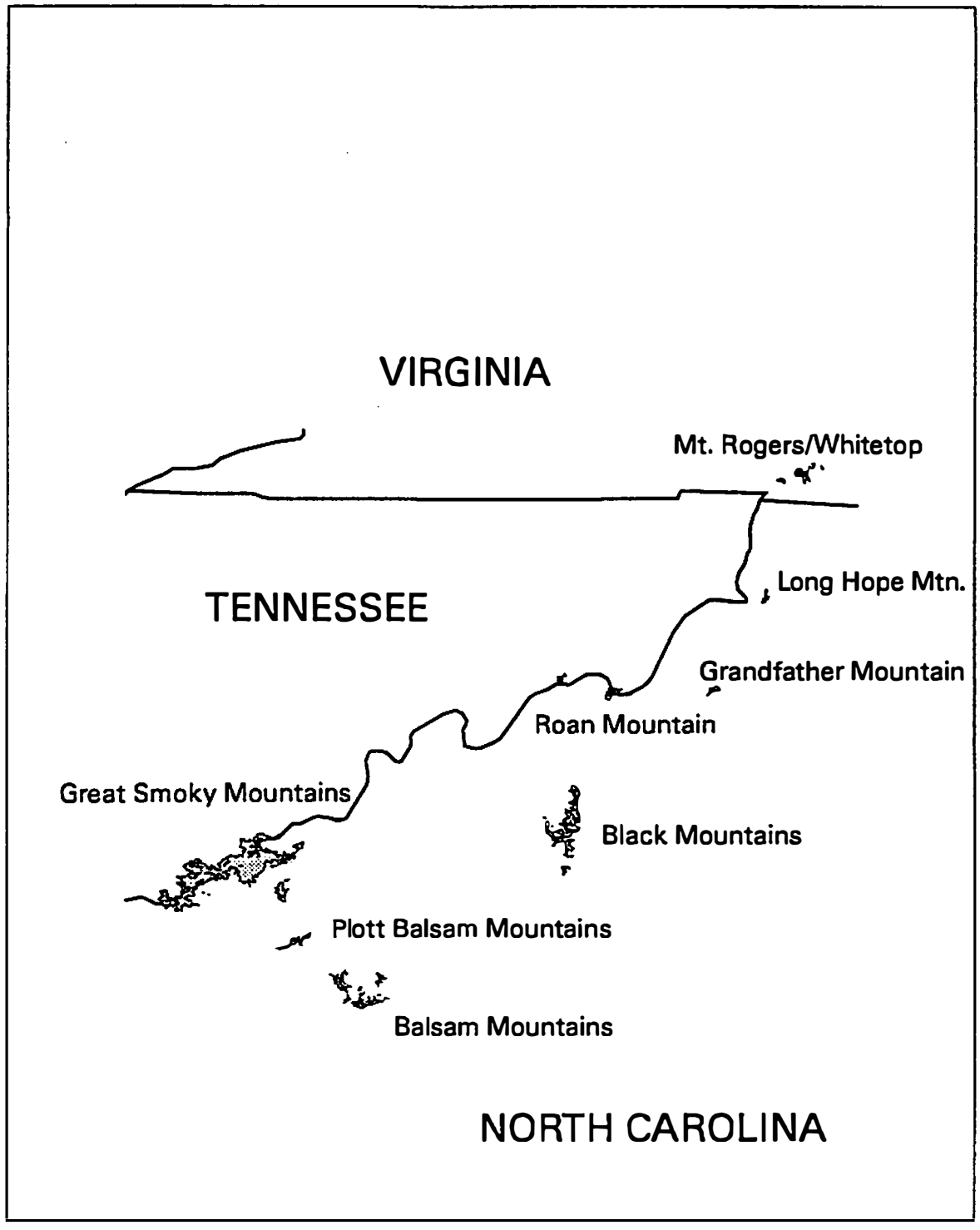

Fig. 2.1. Southern Appalachian spruce-fir forest areas.

for this theory is the abrupt end of the spruce-fir forests at 1680m at Double Springs Gap, in the Great Smoky Mountains, where the forest migrating downward after the hypsithermal period may have failed to invade a well-established beech stand (Whittaker 1956). In addition, Diebel and Feret (1991) found that Fraser fir on Mount Rogers have the low genetic diversity that suggest a severe historical gene pool reduction.

The geographic separation of a single eastern fir species is the more popular of two hypotheses explaining the evolutionary origins of *Abies fraseri* and the northern *Abies balsamea* (L.) Mill., balsam fir. The second hypothesis suggests that the two species were originally distinct but exchanged genes during the Pleistocene migrations. A comprehensive theory of the evolutionary relationships of eastern fir species must also account for the existence of *Abies balsamea* var. *phanerolepis* Fern., which occurs in northern Virginia and West Virginia and is sympatric in the northeast with *Abies balsamea.* According to the distinct species hypothesis, *Abies balsamea* var. *phanerolepis*, which is intermediate in physical characteristics to *Abies fraseri* and *Abies balsamea*, is explained as a hybrid of the two species (Jacobs et al. 1984). Most evidence suggests that Fraser fir originated from monospecific fir populations extending along the Appalachians in a continuous chain during the Pleistocene that was separated following glacial retreat (Robinson and Thor 1969; Thor and Barnett 1974; Jacobs et al. 1984; Hawley and DeHayes 1985). Differences in physical characteristics and wood chemistry between Fraser fir, intermediate fir, and balsam fir are consonant with the disjunct remains of a population that exhibited north to south clinal variation (Robinson and Thor 1969; Thor and Barnett 1974).

2.1.2 Pre-Infestation Physiognomy and Floristics

Ramseur (1960) identified 391 species and varieties of vascular plants in the high mountains of the southern Appalachians, 10.5% of which were characteristic of the region and elevation. White and Renfro (1984) listed 46 species as characteristic of the southern Appalachian spruce-fir type, eight of which were endemics. Despite this relatively high degree of endemism, only three tree taxa dominated the canopy: Fraser fir, red spruce, and yellow birch (*Betula lutea* Michx. f.). All nomenclature of southern Appalachian taxa follows Radford et al. (1968).

Cain (1935) observed that spruce became dominant or codominant in the canopy at about 1370 m elevation with fir increasing in importance at higher elevations until it constituted more than 80% of the stand in sites over 1830 m. Fir forests at the highest elevations, according to Cain, were composed of smaller trees that formed stagnant even-aged "pole stands" in many places. Whittaker (1956) also found that the distribution of spruce and fir followed an elevational gradient with spruce forests descending to 1370 m or lower on ridges and ascending to 1675 m. Spruce-fir forests occurred from 1675 m to 1890 m, above which fir forests dominated, with nearly pure fir stands in many locations. Ramseur (1960) concurred, observing that spruce and fir comprised 95% or more of the canopy individuals above about 1830 m. Crandall (1958) classified the canopy types somewhat differently: spruce-hardwoods (1460-1650 m), spruce (1560-1830 m where more than 80% of overstory basal area was red spruce), spruce-fir (1680-1950 m with less than 60% basal area in fir and less than 80% spruce), fir (1830+ m where more than 60% basal area was fir), and beech-birch gaps. Busing et al. (1993), using data from the 1930s, observed that fir dominated stand basal area in sites over 1800 m elevation, while spruce dominated stands across a broad range from

1100 m to 1900 m. Oosting and Billings (1951) observed that fir was on the average three to five times as abundant as spruce in mixed stands. Spruce, however, grows to a much larger size over its longer life and often comprised a much larger proportion of stand basal area.

Deciduous trees were much less important than spruce or fir. Yellow birch was the major hardwood and comprised 10-15% of overstory stems in some locations (Whittaker 1956). At lower elevation sites it was sometimes codominant with spruce or, in some moist, sheltered draws, it was the dominant species (Whittaker 1956; Busing et al. 1993). Deciduous taxa, usually considered northern hardwood or cove hardwood, that might have been found in lower elevation spruce-fir forests included: *Fagus grandifolia* Ehrh. (which could form nearly pure stands in gaps with some *Aesculus octandra* Marsh.), *Acer saccharum* Marsh., *Acer rubrum* L., *Acer pensylvanicum* L., *Prunus serotina* Ehrh., *Amelanchier arborea* var. *laevis* (Wieg.) Ahles, *Ilex ambigua* var. *montana* (T.&G.) Ahles, *Quercus rubra* L., *Tilia americana* L., and *Halesia carolina* L. (Korstian 1937; Crandall 1958; Whittaker 1956; Oosting and Billings 1951; Ramseur 1960; Busing et al. 1993). *Tsuga canadensis* (L.) Carr sometimes occurred in lower elevation spruce-fir forests (Ramseur 1960). *Betula papyrifera* var. *cordifolia* (Regel) Fernald was rarely found in the Great Smoky Mountains and Black Mountains (Ramseur 1960; White and Renfro 1984), but *Acer spicatum* Lam. was common throughout the spruce-fir forests except at the highest elevations where *Sorbus americana* Marsh. may have been the only deciduous tree present (Whittaker 1956; Ramseur 1960). *Prunus pensylvanica* L. f. was often the first tree species to regenerate after disturbance and could be found as a gap colonizer in the canopy at all but the highest elevations (Korstian 1937; Ramseur 1960).

In the understory, the shrubs *Viburnum alnifolium* Marsh. and *Viburnum cassinoides* L. were omnipresent along with *Vaccinium erythrocarpum* Michx.. *Rhododendron* spp., *Vaccinium corymbosum* L., and *Kalmia latifolia* L. formed dense shrub layers on more xeric ridges. *Sambucus pubens* Michx., *Rubus canadensis* L., and *Rubus idaeus* var. *canadensis* Richardson occurred in canopy gaps (Ramseur 1960; Whittaker 1956; Crandall 1958). Ferns, especially *Dryopteris intermedia* (Willd.) Gray and *Dryopteris spinulosa* (Mueller) Watt, were abundant in many places and percent cover of the small herb *Oxalis acetosella* L. was usually high. Mosses were ubiquitous and greatly increased with elevation; the most common was *Hylocomium splendens* which often covered live fir boles along with many lichens (Ramseur 1960; Crandall 1958; Whittaker 1956; Boner 1979). Whittaker (1956) found that on moist slopes often with a northern aspect, the understory may have consisted of five layers: 1) moss, 2) low herb (such as *Oxalis*), 3) fern, 4) low shrub, and 5) high shrub. Crandall (1958) noted that with decreasing elevation there was a gradual decrease in ground cover but a similar increase in species richness, especially with respect to moss, ferns, and *Oxalis*.

2.1.3 Comparison with the Boreal and Northern Appalachian Spruce-Fir Forests

Given the physiognomic similarities between the northern and southern Appalachian spruce-fir forests and also their similarities with the boreal forests of Canada and Alaska, it is tempting to group the three ecosystems into the unified heading of "boreal forest" (White 1984). Such lumping fails to distinguish the unique characteristics of each forest community. The boreal forest differs in several important ways from the montane spruce-fir forests of the Appalachians. The boreal forest occupies a lower elevation and higher latitude and generally receives less precipitation, much of which falls as snow. With respect to species composition,

Populus tremuloides Michx. and *Pinus banksiana* Lamb. are found in the boreal forests but not the Appalachian forests and the spruce component is *Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) B.S.P. while *Picea rubens* is characteristic of montane spruce-fir forests (White 1984; Oosting and Billings 1951).

Crandall (1958) noted that several site-types she determined for the Great Smoky Mountains spruce-fir communities on the basis of understory composition were very similar to the site-types developed by Heimburger (1934) for the Adirondack Mountains. In addition, Oosting and Billings (1951) estimated that 60% of all plant species they counted in the Great Smoky Mountains and the White Mountains were shared by both spruce-fir types. Similarly, White (1984) noted that 73% of vascular plant species in the Great Smokies spruce-fir forests were also found in northern Appalachian spruce-fir forests. Among the remaining 27% of species, however, many were rare and/or endemic. *Abies fraseri* was one of these endemic species; the fir of the northern Appalachians and boreal forests was *Abies balsamea*. Physiognomic differences existed between the north and south: trees in the south were of greater average size and growth rate, herbs and bryophytes were more abundant in the south, and, unlike the north, a layer of evergreen shrubs (e.g., *Rhododendron* spp.) occupied the more xeric sites (Korstian 1937; White 1984). Some of these differences in vegetation may have been attributable to the long period of genetic separation and others to variation in climate and soil. In the southern spruce-fir ecosystem, temperatures were more moderate and precipitation is higher. Soils in the south tended to have a much shallower organic layer: 2-7 cm as opposed to 20-25 cm in the north (Oosting and Billings 1951). Disturbance regimes in the southern Appalachian spruce-fir forests were dominated more by small-scale windthrows, while the north had a higher incidence of ice storms, insect outbreaks (except the balsam

woolly adelgid), and fires (White 1984). Oosting and Billings (1951) and White (1984) concluded that southern Appalachian spruce-fir forests are a distinct variant of the family of spruce-fir ecosystems with several unique characteristics.

2.2 Disturbance in Spruce-Fir Forests

2.2.1 Stand Dynamics

White et al. (1985) observed that natural disturbances in spruce-fir forests fall into three main categories: lightning fires, relatively unimportant with a return interval of more than 10^7 yr; debris avalanches, locally important and affecting about 2% of the spruce-fir area; and windthrow, the most important. Windthrow can be further divided into relatively large gaps (more than 200 m^2), the more common small gaps, and the qualitatively different large blowdowns found in fir forests over 1900 m elevation. Small gaps, more than 75% of which are caused by a single tree, affect the largest total area. These allow advance regeneration of spruce and fir, which can survive in the understory for over 50 years, to reach the canopy or encourage the germination or sprouting of faster growing deciduous trees. Community structure has been found to remain relatively stable and uneven-aged over time (White et al. 1985). The rarer large gaps tend to favor hardwoods, especially *Prunus pensylvanica*. Windthrow of fir in large patches, however, fosters the establishment of even-aged fir stands that ultimately form the stagnant "pole stands" observed by Cain (1935).

Nicholas and Zedaker (1989) suggested that the small-scale disturbance model may not be applicable to second-growth spruce-fir stands. They encountered widespread damage and significant mortality of previously intact spruce trees in formerly logged stands in the Black Mountains after a winter of severe ice storms. Fir had the largest survivorship after the

storms and damaged fir proved three times as adept at reestablishing apical dominance than spruce after losing their tops. This observation suggests an adaptation to a historically important disturbance regime at high elevations. Busing et al. (1993) suggested that the impact of wind and ice storms at high elevations favors canopy dominance by fir rather than spruce. They noted that at high elevations, spruce is largely confined to sheltered draws and rarely achieves the larger diameters observed at lower elevations while fir is abundant on shallow-soiled ridges and summits.

In balsam fir forests in the northern Appalachians and in montane forests of *Abies veitchii* Lindl. and *Abies mariesii* Mast. in Japan, unique patterns of regeneration known as "fir waves" are observed (Sprugel 1976; Kohyama and Fujita 1981). Fir waves are characterized by a crescent-shaped wave of mortality moving through a stand at a rate of 0.6 to 3.1 m/yr (Moloney 1986). Canopy trees at the edge of the wave are killed by exposure to prevailing winds (Sprugel 1976). In the wake of the wave of mortality, the fir forest regenerates as a series of even-aged stages from seedling to canopy fir until the next wave edge is reached. Moloney (1986) observed similarities between fir wave regeneration cycles and patch regeneration in non-wave areas. He proposed that rather than a major alteration of the size and age structure of balsam fir populations, fir waves arise from a spatial reorganization of regeneration stages. Fir waves have not been observed in the southern Appalachians (White 1984).

2.2.2 **Insects and Disease**

The southern Appalachian spruce-fir forests are more fortunate than those in the north in that biotic disturbance agents in the form of insects (except the balsam woolly adelgid),

fungi, and other pathogens are rare or generally innocuous. Bruck (1989) described as "remarkable" the lack of non-adelgid insect damage suffered by spruce and fir. He found eight different insect parasites or predators on spruce and fir, but none had important deleterious effects; spruce budworm was not found. Similarly, 21 spruce and fir fungal pathogens were identified, but all, including the lethal *Cytospora* canker and *Armillaria* root rot, were rare and of negligible importance. The spruce bark beetle was found on Whitetop, VA, in 1988 but did not appear to be a major cause of mortality (Nicholas 1992). Predation of Fraser fir seed by the seed chalcid, *Megastigmus specularis* Walley, was not included in Bruck's survey. From studies on Roan Mountain, Fedde (1973a) discovered that about 3% of seeds are damaged by the chalcid, but that this amount increased tenfold when the cone-bearing fir is or has been infested by the balsam woolly adelgid.

2.2.3 Early Anthropogenic Impacts

Anthropogenic disturbances in the southern Appalachian spruce-fir forests vary widely by mountain area. As a general rule because of the inaccessibility of the high mountain forests, the spruce-fir forests were frequented by few European settlers and probably few Native Americans before the construction of logging railroads. Some livestock grazing occurred and certain mountains, such as Mount Mitchell (in the Black Mountains) and Mount Rogers, were popular tourist destinations in the nineteenth century (Pyle and Schafale 1988). Fires occasionally spread into the spruce-fir forests from deciduous forests being cleared for farming below; also some forest fires were accidentally set by hunters. Pyle and Schafale (1988) estimated that 10% of the spruce-fir forests on the east slope of Mount Mitchell burned

in such fires before logging occurred. Overall, pre-logging human disturbances to the spruce-fir forests were minor compared to the damage caused to the deciduous forests downslope.

When timber in the red spruce forests of the northeast became scarce, logging companies moved south to exploit this commercially valuable tree. Logging for spruce in the southern Appalachians began in 1905 on Mount Rogers and quickly spread south, with the most inaccessible area, the Great Smoky Mountains, cut last (Pyle and Schafale 1988). Logging in the rugged southern Appalachians required large capital outlays for railroad construction and land or timber right purchases. To profit, large scale mechanized operations were necessary. Korstian (1937) documented that the mechanized steam or cable skidding practiced to remove the logs was extremely destructive to spruce and fir seedlings and saplings. Buildup of logging slash between the skidder lanes often covered the young trees that remained. Regeneration or planting after logging, however, was generally successful with fast-growing hardwoods and shrubs dominating for a length of time depending upon site quality before being overtopped by spruce and fir (Korstian 1937; Minckler 1940). Korstian (1937) qualified this scenario with the observation that after logging most spruce-fir land was laden with slash and increased sunlight desiccated the organic soil. Such land usually burned one to several times. Fire destroyed the advance regeneration of spruce and fir and removed much of the soil organic layer, increasing soil erosion.

On burned sites, if the soil had not completely eroded to rock as was the case in many locations, *Rubus* was usually the first colonizer, followed by fire cherry, *Prunus pensylvanica* (Korstian 1937). Spruce and fir were often unsuccessful in germinating under these conditions, especially if an established deciduous population has covered the ground with a tough layer of leaf litter that germinal conifer roots cannot penetrate (Korstian 1937; Pyle

1984). Pyle and Schafale (1988) observed burned sites previously supporting spruce-fir forest that sustained open stands of yellow birch, fire cherry, shrubs (especially *Rubus*), and grasses. Estimates vary, but it is possible that 50-90% of former spruce and spruce-fir forests in the central and southern Appalachians (including West Virginia) no longer exist because of failed regeneration (Korstian 1937; Pyle 1984). The Great Smoky Mountains was logged the least and lost only 4540 ha of the original 17,910 ha of spruce-fir forests, according to Pyle (1984).

After the post-World War I logging bust, state and federal agencies bought many spruce-fir forests, some logged over, out of a mixture of conservation motives goaded by public outcry and desire to protect important watersheds. Protection did not immediately halt the logging fires and small-scale logging and grazing occurred in areas like Mount Rogers that remained privately owned until recently (Pyle 1984; Pyle and Schafale 1988). Other post-logging disturbances varied widely among mountains and depended on ownership and land use, but included development for tourism and Fraser fir Christmas tree farming or harvesting. Most areas were allowed to regenerate naturally, but planting of native and exotic species was carried out in highly visible and/or badly burned areas. On Mt. Mitchell, twenty species of conifers, mostly exotics from the western U.S., Europe, and Asia, were widely planted. Minckler (1940) remarked on the fact that the two natives, *Abies fraseri* and *Picea rubens*, grew best while most others died out fairly quickly or survived only in stunted form. Two other species that Minckler also designated as successes were *Pinus resinosa* Ait., red pine, and *Picea abies* (L.) Karst., Norway spruce. Healthy individuals of the latter species, and possibly some of the others, are still present (Nicholas 1992).

2.2.4 Air Pollution

Reports of red spruce decline in the northern Appalachians (Siccama et al. 1982) have been attributed by many to air pollution and have raised concerns over its possible role in the southern Appalachian spruce-fir forests (White 1984). McLaughlin et al. (1987) found a similar annual growth increment decline in southern red spruce beginning in the early 1960s. Two forms of pollution that may be partially responsible for spruce decline are ozone and atmospheric deposition of anionic sulfur and nitrogen compounds.

Higher elevation sites tend to have greater atmospheric concentrations of ozone because they tend to remain above the surface boundary layer where ozone depletion occurs at night (Mueller 1994). Based on the effects of ozone on other species, such as loblolly pine (*Pinus taeda* L.), researchers were concerned that ozone may damage spruce chlorophyll or the wax layer on needle surfaces, thus leading to reductions in photosynthesis, decreased cold tolerance, and/or alterations in carbon allocation. Laboratory and field studies, however, have shown that red spruce is tolerant of ambient ozone concentrations and do not support ozone as a causal factor in spruce decline (DeHayes et al. 1991; McLaughlin and Kohut 1992; Thornton et al. 1994).

High elevation ecosystems in the southern Appalachians may be particularly susceptible to atmospheric deposition of sulfate and nitrogen compounds because of higher precipitation and cloud immersion levels. The large surface area of the needle-leafed spruce and fir trees collects large amounts of cloud moisture (White 1984). Shubzda et al. (1995) estimated cloudwater inputs of 40 cm/yr and 70 cm/yr at two sites on Clingmans Dome at 1740 m and 1920 m elevation. They found that cloudwater inputs of sulfate on Clingmans Dome comprise 40% and 50% of the total sulfate deposition at the two sites. Laboratory acid mist

and/or rain treatments of red spruce seedlings and field experiments excluding ambient cloudwater from spruce seedlings and branches of mature trees have suggested several mechanisms by which atmospheric deposition may contribute to spruce decline. Thornton et al. (1994) found that exposure to ambient cloudwater reduced spruce seedling foliar concentrations of calcium, magnesium, and zinc and suggested three possible mechanisms: foliar leaching by acidic cloudwater, soil leaching and reduced uptake, and interference with uptake by elevated soil levels of aluminum. Ambient cloud deposition has been found to reduce the cold tolerance of seedlings (DeHayes et al. 1991) and mature branches (Vann et al. 1992). Results of acid deposition studies, however, have produced contradictory results regarding effects on photosynthesis and growth (Kohut et al. 1990; Patton et al. 1991; McLaughlin et al. 1993; Thornton et al. 1994).

Another potential factor in spruce decline arising from atmospheric deposition is nitrogen availability in excess of plant demand, or nitrogen saturation. Stream exports of nitrate from spruce-fir forests in the Great Smoky Mountains are high throughout the year and contribute to chronic and episodic stream acidification, indicating that these ecosystems are nitrogen saturated (Flum and Nodvin 1995; Nodvin et al. 1995). McNulty et al. (1996) fertilized a Vermont montane spruce-fir stand with NH_4-N and NO_3-N for six years. In contrast to research on strong acid anion inputs, they found no differences in the form of nitrogen applied. Net basal area growth moderately decreased in plots receiving > 25 kg N/ha·yr. Foliar concentrations of nitrogen were positively correlated with added nitrogen and negatively correlated with changes in net basal area growth. McNulty et al. (1996) suggested that excess nitrate was being exported from the system, which may leach calcium and magnesium from the soil. Cation leaching may have resulted in nutrient imbalances, as foliar

calcium : aluminum ratios inversely related to nitrogen fertilization suggested. Nutrient imbalances and deficiencies have been found to cause changes in carbon allocation which predispose trees to other stresses such as drought or freezing injury (McLaughlin and Kohut 1992). In addition, increases in nitrogen saturation may favor nitrogen demanding deciduous species and cause a species shift away from the slower growing spruce and fir (McNulty et al. 1996).

Some researchers doubtful whether southern Appalachian red spruce is in significant decline (Busing et al. 1988; Nicholas et al. 1992a). LeBlanc et al. (1992) suggested that the current decrease in incremental growth of southern red spruce is not greater than historical levels. Reams et al. (1993) quantified the cyclic behavior of radial growth trends and revealed that since the mid-1960s, radial growth has not simply decreased but has increased and decreased twice. They also speculated that overall spruce growth decrease is part of a long-term, climate-induced cyclic fluctuation. In support of this idea, they pointed out that a local maximum in radial growth preceded the 1960s decline. They concurred with LeBlanc et al. that the recent downward trend is not unusual when compared with data from the past 200 years. If southern spruce is suffering unusual incremental growth reductions, other factors may be responsible, including drought (Adams et al. 1985) and the sudden increase in exposure to wind and ice storms after the death of neighboring fir (Zedaker et al. 1988; Nicholas et al. 1992a).

Hain and Arthur (1985) proposed that atmospheric deposition may weaken or predispose Fraser fir to attack by the balsam woolly adelgid and noted that *Abies alba* Mill. in Germany seems to be highly pollution sensitive. Hollingsworth and Hain (1991) and McLaughlin et al. (1994) suggested that calcium deficiencies in fir caused by leaching of basic

cations from the soil may increase fir vulnerability to the adelgid. Since calcium may be limiting for cambial growth, infested trees lacking the nutrient may have a slower and less complete wound response to adelgid attack.

2.3 The Balsam Woolly Adelgid

2.3.1 Life Cycle

The balsam woolly adelgid, *Adelges piceae* Ratz., is a small, wingless insect whose North American populations are entirely female and parthenogenic (Balch 1952; Eagar 1984). An adelgid lays an average of 100 eggs and as many as 250 (Balch 1952; Amman and Speers 1965). The first instar, less than 0.5 mm long, is the only motile stage of the insect. This "crawler" locates a suitable feeding spot on the fissured bark of a mature fir, inserts its stylet, and enters diapause for two to eight weeks during which its legs and antennae atrophy. After diapause, the adelgid begins feeding and rapidly passes through the second and third instars to the adult stage, which is purplish-black and less than 1 mm in length. After breaking diapause, the adelgid begins producing long, curling, white wax threads that entirely cover it by adulthood (Balch 1952; Amman 1962; Amman 1970; Amman and Speers 1965; Eagar 1984). The balsam woolly adelgid populations produce at least two generations per year in North America (Balch 1952), three under more temperate conditions not uncommon in the south, and Amman and Speers (1965) observed as many as four generations during one year. The adelgid overwinters as a first instar with that generation known as the hiemosistens and the other(s) known as the aestivosistens, though there is little biological difference between them (Balch 1952; Eagar 1984). The adelgid is primarily disseminated by wind, but also by gravity, humans, other animals, and nursery stock.

2.3.2 Introduction and Spread

The balsam woolly adelgid is thought to be native to Caucasia. It exhibits a complex life cycle with sexual forms on its primary host, *Picea orientalis* Carr., and parthenogenic forms on any true fir. In the nineteenth century, it spread throughout Europe, possibly losing sexual reproduction outside the range of its primary host (Balch 1952). In central and western Europe, it feeds on *Abies alba,* causing only minor damage (Eagar 1984).

It was first discovered in Maine in August, 1908, after apparently being introduced on imported nursery stock several years prior (Kotinsky 1916). In the southern Appalachian spruce-fir forests, it was encountered first on Mount Mitchell in October, 1957 (Speers 1958). Severe mortality of Fraser fir and rapid spread of the adelgid followed: in 1958 11,000 trees were estimated dead and an aerial survey in 1960 found over 200,000 trees dead, representing about 7% of the Black Mountains area (Amman and Speers 1965). Since the first infestation in the southern Appalachians was in the center of distribution of Fraser fir, it seems unlikely that the adelgid was carried by the wind over the great distance to the Blacks from infested balsam fir in the north while missing the more northerly Mount Rogers, Roan Mountain, and Grandfather Mountain, but rather was introduced by human activity. It seems more likely that the adelgid was introduced to Mount Mitchell on trees planted to restore logging damage to the spruce-fir forests. Other possible vectors include the aforementioned transport on clothes, vehicles, or animals (Eagar 1984).

From Mount Mitchell, the adelgid spread throughout the Black Mountains and was detected on Roan Mountain in 1962 and Grandfather Mountain in 1963. In 1963, aerial surveys detected 45 dead and dying trees north of Mount Sterling on the east side of the Great Smoky Mountains National Park; ground truthing revealed the presence of the adelgid (Ciesla

et al. 1963). Subsequent surveys tracked the spread of the adelgid west through the Great Smokies first to Cataloochee Knob and then the southeast slope of Mount Guyot (Ciesla et al. 1963, 1965; Lambert and Ciesla 1966, 1967). During the 1970s, spread of the adelgid was not well monitored. Eagar (1978) deduced from patterns of mortality that it moved directly from Mount Guyot to Mount LeConte and Clingmans Dome, creating a discontinuous pattern of infestation that later coalesced. Mount Rogers was believed to be free of infestation until small populations were discovered in 1979. Stem analysis of infested trees revealed adelgid-caused redwood, or "rotholz," beginning in 1962 in a pattern that indicated repeated infestation and recovery (Eagar 1984). At present, the balsam woolly adelgid is found throughout the native range of Fraser fir.

2.3.3 Infestation Symptomology and Mechanisms

Since the balsam woolly adelgid is usually wind disseminated, initial infestation of a stand typically began in the lower elevation spruce-fir forests on the lee side of the mountain where wind speed was sufficiently reduced to allow the insect to intercept the tallest trees of the stand. Although the dominant canopy trees are the first to be infested, suppressed trees with little vigor are the first to die (Eagar 1984). Amman and Speers (1965) found that death occurs rapidly, usually within two to five years depending on tree size and vigor and degree of infestation.

Amman and Talerico (1967) described two different manifestations of infestation in Fraser fir: crown infestation of branches, twigs, nodes, and bud bases and stem infestation. Stem infestation is the predominant form and is lethal to trees over about 4 cm diameter at breast height (dbh) that have the bark fissures in which the adelgid feeds. Smooth-barked

young trees are impervious to stem attack but may suffer from crown infestations which result in a set of symptoms collectively known as "gout": nodal swelling, shoot thickening, and tip inhibition. Defoliation, dieback, and/or increased stem taper may also occur (Amman and Talerico 1967; Eagar 1984). Crown infestation of the understory is usually lethal only under a heavily infested overstory and recovery is possible if the young tree is not seriously damaged by the time the older trees die and the rain of insects ceases (Eagar 1984). Unless infestation is particularly heavy, needle color change to yellow-green then red then brown is often the first sign of a stem attack since the majority of adelgids tend to feed within the base and lower two-thirds of the crown and can be best detected by tree climbers (Ciesla et al. 1965).

During feeding, the balsam woolly adelgid injects salivary compounds into the bole of the host tree which stimulates the cambium to produce abnormal xylem composed of shorter, heavily lignified tracheids and increased numbers of ray cells. Balch (1952) demonstrated similarities in tissue response to auxins and adelgid saliva. The affected xylem forms wider than normal annual rings that are a dark red in color, anatomically resembling compression wood, that are called "rotholz" (Balch 1952; Puritch 1971). Hollingsworth et al. (1991) discovered that increasing levels of infestation cause the tree to produce proportionally greater amounts of rotholz which in turn cause an increasing and significant reduction in sapwood conductance. In other words, the balsam woolly adelgid produces water stress in infested Fraser fir.

In permeability experiments with the wood of infested grand fir (*Abies grandis* (Doug.) Lindl.), Puritch (1971) observed that sapwood permeability of the damaged trees was only about 5% of that of non-infested sapwood although no rotholz was produced. Subsequent experiments revealed that reduced conductivity was caused by a combination of larger

amounts of air-filled tracheids and lignification of the pores in bordered-pit membranes in infested xylem (Puritch and Petty 1971; Puritch and Johnson 1971). The infested sapwood had conductive properties, color reaction with perchloric acid, and appearance of pit membranes under electron microscopy similar to those of heartwood. Puritch and Johnson (1971) concluded that the adelgid causes water stress in infested trees by inducing premature heartwood formation. Hollingsworth and Hain (1991) concurred and further suggested that adelgid feeding reduces xylem pressure potential which leads to cavitation of tracheids which may accelerate heartwood formation. A further hypothesis associating rotholz and heartwood formation suggests that the increase in flow resistance generated by rotholz also causes a more negative xylem pressure leading to heartwood production as described above (Hollingsworth et al. 1991).

Observations that heavily infested areas on fir bark may support only a few insects in the next adelgid generation appears to be the result of the formation of a secondary periderm layer (Hollingsworth et al. 1991). This wound response mechanism seems to be incomplete in most Fraser fir, although *Abies alba* and *Abies balsamea* respond more vigorously and may recover (Balch 1952). Hollingsworth and Hain (1992) observed that infested Fraser fir on Mount Rogers produce more outer bark at a higher rate than infested fir on Mount Mitchell and suggested that this difference in bark response explains the resistance of the Mount Rogers population to adelgid attack.

2.3.4 Population Dynamics and Control

The balsam woolly adelgid is extremely resistant to climate-induced mortality. Direct sunlight causing high bark surface temperatures can kill by desiccation, although the waxy

exudate of the second instar and older stages offers some protection. There is no indication that this is a significant cause of mortality (Eagar 1984). Temperatures as low as -8°C are needed to kill eggs and are not found in the southern Appalachians during the time of year when adelgids lay eggs. Other stages are more resistant. Overwintering first instar populations were once observed to partially withstand an overnight temperature of -33.8°C on Mount Mitchell (Amman 1970) and two nights of -35°C in Canada (Balch 1952).

In North America, there are no known diseases or parasites of the adelgid (Balch 1952; Eagar 1984). Native and introduced predators of the adelgid have had little effect (Amman 1970). One introduced coccinellid species has been recovered recently at Mount Mitchell (Humble 1994); Balch (1952) described the successful introduction and rapid spread of *Leucopis obscura* Hal. (Diptera: Chamaemyiidae), a predaceous fly. Failure of predators to control the adelgid is caused by limited searching ability, failure to prey upon eggs or first instars, and the high fecundity of the adelgid (Balch 1952; Eagar 1984). The only biotic factor limiting adelgid populations, and the most important limiting factor overall, appears to be the carrying capacity of the host tree. The most vigorous trees prior to infestation will ultimately support the highest adelgid populations. Adelgid numbers increase throughout infestation until one to two years prior to host death when they dramatically decline (Amman 1970; Fedde 1973b).

Human applied control efforts to reduce the spread of the adelgid have likewise failed. The first infested trees detected in the Great Smoky Mountains were cut down to slow the rate of infestation, but these sanitation cuts were soon discontinued when it was discovered that eggs and crawlers are detached during the felling and could be carried a considerable distance by wind (Ciesla et al. 1965; Lambert and Ciesla 1966). Various insecticides have been tested

and proved effective, with application of $^1/_8$% lindane emulsion (gamma isomer of benzene hexachloride) found to be the most effective (Amman and Speers 1965). Since the adelgid is a stem-feeder, aerial application techniques do not work and spraying the entire bole by hand is required. Stands in a 60 m wide margin on either side of access roads have been sprayed with lindane annually during the 1960s and '70s at Mount Mitchell and during the 1970s at Roan Mountain (Eagar 1984). At present this practice has been discontinued due to cost and limited effectiveness as well as concerns about lindane's persistence and toxicity. A less toxic alternative, potassium oleate soap, is currently applied annually to stands in the Great Smoky Mountains National Park around the parking lot at Clingmans Dome and the trail to the observation tower, and roadside accessible stands on Balsam Mountain (Eagar 1984; K. Johnson, personal communication). Currently, the program is budgeted on an annual basis and may be eliminated in the near future because of cost, limited effectiveness (only one generation is impacted), and the negative reaction of Park visitors when access to Clingmans Dome is closed for a week for treatment (K. Johnson, personal communication).

2.4 Current Status of the Spruce-Fir Ecosystem

2.4.1 Overstory Changes

The spruce-fir ecosystems of the southern Appalachians have changed dramatically following adelgid infestation. Directly comparable data from pre- and post-adelgid periods, however, is rare. Busing et al. (1988) and Busing and Clebsch (1988) resampled three 0.405 ha plots established in the Great Smoky Mountains before adelgid attack. They found that live basal area has seriously decreased from the death of large fir.

Nicholas et al. (1992a) compared data collected from 66 plots in the Great Smoky Mountains in 1985 and 1986 with measurements from 1946 by Oosting and Billings (1951) in 7 plots in the Smokies. Total live basal area in 1985 and 1986 was found to decrease with elevation, similar to 1946 patterns; however, live fir basal area values were only 8-62% of those recorded by Oosting and Billings. When recently dead fir basal areas were added, Nicholas et al. observed that fir basal areas of the two studies compared fairly well. Spruce basal areas were found to have increased somewhat. In 1985 and 1986, overstory fir density had decreased to 576 stems/ha at 1830m elevation and 744 stems/ha at 1980m from 1946 densities of 897 stems/ha and 1310 stems/ha, respectively (Oosting and Billings 1951; Nicholas et al. 1992a). Although no quantitative studies were performed in the Black Mountains prior to infestation, Nicholas et al. (1992a) failed to find notable differences between overstory structure among their 40 Black Mountains plots and the 66 Smokies plots when logging disturbances and differences in time of infestation were taken into account. In contrast to the decimation at the these sites, Nicholas et al. (1992a) noted that current basal areas and densities of live fir at Mount Rogers were more than an order of magnitude greater than those in the Blacks or Smokies, reflecting the much smaller impact of the adelgid.

Other studies have revealed similar patterns. Boner (1979) compared relatively uninfested stands in the western part of the Great Smoky Mountains with stands in the Smokies and Black Mountains where canopies had been opened due to fir death for up to twenty years. Although his results were somewhat confounded with elevation and site differences, he found that total overstory density and basal area and fir density and basal area were negatively correlated with length of time since infestation. Boner (1979) and DeSelm

and Boner (1984) reported, however, that by 11-20 years after canopy opening, young fir were beginning to enter the overstory again.

2.4.2 Community and Ecosystem Implications

There are many implications of the decimation of Fraser fir and subsequent canopy opening. As mentioned above, spruce may be exposed to greater amounts of wind and sun with detrimental effects to incremental growth and total density (Nicholas et al. 1992a). On the other hand, in sites with originally lower numbers of fir, spruce may respond positively to the loss of competing fir (Zedaker et al. 1988; Reams et al. 1993). Other, mostly understory, arboreal taxa seem to be increasing in numbers over time since canopy opening, including: *Acer pensylvanicum, Ilex ambigua* var. *montana, Acer spicatum, Amelanchier arborea* var. *laevis, Betula lutea,* and *Prunus pensylvanica* (DeSelm and Boner 1984). Responses of *Sorbus americana* to increased levels of light are unclear because of significant mortality rates observed in the late 1980s. Damage from the exotic mountain-ash sawfly (*Pristiphora geniculata* Hartig) is thought to be at least partially responsible (Nicholas 1992).

Understory shrub, herb, and bryophyte changes have been quantified by Boner (1979), and DeSelm and Boner (1984). Shrubs that increased markedly in density or cover in adelgid-disturbed plots included *Sambucus pubens, Vaccinium erythrocarpum,* and especially *Rubus canadensis,* while *Viburnum cassinoides* was not detected in any disturbed plots. *Rubus* density, in fact, was found to increase nearly tenfold from the average undisturbed sites compared with the plots that had been impacted by the adelgid for 16-20 years (Boner 1979). Busing et al. (1988) similarly noted that *Rubus* occupied 25-50% of two 0.405 ha plots that were without the shrub prior to the adelgid and most likely invaded in response to increased

levels of light and temperature. Boner (1979) and Pauley (1989) both found that *Rubus* density was correlated with southwestern aspect and lower elevation, providing further evidence that *Rubus* responded to increased light and temperature. Fraser fir tends to support more epiphytic lichens, mosses, and liverworts than red spruce. Nearly half of the 203 known bryophyte species in the Great Smoky Mountains spruce-fir forests may be affected by changes in the canopy, including six endemic or widely disjunct obligate fir epiphytes (Harmon et al. 1983; Smith 1984).

Total ground cover of herbs and bryophytes has remained relatively constant since adelgid infestation for a given elevation, although composition has changed. Boner (1979) found that *Oxalis acetosella* decreased from an average of 32% cover in uninfested stands to 6% in stands that had experienced major canopy fir mortality 16-20 years earlier. Moss cover had similarly declined by about 9% over the same time period. These floristic changes resemble those observed in large canopy gaps prior to infestation. After investigating a large blowdown in a fir forest on Clingmans Dome, Crandall (1958) reported that moss and *Oxalis* together comprised less than 1% of the ground cover while fern cover was 60% and herb cover 57 percent. In a nearby undisturbed stand, moss covered 38% of the area, *Oxalis* nearly 50%, ferns 94%, and herbs only 8 percent. Although it appears that death of the fir overstory and resultant canopy opening has and will continue to have serious impacts on relative abundance of understory species, little is known about the autecology of many of them (DeSelm and Boner 1984). This fact hampers accurate predictions of future abundance, especially with respect to the many rare and endemic taxa found in the southern Appalachian spruce-fir forests.

In addition to impacts on vegetation, relative abundances of animals may be affected by the demise of Fraser fir. Changes in canopy structure and fir seed availability may adversely impact some species of birds and mammals. Censuses in 1969 and 1985 on Mt. Guyot in the Great Smoky Mountains documented a decrease in total bird density with decreases in 10 species and increases in six (Hall 1989). Increased insolation may desiccate and warm the soil of this perpetually moist and cool habitat, possibly impacting species of salamander and invertebrates (Matthews and Echternacht 1984). The federally endangered spruce-fir moss spider (*Microhexura montivaga*) is probably declining because of desiccation of the moss mats in which it lives (USDI Fish and Wildlife Service 1995).

Ecosystem processes, such as nutrient cycling and energy flow and disturbance regimes, may also be affected. Decomposition processes, and thus the rate of nutrient cycling, may accelerate with greater soil insolation. Large amounts of dead fir wood provide greater nutrient influxes over the short term. Such changes in ecosystem processes are not limited to the spruce-fir forests, however, since these high elevation sites are found at the headwaters of important southern Appalachian watersheds, including 17 of 28 major watersheds in the Great Smoky Mountains National Park (Pyle 1984) and the Asheville, NC watershed. Potential changes in disturbance regime include the greater possibility of windthrow and ice storm damage discussed above and increased probability of fire. Adelgid-caused mortality has increased fuel loading in spruce-fir forests with greater fuel levels occurring at higher elevations, corresponding with pre-infestation fir densities (Nicholas and White 1985). Nicholas and White also found that the most recently infested stands tend to support the highest coarse woody debris loadings. Standing dead basal area remained greater than downed bole basal area, probably because of the lower rate of decomposition of standing boles, which

could contribute over the long term to increased fire probability. Spruce, as a thin-barked, resinous, and shallow-rooted tree with a relatively low crown and poor self-pruning, is particularly susceptible to fire damage (Korstian 1937).

2.4.3 Fraser Fir Regeneration and Species Survival

One important result of canopy opening is the proliferation of Fraser fir seedlings. Boner (1979) reported that fir subsapling (0.6 m tall to 2.5 cm dbh) density was positively correlated with time since canopy opening and that percent cover of seedlings less than 0.6 m in height appeared to be stable over time. Nicholas et al. (1992b) found that proportions of seedling densities in the Great Smoky Mountains, excluding germinals, remained in a stable, inverse J-shaped survivorship curve. The exception to this was the declining numbers of 1-4 year old seedlings, possibly attributed to drought and/or the sporadic nature of seed crop germination. Nicholas et al. (1992b) also reported a total seedling (1 year to 1.37 m tall) density of 23,828 stems/ha, with 82% ≤ 0.25 m height, and germinal seedling density of 1389 stems/ha. In a study on Mount Collins using transects, Pauley and Clebsch (1990) found an average seedling density of 33,000 stems/ha, with 87% of seedlings ≤ 0.25 m. Witter and Ragenovich (1986) and Witter (1988) collected data on fir seedlings ≤ 244 cm tall on Mount Mitchell. When the plots were first sampled in 1966, more than 90% of the fir > 244 cm tall were dead; however, fir seedling densities were greater than 33,000 stems/ha for site-types designated "fir" or "spruce-fir" with considerably lesser densities in "spruce-fir-hardwood" low elevation stands. The plots were resampled in 1978 and 1985. Witter (1988) determined that seedling density declined over 19 years by 78% in fir sites and 68% in spruce-fir sites. A large part of this decrease was explained by growth of the young fir. In 1966, 1% of fir

seedlings were > 61 cm tall while 75% were > 61 cm in 1978, and the majority were over 1.5 m in 1985. Witter (1988) described live fir between 3 and 7 m tall as a "common sight" in the Mount Mitchell area. Nicholas et al. (1992b) cautioned against expecting future regeneration patterns in the Great Smoky Mountains and elsewhere to be identical to those in Mount Mitchell, since most plots used in the Mount Mitchell studies were in second-growth stands.

Perpetuation of Fraser fir requires not only survival of existing seedlings and saplings to cone-bearing age (20-30 years), but also the viability of seeds produced and successful growth of those seedlings in an altered environment. Fraser fir bear large seed crops every two to four years (USDA Forest Service 1974); one such bumper crop was produced in the Great Smoky Mountains in 1987 which yielded nearly 2.5 million seeds/ha at the highest elevations (Nicholas et al. 1992b). The same study, however, discovered that 88-100% of seeds were unfilled over a five year period. The best germination rate, which also occurred at the highest elevation fir forests, was only 0.3% including both filled and unfilled seeds. Whether germination rates were this low prior to the adelgid is unknown. Since adelgid infestation impairs seed production, however, mean germination rates may have been higher before adelgid infestation (Fedde 1973a). According to Fedde's (1973a) study on Roan Mountain, infestation reduced numbers of filled seeds by about 42%, including the aforementioned *Megastigmus* predation. Fedde (1973a, b) also reported that germination of filled seed decreases by 40% when the parent tree is infested and that cones were produced by infested trees only on the upper third of the crown and often only at the extreme tip.

Observations of the great increase in *Rubus* densities have prompted questions about the ability of this gap-invading species, and possibly others, to outcompete fir seedlings. Witter and Ragenovich (1986) investigated fir seedling occurrence by estimated competition

class and found that seedling numbers decrease significantly as competition increases. They identified competition as the major factor in the lesser numbers of fir seedlings found between 1966 and 1978 and indict *Rubus* as being by far the prime competitor. No mention was made, however, of the potential role of intraspecific competition as growing seedlings begin crowding each other. Data collected by Pauley (1989) and Pauley and Clebsch (1990) supported this conclusion by noting the negative correlation between fir seedling and *Rubus* densities, though not between *Rubus* densities and fir seedling annual growth rates.

The question of the probability of Fraser fir extirpation from southern Appalachian spruce-fir forests has not yet been answered satisfactorily. This uncertainty was reflected by the USDI Fish and Wildlife Service (1993) review of Fraser fir for possible listing as a threatened or endangered species. *Abies fraseri* was designated as Category 2, "...propos[al] to list as endangered or threatened is possibly appropriate...," and was marked as "declining." In February, 1996, however, the USDI Fish and Wildlife Service discontinued the Category 2 designation, citing confusion about the conservation status of such taxa. Fraser fir is currently not a candidate for listing under the Endangered Species Act (USDI Fish and Wildlife Service 1996).

Witter (1988) predicted that fir will survive based on observations of successful regeneration and cone-bearing trees. Witter and Ragenovich (1986) speculated that Fraser fir may evolve resistance to the adelgid. Eagar (1984) believed a cycle of infestation followed by regeneration, which survives to produce viable seed before death, is likely. Nicholas et al. (1992b) were more skeptical and suggested that neither is enough known about future seed viability nor if sufficient regeneration exists to mature and produce a vigorous understory numerous enough for perpetuation. Dale et al. (1991) used a Leslie matrix model of fir and

adelgid populations and predicted that both populations would persist and oscillate over space and time. Their model, however, overestimated fir germination in the field by an order of magnitude, used age rather than size as the determinant of infestation and reproduction, and failed to take into account community and disturbance factors, such as competition, windthrow, and alteration of the seedling environment due to canopy opening. Using a canopy gap replacement model, Busing and Clebsch (1987) simulated two scenarios over 300 years: 1) recurrent adelgid infestation with repeated fir regeneration and 2) fir extinction. In the first model, total stand basal area is predicted to decline, but recover in 65 years with fir remaining at only 20% basal area in a spruce-dominated system. In the second model, a low total stand density with a greater amount of spruce is the final outcome. Rheinhardt (1984) suggested that in the case of fir extinction, the remains of the southern Appalachian spruce-fir ecosystem will resemble Whitetop, VA.

Chapter III

Patterns of Overstory Composition

3.1 Abstract

In 1957, the exotic balsam woolly adelgid (*Adelges piceae* Ratz.) was discovered in the southern Appalachians. Soon after, it quickly spread throughout the spruce-fir forests, decimating adult Fraser fir (*Abies fraseri* (Pursh) Poir.) populations. In 1990 and 1991, a system of temporary and permanent plots was established on five mountains in the Great Smoky Mountains. Over the study area, almost 70% of total standing fir basal area is dead. Large scale patterns of overstory abundance are primarily dependent on elevation. Live fir density is positively associated with time since the major wave of mortality. Patterns of fir mortality, treefall rates, and recruitment determine the proportion of dead fir stems in the overstory. These three factors in turn are primarily dependent on time since major mortality. The interaction of mortality, treefall, and recruitment results in a right-skewed bell-shaped curve when the proportion of dead fir is plotted over time.

3.2 Introduction

Southern Appalachian spruce-fir forests occur in an island-like distribution on the peaks of the seven highest mountain areas in North Carolina, Tennessee, and southwestern Virginia (Oosting and Billings 1951; Ramseur 1960). The forest communities, relicts of the last glaciation, are rich in disjunct, rare, and endemic species (Delcourt and Delcourt 1984; White and Renfro 1984). Red spruce (*Picea rubens* Sarg.) and the endemic Fraser fir (*Abies fraseri* (Pursh) Poir.) are the characteristic tree species of the spruce-fir forests (nomenclature follows Radford et al. 1968). Fir typically dominates the canopy above 1890 m elevation; at

elevations of about 1675-1890 m, spruce is codominant (Whittaker 1956). Yellow birch (*Betula lutea* Michx. f.) is the most important deciduous tree species and sometimes dominates the canopy near lower elevation streams and seeps (Oosting and Billings 1951; Whittaker 1956). Mountain maple (*Acer spicatum* Lam.), fire cherry (*Prunus pensylvanica* L. f.), and mountain-ash (*Sorbus americana* Marsh.) are smaller hardwoods often found in spruce-fir forests (Whittaker 1956; Ramseur 1960).

These forests have been profoundly impacted by an exotic insect, the balsam woolly adelgid (*Adelges piceae* Ratz.). The adelgid was first detected in the southern Appalachians in 1957 (Speers, 1958), and has since spread throughout the fir and spruce-fir forests, killing enormous numbers of Fraser fir. The North American populations of this small wingless insect are parthenogenic and very fecund. An adelgid lays an average of 96 eggs, and in the southern Appalachians there are often three generations per year (Balch 1952; Amman and Speers 1965; Eagar 1984). The balsam woolly adelgid has no known parasites or diseases in North America. Native and introduced predators have had no success in controlling adelgid populations and human-applied control efforts have largely failed (Amman 1970; Eagar 1984). At present, the balsam woolly adelgid is found throughout the native range of Fraser fir and has greatly reduced the numbers of adult fir in all areas, except for Mt. Rogers, VA, where the trees are more resistant to the adelgid (Eagar 1984; Dull et al. 1988).

The adelgid feeds primarily in bark fissures of trees over about 4 cm diameter at breast height (dbh) (Eagar 1984). During feeding, the adelgid injects salivary compounds that cause the host tree to produce abnormally short and heavily lignified tracheids (Puritch 1971; Hollingsworth et al. 1991). This reduces sapwood conductance and produces water stress in infested Fraser fir, which usually die in two to seven years (Amman and Speers 1965; Eagar

1984). Smaller, smooth-barked trees are generally impervious to stem attack but may suffer from crown infestations which are usually lethal only under a heavily infested overstory (Eagar 1984).

The spruce-fir forest communities are changing rapidly in response to the catastrophic mortality of canopy fir. The resulting sudden increase in exposure to wind and ice storms ("thinning shock") may be partially responsible for red spruce mortality reported at some sites (Zedaker et al. 1988; Nicholas and Zedaker 1989; Nicholas et al. 1992; Busing and Pauley 1994). Abundances of some deciduous tree and shrub taxa are increasing in response to increased insolation (Boner 1979; DeSelm and Boner 1984). Nearly half of the 203 known bryophyte species in the Great Smoky Mountains spruce-fir forests may be affected by changes in the canopy, including six endemic or widely disjunct obligate fir epiphytes (Smith 1984). The endangered spruce-fir moss spider (*Microhexura montivaga*) is probably declining because of desiccation of the moss mats in which they live (USDI Fish and Wildlife Service 1995).

The large scale of this study allows investigation of differences in community dynamics among peaks that were subjected to major fir mortality at different times. I describe patterns in the overstory abundance in fir and fir-spruce forests at the highest elevations of five mountains in the Great Smoky Mountains National Park. Specific questions addressed by this study are: (1) what environmental variables are important in controlling overstory abundance and how they have changed from historical patterns; (2) how the proportion of standing dead fir stems (relative to live and dead standing stems) varies among mountains; and (3) what environmental variables determine the proportion of dead stems.

3.3 Methods

3.3.1 Study site and data collection

The study was initiated and data were collected by the Uplands Field Research Laboratory staff at the Great Smoky Mountains National Park. The study sites were five peaks in the Great Smoky Mountains National Park (GSMNP), from northeast to southwest: Mt. Sterling (1781 m elevation), Mt. Guyot (2019 m), Mt. LeConte (2010 m), Mt. Collins (1887 m), and Clingmans Dome (2025 m). Clingmans Dome and Mt. Collins were sampled in 1990; Mt. LeConte, Mt. Guyot, and Mt. Sterling were sampled in 1991. These five were chosen because as a group they include nearly the entire range of Fraser fir in the park. Areas that had been logged or burned were avoided when placing the permanent plots. Mt. Sterling was the first mountain to be infested by the adelgid, which subsequently spread westward throughout the Park. Major fir mortality occurred at the summit of Mt. Sterling in 1970-1972, on Mt. Guyot in 1980-1982, on Mt. LeConte in 1982-1984, on Mt. Collins in 1985-1987, and on Clingmans Dome in 1990-1992 (C. Eagar, personal communication). The median values of these intervals were used in estimating the number of years since major mortality in the statistical analyses below. Three permanent plots on Clingmans Dome and two on Mt. Collins were originally established in 1985 for the National Acid Precipitation Assessment Program and used by Nicholas et al. (1992a, 1992b). In 1995, these five plots were also resampled for a separate study using the methodology below.

To estimate overstory abundance, a total of 1337 temporary plots among all five mountains were established. Temporary plots were taken using horizontal point sampling (Husch et al. 1982) with a prism at sample points located at the intersections of a 50 × 50 m grid overlaying the summit of each peak to an elevation of 100 m below the summit. Basal

areas by species and live/dead status were calculated at each sampling point. (All discussion of "basal area" refers to stand basal area.)

Thirty-six 400 m^2 (20 × 20 m) permanent plots, corrected for slope, were established within 100 m elevation of the summits of the five mountains. Each mountain was to have two replicate plots in each of four stand types:

- pure live fir (PLF) with ≥65% overstory basal area in fir and ≥65% of those trees living
- pure dead fir (PDF) with ≥65% of overstory basal area in fir and ≥65% of those trees dead
- mixed live fir (MLF) with ≤35% of overstory basal area in fir, ≥65% of which is live, mixed with spruce and/or hardwoods
- mixed dead fir (MDF) with ≤35% of overstory basal area in fir, ≥65% of which is dead, mixed with spruce and/or hardwoods.

One PLF plot from Clingmans Dome, one PLF plot on Mount Sterling, one PDF plot from Mount Sterling, and one MLF plot on Mount Guyot were never established because a second replicate of the stand type could not be found on those peaks. Site variables, such as aspect, elevation, and percent slope, were measured and all live and dead overstory (diameter at breast height (dbh) (1.37 m above ground) ≥ 5 cm dbh) trees were tallied by species and measured for dbh.

3.3.2 Data analysis

I used multivariate analysis-of-variance (MANOVA) to test for differences in temporary plot basal areas among mountains. I also used MANOVA to test for differences among mountains, stand types, and mountain × stand type interactions for species basal areas and densities in the permanent plots. I followed significant MANOVAs with Ryan's Q

multiple comparisons tests to detect differences among particular mountains or stand types (Day and Quinn 1989). I performed a multivariate regression of live fir, spruce, and hardwood density and basal area on years since major mortality, elevation, slope, and aspect using the permanent plot data. Before use in the regression, aspect in degrees was transformed to a linear scale (Beers et al. 1966).

I used logistic regression to determine the importance of environmental variables in determining the percentage of currently standing dead stems. Logistic regression utilizes bivariate frequency data to predict the probabilities or proportions of the alternate values of the dependent variable, in this case, live and dead individuals (Hosmer and Lemeshow 1989). For the temporary plot data, I fit separate logistic models for fir, spruce, and hardwoods. Live and dead stem counts on all five mountains were regressed on the number of years since major mortality occurred on each peak and the elevation at the summit. A plot of the model coefficients versus the variable values for years since major mortality suggested that a quadratic term was also needed in the model. For the logistic regression of fir, spruce, and hardwood live and dead stem counts using the permanent plot data, the independent variables analyzed were years since major mortality, plot elevation, percent slope, and transformed aspect. Model coefficient plots did not indicate that a quadratic term for years since major mortality was needed for the permanent plot logistic regression. I conducted all statistical tests using SAS (SAS Institute 1989).

3.4 Results

3.4.1 Temporary plots

Fraser fir and red spruce occurred with four deciduous tree species (mountain maple, yellow birch, fire cherry, and mountain-ash) on each of the five peaks. Nine additional species occurred on Mt. Sterling, the lowest peak in the study, including black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.), and American beech (*Fagus grandifolia* Ehrh.). For comparison with spruce and fir, the other species were combined into a "hardwood" category in all figures and discussion below.

Despite a 15 year difference in time of major fir mortality at the summits, live fir basal area was lowest on the two lowest elevation peaks, Mt. Collins and Mt. Sterling (Fig. 3.1). The distribution of dead fir basal area among mountains was not well correlated ($r = -0.170$, $P < 0.0001$) with live fir basal area. Dead fir basal area was lowest on Mt. Sterling, the lowest and first infested peak. Basal areas of live spruce and live hardwoods were greater on the lower elevation Mt. Collins and Mt. Sterling than on the other three mountains.

The mean percentage of standing dead fir basal area, as a function of total standing fir basal area, for all five mountains was 68.2 percent. Mt. Collins had by far the largest percentage of standing dead fir while the nearby Clingmans Dome had the lowest (Table 3.1). Clingmans Dome had a much higher percentage of dead hardwood basal area than the other peaks.

To determine what variables best predict the proportion of standing stems that were dead, logistic regressions were fit for frequencies of live and dead fir and hardwoods (Table 3.2). The Pearson χ^2 goodness-of-fit tests showed a good fit for the hardwood model. The fit of the Fraser fir model was poor, although elevation, years since major mortality, and years

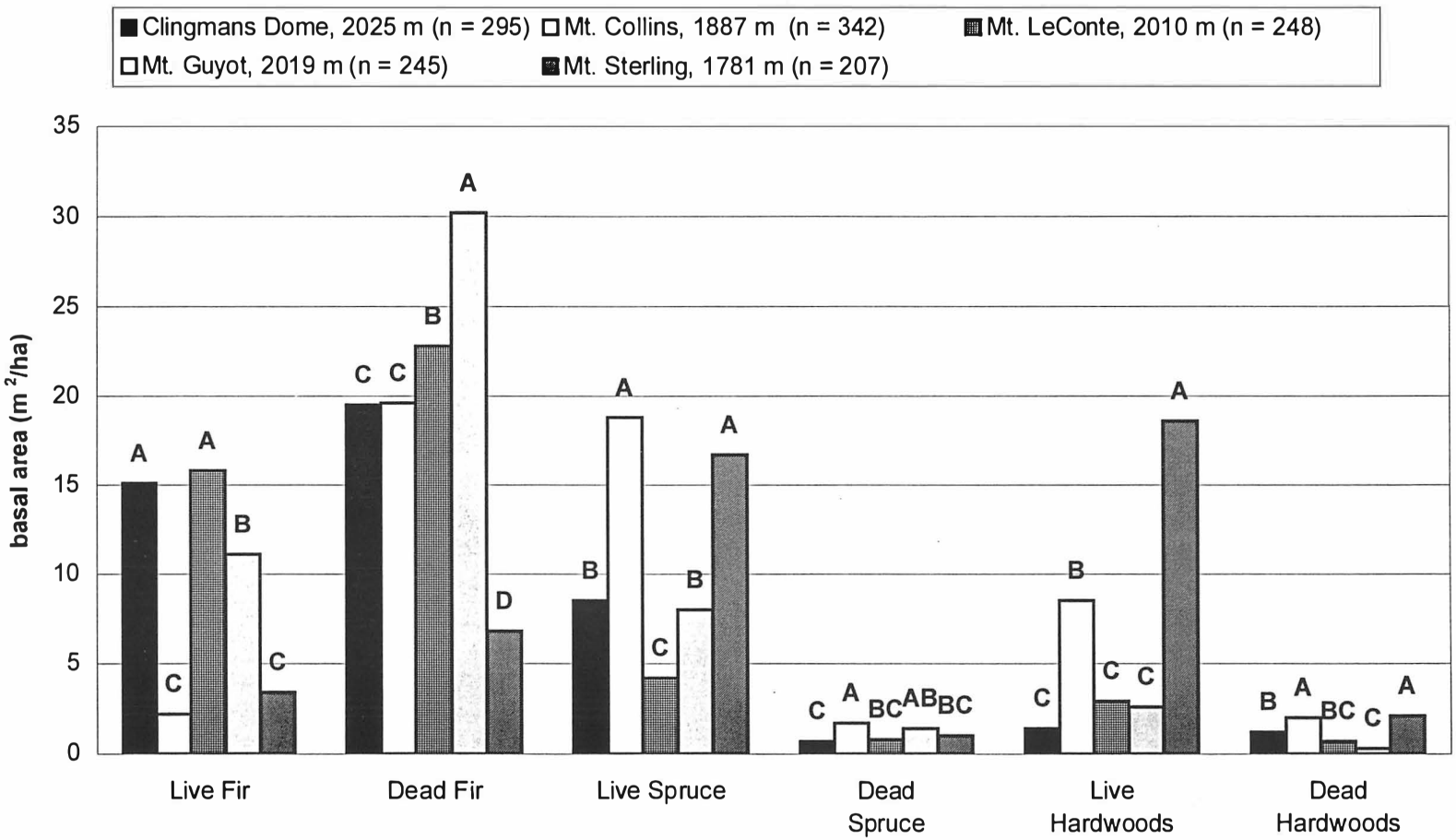

Figure 3.1. Temporary plot data- Live and dead fir, spruce, and hardwood stand basal area (m^2/ha) for five locations in GSMNP. Sample size (n) is the number of temporary plots. Means in the same live/dead-species category with the same letter are not significantly different ($\alpha = 0.05$) by Ryan's Q multiple comparisons tests following a significant MANOVA (F = 56.5286, 24 df, P = 0.0001).

Table 3.1. Temporary plot data—Percent of standing basal area that is dead (% ± standard error) for five locations in GSMNP.

	Clingmans Dome	Mt. Collins	Mt. LeConte	Mt. Guyot	Mt. Sterling
Fir	58.6 ± 1.9 (n = 291)[1]	90.9 ± 1.1 (n = 324)	65.9 ± 2.3 (n = 244)	78.6 ± 1.9 (n = 244)	67.3 ± 3.5 (n = 137)
Spruce	7.4 ± 1.5 (n = 187)	7.0 ± 0.8 (n = 319)	18.1 ± 3.4 (n = 99)	14.8 ± 2.2 (n = 160)	5.5 ± 1.2 (n = 175)
Hardwood	45.1 ± 5.0 (n = 89)	18.3 ± 1.8 (n = 279)	18.9 ± 3.5 (n = 101)	13.2 ± 3.9 (n = 64)	10.0 ± 1.4 (n = 183)

[1] Sample size (n) is the number of temporary plots.

Table 3.2. Temporary plot data—Logistic regressions of live and dead overstory fir, spruce, and hardwood frequencies on elevation, years since major mortality, and (years since major mortality)^2 for five locations in GSMNP. No independent variables were significant for spruce.

	Intercept	Elevation	Years	Years^2	Likelihood Ratio Test	Pearson χ^2
Fir (n = 1240)[a]	12.2528	-0.0059	0.0978	-0.0078	67.02 (df = 3, P<0.0001)[b]	6.57 (df = 1, P = 0.0104)[c]
Hardwood (n = 716)	-0.4045	-	-0.1969	0.0074	29.75 (df = 2, P<0.0001)	1.19 (df = 2, P = 0.5525)

[a] Sample size (n) is the number of temporary plots.

[b] Significant values for the likelihood ratio test indicate that one or more independent variables have a nonzero slope.

[c] Significant values for the Pearson χ^2 goodness-of-fit test indicate poor fit between observed and predicted distributions.

squared were all significant. I then assumed that the different proportions of dead fir on the five mountains could provide an adequate estimate of how the proportion of dead fir at one location changes over time. I used the Fraser fir equation to model the change in proportion of standing dead stems for one mountain of 1891 m elevation over time (the mean elevation of all permanent plots) (Fig. 3.2).

4.2 Permanent plots

Except for Mt. Sterling, mean live fir basal areas increased from west to east (Fig. 3.3). Mt. Sterling had significantly smaller mean live and dead fir basal areas and a significantly higher mean live hardwood basal area than the other four peaks. Live fir density was lower on the lower elevation sites (Mt. Collins and Mt. Sterling) than on Mt. Guyot and Mt. LeConte (Fig 3.4). No differences by mountain were detected for live or dead spruce or hardwood density. For the most part, overstory species abundances in the four stand types reflect stand type establishment criteria and are presented for completeness and to better characterize overstory composition in the stand types for the following chapters (Figs. 3.5 and 3.6). There are, however, two important differences between the mixed stand types. MLF stands have higher hardwood basal areas and densities than MDF stands. The live spruce in MDF stands are much larger than those in MLF stands as can be seen by comparing live spruce density and basal area in the two stand types.

Elevation and years since major mortality were significant independent variables for live fir density (Table 3.3). Both variables had positive regression coefficients, indicating that fir density is greater at higher elevations and on mountains that suffered major canopy mortality at earlier dates. Red spruce density and hardwood basal area had significant negative

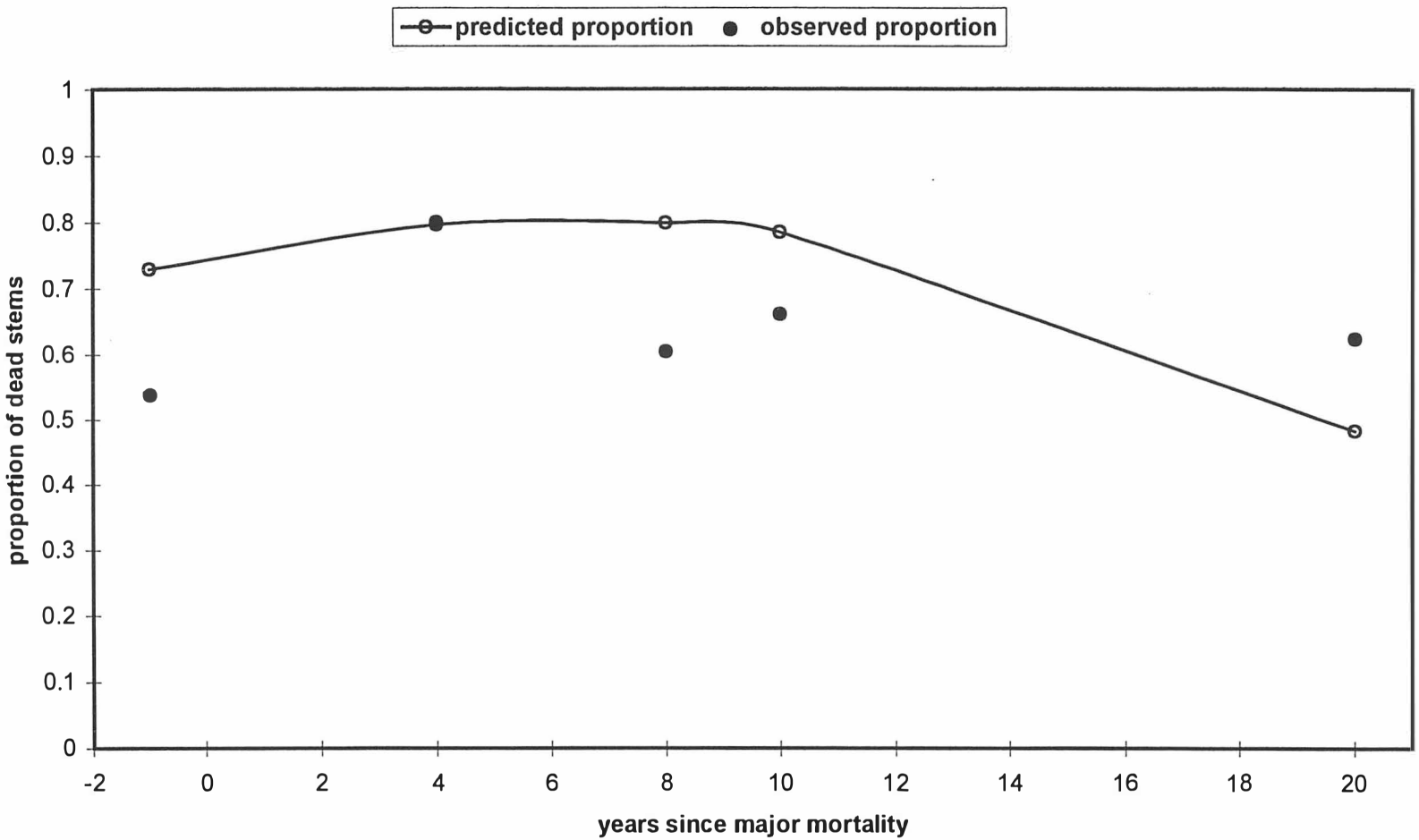

Figure 3.2. Temporary plot data- Predictions of the proportion of standing Fraser fir stems that would be dead on an 1891 m elevation mountain over time since major mortality based on logistic regression and data from five locations in GSMNP.

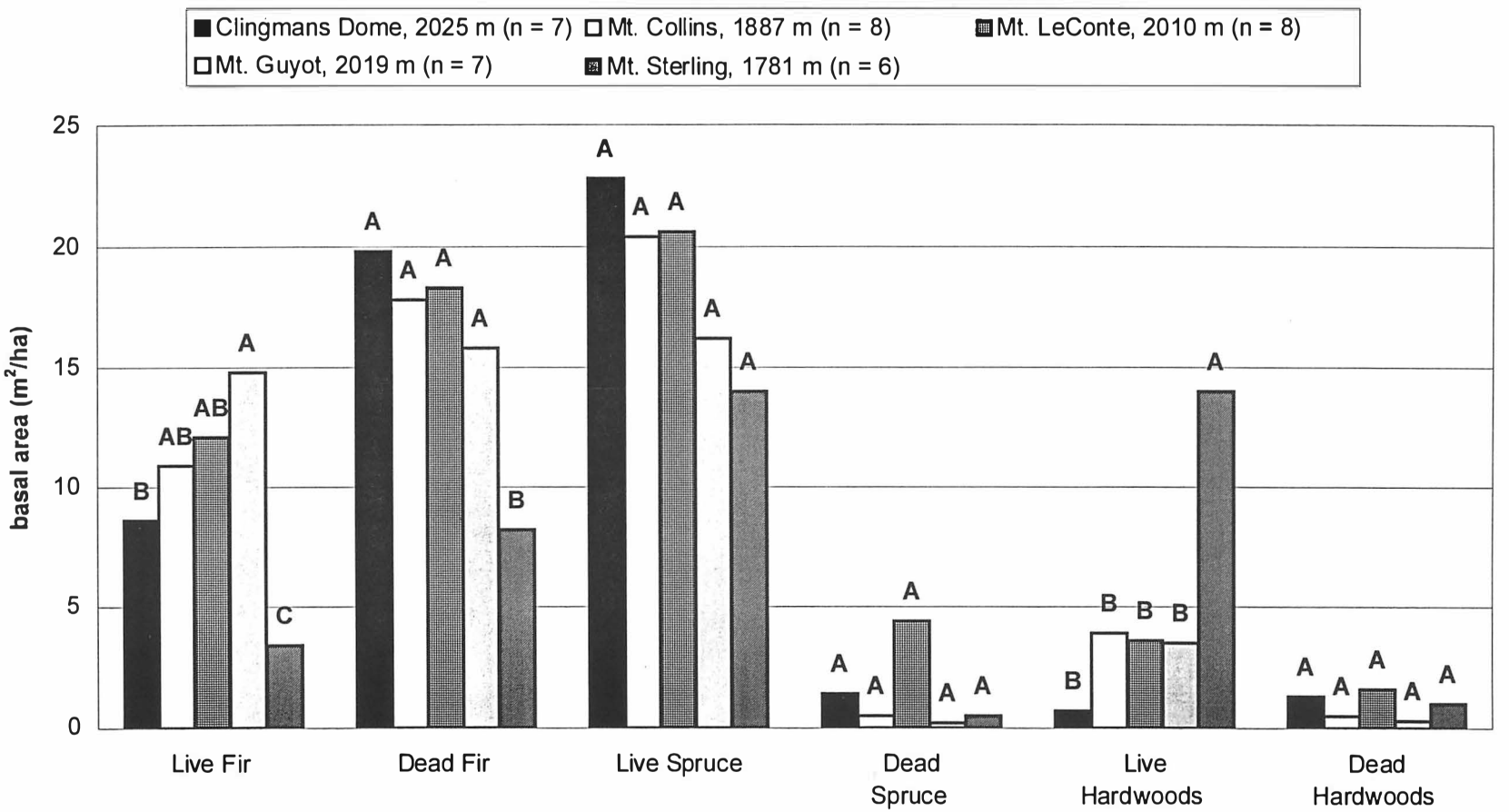

Figure 3.3. Permanent plot data- Live and dead fir, spruce, and hardwood basal area (m^2/ha) for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means in the same live/dead-species category with the same letter are not significantly different ($\alpha = 0.05$) by Ryan's Q multiple comparisons tests following a significant MANOVA (F = 2.5559, 24 df; P = 0.0043).

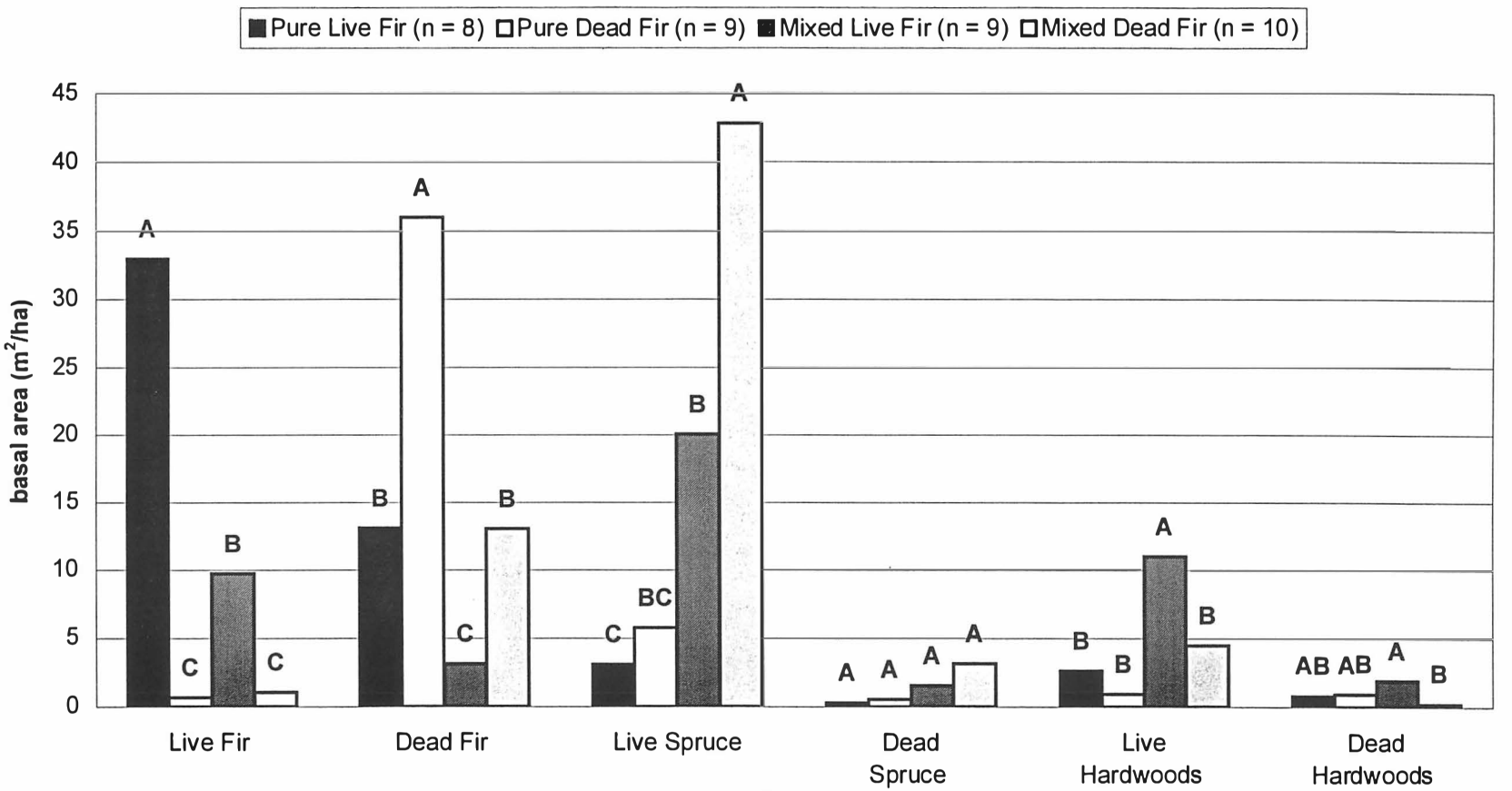

Figure 3.4. Permanent plot data- Live and dead fir, spruce, and hardwood basal area (m^2/ha) by stand type for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means in the same live/dead-species category with the same letter are not significantly different ($\alpha = 0.05$) by Ryan's Q multiple comparisons tests following a significant MANOVA ($F = 25.2075$, 18 df; $P < 0.0001$).

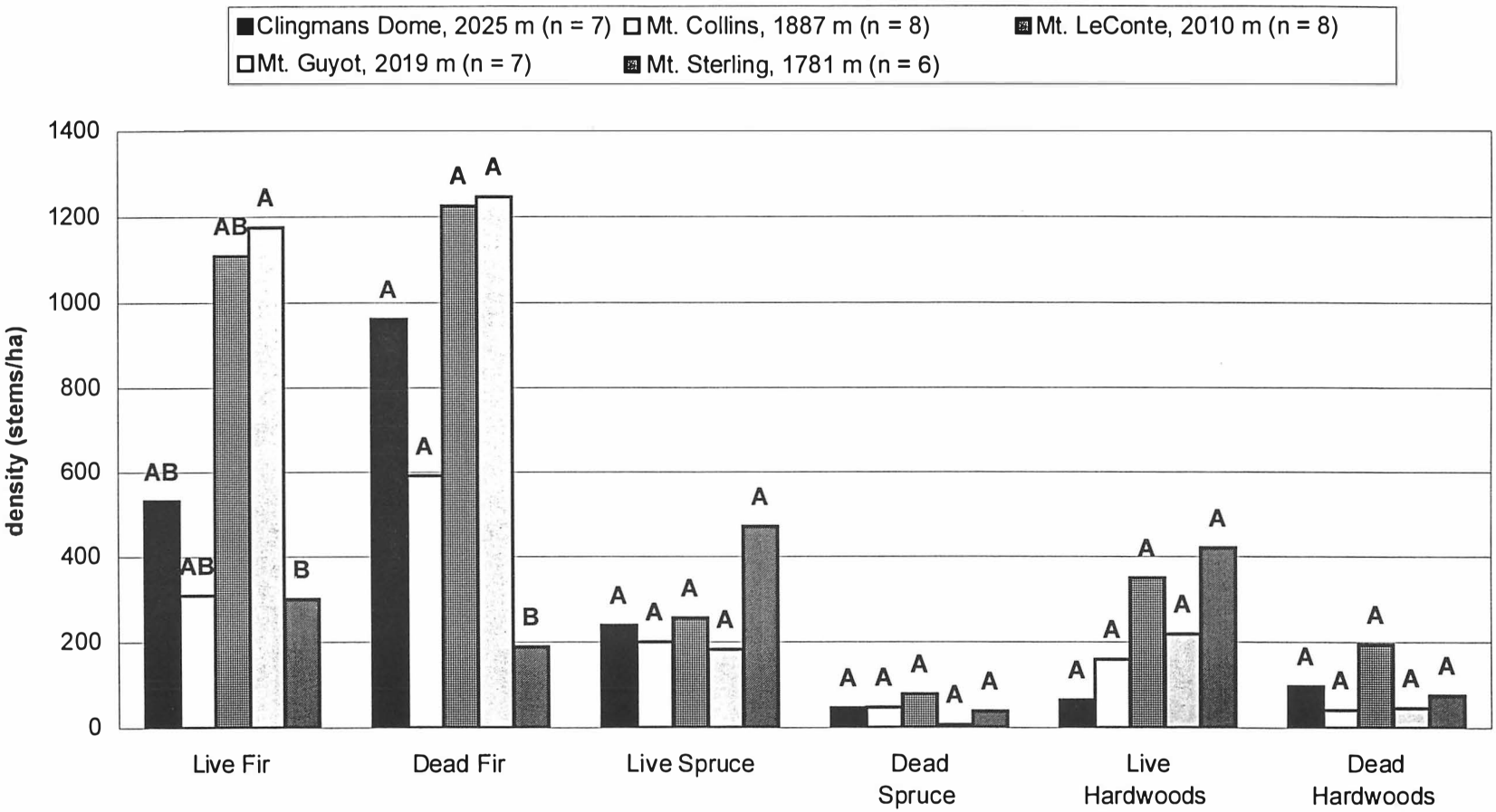

Figure 3.5. Permanent plot data- Live and dead fir, spruce, and hardwood density (m^2/ha) for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means in the same live/dead-species category with the same letter are not significantly different ($\alpha = 0.05$) by Ryan's Q multiple comparisons tests following a significant MANOVA ($F = 2.7106$, 24 df; $P = 0.0026$).

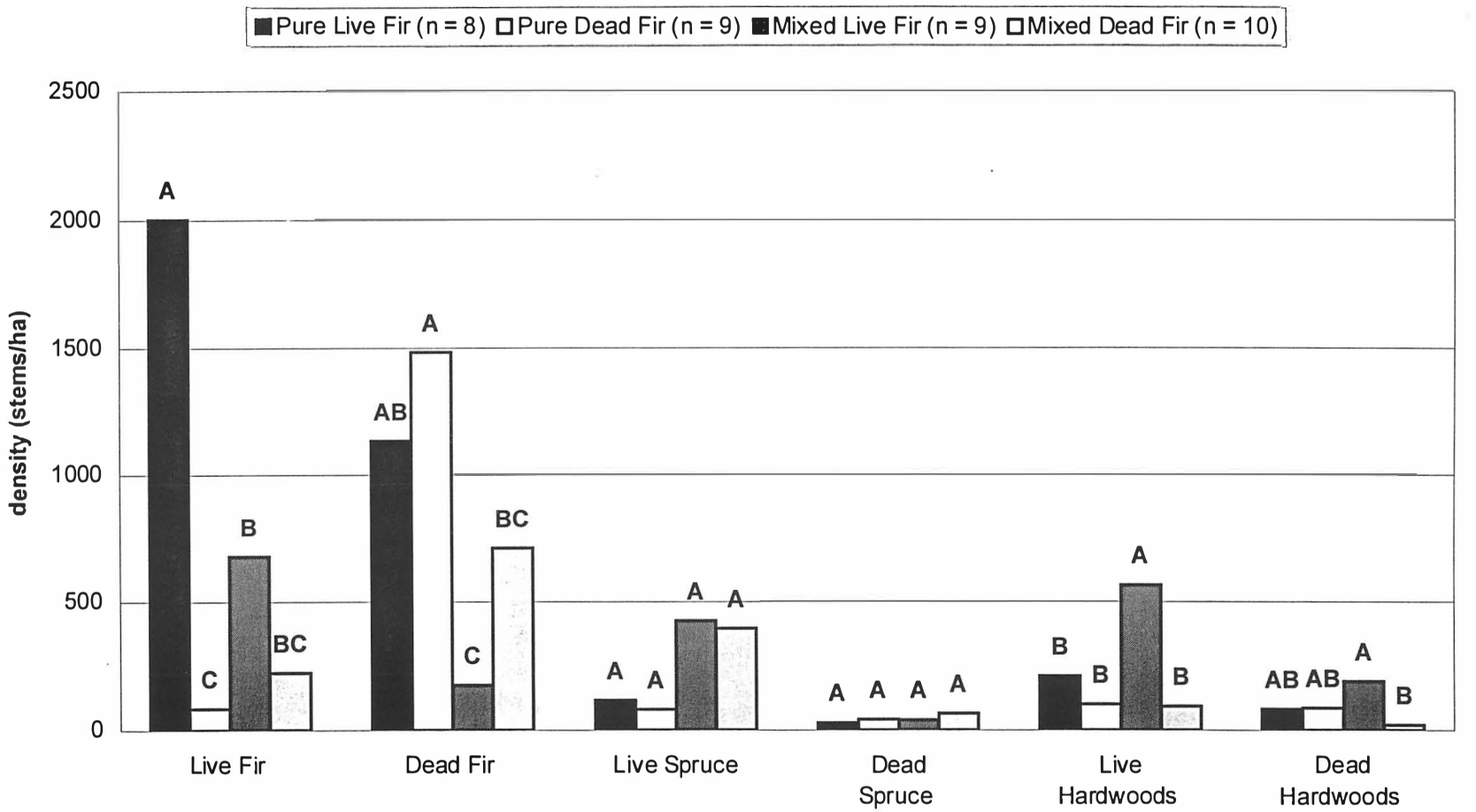

Figure 3.6. Permanent plot data- Live and dead fir, spruce, and hardwood density (stems/ha) by stand type for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means in the same live/dead-species category with the same letter are not significantly different ($\alpha = 0.05$) by Ryan's Q multiple comparisons tests following a significant MANOVA ($F = 8.5544$, 18 df; $P < 0.0001$).

Table 3.3. Permanent plot data— Multivariate regression of live fir, spruce, and hardwood basal area and density on elevation, years since major mortality, percent slope, and linearly transformed aspect for five locations in GSMNP. Shown are the regression coefficients for independent variables significant at $\alpha = 0.1$ and the partial R^2 values for the variables. No independent variables were significant for live fir basal area and live hardwood density.[1]

	Elevation	Years	Slope	Aspect[2]	P
Fir density ($R^2 = 0.1782$)	1.9792 ($r^2 = 0.1049$)	52.6116 ($r^2 = 0.0733$)	-	-	P = 0.0392 F = 3.58
Spruce density ($R^2 = 0.2710$)	-0.3749 ($r^2 = 0.1169$)	-	9.1501 ($r^2 = 0.1541$)	-	P = 0.0054 F = 6.13
Spruce basal area ($R^2 = 0.2985$)	-	-	0.7265 ($r^2 = 0.2985$)	-	P = 0.0006 F = 14.47
Hardwood basal area ($R^2 = 0.3522$)	-0.0155 ($r^2 = 0.2932$)	-	-	2.9349 ($r^2 = 0.0590$)	P = 0.0008 F = 8.97

[1] Sample size in all cases is the number of permanent plots, 36, and all significance tests have df = 35.

[2] Transformed aspect measures distance on a linear scale from 225° (southwest). An aspect of 225° yields a transformed aspect of 0; an aspect of 45° (northeast) yields a transformed aspect of 2 (Beers et al. 1966).

coefficients for elevation. Spruce density and basal area were positively associated with steeper slopes. No significant independent variables were found for live fir basal area or live hardwood density. The R^2 values for the equations were fairly low, indicating a large degree of variability in the responses of overstory abundance to the environmental factors included in the model. The multivariate regression model, while identifying biologically meaningful functional relationships, was not a good predictor of overstory abundances.

Logistic regressions were fit using frequencies of live and dead fir, spruce, and hardwoods (Table 3.4). The model fit was very good for spruce and hardwoods and fairly good for fir based on the Hosmer-Lemeshow statistics. Odds ratios were calculated for significant independent variables to measure the predicted increase in the proportion of dead stems for a change of c units of the independent variable (Table 3.4). For example, the model predicted that for a decrease of 100 m elevation, the proportion of standing dead fir stems will increase 1.185 times. Unlike the temporary plot data, the permanent plot logistic regression model resulted in a linear decrease in the proportion of standing dead fir over time, since the quadratic term for years since major mortality was not included in the model. The plot of the model coefficients did not show that a quadratic term was needed. This was probably because the permanent plots were not randomly selected, but chosen in part based on the proportions of live and dead fir.

3.5 Discussion

Since the permanent plots were not established randomly and because the temporary plot sample size is much larger, the temporary plots provide better estimates of the mean overstory basal area on each mountain. Since the initial adelgid outbreaks occurred as spot

Table 3.4. Permanent plot data—Logistic regressions of live and dead overstory fir, spruce, and hardwood frequencies on plot elevation, years since major mortality, percent slope, and transformed aspect for five locations in GSMNP. Shown are regression equation coefficients followed by the estimated odds ratio in parentheses. The estimated odds ratio is the increase in the proportion of dead stems for an increase (or decrease if the coefficient is negative) of *c* units of the independent variable.

	Intercept	Elevation c = 100 m	Years c = 10 yr	Slope c = 10%	Aspect [1] c = 0.5 unit	Likelihood Ratio Test	Hosmer-Lemeshow $\hat{C}$ [2]
Fir (n = 36)[3]	3.0538	-0.0017 (1.185)	-0.0597 (1.817)	0.0098 (1.103)	0.6330 (1.372)	169.72 (df = 4; P < 0.0001)	4.0654 (df = 5; P ≈ 0.5417)
Hardwoods (n = 30)	-8.1957	0.0033 (1.391)	-0.0466 (1.594)	0.0406 (1.501)	-	47.73 (df = 3; P < 0.0001)	0.6721 (df = 5; P ≈ 0.9826)
Spruce (n = 35)	-0.8890	-	-0.0540 (1.716)	-	-0.5908 (1.344)	15.51 (df = 2; P = 0.0004)	0.2767 (df = 8; P > 0.995)

[1] Transformed aspect measures distance on a linear scale from 225° (southwest). An aspect of 225° yields a transformed aspect of 0; an aspect of 45° (northeast) yields a transformed aspect of 2 (Beers et al. 1966).

[2] The Hosmer-Lemeshow statistic is a goodness-of-fit test distributed as χ^2 that corrects for the situation where the number of different combinations of independent variables equals or nearly equals the number of observations (Hosmer and Lemeshow 1989).

[3] The sample size (n) is the number of permanent plots.

infestations that later coalesced (Eagar 1978), differences between the two data sets are greater on the two peaks last and least uniformly infested. The large live fir stand basal area relative to live fir density on Mt. Collins indicates that the permanent plots on this peak contain large fir not yet killed by the adelgid (Figs. 3.3 and 3.4). Live fir density measured on Clingmans Dome most likely underestimates the mean density for the peak as a whole, but also probably indicates that live fir are larger on average than on the three eastern mountains (Figs. 3.1 and 3.4). Since the adelgid selectively infests larger stems, larger mean fir size would be expected on peaks that have suffered less infestation and mortality (c.f. Chapter 5).

The overrepresentation of live spruce basal area and underrepresentation of live fir basal area in the permanent plots on the three highest peaks are the result of plot structure (Fig. 3.1 and 3.3). While the study design included equal numbers of pure and mixed fir plots, the upper 100 m elevation of the three higher elevation mountains are fir dominated (Fig. 3.1). An unanticipated result of stand type stratification is the significantly larger mean size of live spruce in the MDF plots. Eagar (1978, 1984) has suggested that stands with large spruce that have crowns projecting above the average canopy height intercept the wind-disseminated adelgid much better than more regular canopies. From these superdominant spruce, the adelgid then crawls or falls into the fir crowns below. The larger mean size of spruce in dead fir stands supports this spruce-filter hypothesis.

Differences in the relative abundance of the overstory tree taxa among the peaks were primarily due to elevation (Cain 1935; Korstian 1937; Oosting and Billings 1951; Whittaker 1956). On Clingmans Dome, Mt. LeConte, and Mt. Guyot, where the plots were established at higher elevations, live fir still dominated several years after catastrophic mortality. At lower elevations, Mt. Collins and especially Mt. Sterling, spruce and hardwoods were more important

than fir (Fig. 3.1). The results from the permanent plot multivariate regression of live fir, spruce, and hardwoods also supported the dependence of relative abundance on elevation.

Other environmental variables also contributed to the distribution of overstory density and basal area. Live fir density increased with time since major mortality. As overstory fir die, the canopy opens, permitting recruitment of suppressed understory survivors and seedlings (DeSelm and Boner 1984; Witter 1988). The release caused by the adelgid is qualitatively similar to that caused by large blowdowns in fir dominated forests prior to the adelgid (Cain 1935; Crandall 1958). In many places, the regeneration will form dense thickets of young fir, dubbed "pole stands" by Cain (1935). Unfortunately, the pole-sized fir will be undergoing intense intraspecific competition during stand thinning at nearly the same size as they become susceptible to stem infestation by the adelgid.

Since, in this study, moderate slope is associated with ridgetop plots that are more exposed to winds, the greater amounts of red spruce found on steeper slopes can be explained in part by the more sheltered conditions found there. The larger partial R^2 value for slope in the spruce basal area equation compared to the spruce density equation suggests that this effect is skewed toward larger trees, as would be expected. Busing et al. (1993), analyzing data from the mid-1930s, also found greater abundances of spruce in sheltered sites than in exposed sites at higher elevations. The same pattern would be expected for hardwood species that favor sheltered sites, such as yellow birch (Oosting and Billings 1951; Whittaker 1956), if these species were not combined with others more tolerant of exposed conditions, such as mountain-ash. Although Clingmans Dome has the lowest basal area in live hardwoods of the five mountains, it has the largest percentage of standing dead hardwood basal area. It is possible that this is partially due to more exposure to wind and ice storms at higher elevations. Since

mountain-ash comprises the largest fraction of dead hardwood basal area, it is likely that infestation by the exotic mountain-ash sawfly (*Pristiphora geniculata* Hartig) has contributed to mortality (Nicholas 1992).

To some extent, the proportion of standing dead fir out of the total of standing live and dead fir is a measure of the stage of adelgid infestation, mortality, and recovery in a stand. In studies, such as this one, that do not measure changes in forest composition over time, standing dead trees are the only measure of mortality available. Thus it is important to analyze the processes that control the proportion of standing dead stems: fir death, the fall of dead fir stems, and recruitment of understory fir into the overstory. The rates of these three processes depend primarily on time since initial infestation by the adelgid. At any given location, there will be a relatively small amount of standing dead fir prior to infestation. In the Great Smoky Mountains, Nicholas and White (1985) reported that 20.1% of standing Fraser fir stems were dead at 1829 - 1981 m elevation sites that had been infested for 0 - 3 years and had suffered little adelgid-caused mortality. Once a patch of fir is infested, mortality is rapid (the death of an individual tree usually occurs within two to seven years) and virtually complete (Amman and Talerico 1967; Eagar 1978, 1984). The proportion of standing dead fir in a stand during the initial wave of catastrophic mortality may be visualized as a sigmoid curve: first, a slow increase as the most susceptible individuals die, followed by an exponential increase over a short period of time, and finally another slow increase as healthier or more isolated individuals gradually die. Major mortality was nearly complete throughout the Great Smoky Mountains, except for Clingmans Dome which was sampled in 1990 during or slightly before completion of the initial wave of mortality (Table 3.1) (C. Eagar, personal communication). The predictions of the temporary plot data logistic regression model in Fig. 3.2 shows an increase in

the proportion of standing dead fir stems over time in the part of the curve representing the early years since major mortality.

Data on treefall rates for adelgid-killed fir are scanty. Between 1985 and 1989 in the Smokies, only 4.4% of stems fell in the same year in which they died (Nicholas, 1992). In a study concentrating on Fraser fir mortality in the Smokies, Nicholas and White (1985) found that for high elevation stands that had been infested for 7 - 17 years, 92.1% of standing stems were dead, suggesting a slow rate of treefall. In each of three of the five permanent plots in this study resampled in 1995, only one dead fir standing in 1990 had fallen by 1995. In the other two plots, 25.8% and 38.5% of the standing dead fir had fallen. It is interesting that standing dead fir in these two plots were more than twice as numerous as dead fir in the three plots with a low rate of fall. Treefall rates at the stand level are probably controlled by random wind storms. The logistic regression based on permanent plot data shows that the proportions of standing dead fir and hardwoods tend to be lower in plots with less slope (Table 3.4). Most of these plots are located on ridgetops that are more exposed to winds. In several sites, wind storms caused more dead trees to fall in one year than had fallen in the preceding ten years (personal observation). Over time, patches of heavy treefall will contribute to a gradual decrease in the percentage of standing dead fir at the mountain or landscape level.

Recruitment of young fir from the understory to the canopy is the second factor contributing to decreases in the proportion of standing dead fir. The proportion of dead stems decreases as suppressed survivors in the understory and later as the second generation seedlings capture the canopy. Although several studies have focused on Fraser fir seedlings and saplings, fir recruitment rates have received little research attention. DeSelm and Boner (1984) compared stand composition in several sites in the Smokies and the Black Mountains, NC at

elevations < 1829 m that had suffered major fir death up to 15 years prior to sampling in 1974. They found that densities of fir stems that were 2.5 - 12.4 cm dbh were much lower in stands impacted 5 - 6 years before sampling (17.4 stems/ha) than in unimpacted stands (275.8 stems/ha). In stands that experienced mortality 11 - 15 years previously, however, densities were greater than in the unimpacted stands (359.8 stems/ha). Witter (1988) presented results from a study of fir regeneration in fir and spruce-fir stands on Mt. Mitchell, NC, which underwent severe infestation and mortality around 1965. He reported that in fir stands, densities of live fir > 244 cm tall increased from 798 stems/ha in 1966 to 790 stems/ha in 1978 to 4090 stems/ha in 1985. In spruce-fir stands, fir densities increased from 17 stems/ha to 1097 stems/ha to 4913 stems/ha over the same period. In the five permanent plots of this study resampled in 1995, five-year recruitment of fir ≥ 5 cm dbh varied from 25 stems/ha to 250 stems/ha representing 5.6% to 83.3% of the total 1995 live fir density. Since the resampled plots were located on Clingmans Dome and Mt. Collins, these data represent recruitment 4 to 9 years after major mortality. The predicted decline in the proportion of dead stems in the logistic regression of the temporary plot data (Fig. 3.2) reflects the combined effects of increasing treefall and recruitment over time.

The influence of elevation on the percentage of standing dead fir, which increases with decreasing elevation, is difficult to assess. Elevation of the permanent plots is negatively correlated with time since major mortality ($r = -0.689$; $P < 0.0001$), which is probably the main reason for the significance of elevation in the logistic regressions based on the temporary and permanent plots. Higher rates of treefall in areas more exposed to wind and ice storms would be expected, but elevation is not significantly correlated with exposed sites in my data. Fir seedlings and saplings are more abundant at higher elevations (Nicholas *et al.*, 1992b), which

should lead to higher rates of recruitment into the overstory. In the logistic regression of the permanent plots, the negative relationship between elevation and percentage of standing dead on the more recently infested mountains is most likely the product of patterns of adelgid infestation and spread. Eagar (1978, 1984) documented that infestation and mortality usually began at the lower elevations and spread upslope.

Eagar (1984) suggested that an approximately 35 to 60 year cycle of infestation, mortality, and recovery may occur in the Great Smoky Mountains. With mortality on Clingmans Dome, the last mountain in the Smokies to become infested, quickly approaching that on earlier infested mountains, the first wave of the cycle is nearly complete. With fir recruitment entering the canopy of Mt. Sterling, a second cycle may begin soon. Although it is not possible to explicitly model recovery and reinfestation with these data, I would expect the decrease in the proportion of standing dead fir to approach the minimum asymptotically as the second generation of fir begin to die in numbers. It is not known if sufficient numbers of fir will survive to cone-bearing age and produce another vigorous seedling population to maintain the cycle at high population levels. The alternatives are a dampening cycle or a less uniform mosaic of infested, dead, and recovering patches that will lead to local extirpations as stands of Fraser fir fail to reproduce or seedlings become excluded by competing vegetation better adapted to more open and drier conditions.

The logistic regression based on the permanent plots allows analysis of two additional variables and provides insights into the dynamics of spruce and hardwoods. The proportions of standing dead fir, spruce, and hardwood stems are all inversely related to years since major mortality. For hardwoods, this trend is consistent with the results of DeSelm and Boner (1984) who reported greater overstory and subsapling densities of some hardwood species in longer

infested stands in the Smokies and Black Mountains. It is also likely that understory red spruce are responding positively to increased canopy openness in formerly fir-dominated stands. If thinning shock has increased mortality of large, exposed red spruce, it might be expected that the percentage of standing dead spruce would increase with time since fir death (Zedaker et al. 1988; Nicholas and Zedaker 1989; Nicholas et al. 1992; Busing and Pauley 1994). Busing and Pauley (1994), however, found that the majority of large spruce mortality in their study occurred by windthrow. The positive relationship between fir mortality and plots with a more northeastern aspect (transformed aspect approaching a value of 2) is perhaps the result of historical patterns of infestation; the first fir stands infested on a given peak were generally those with a southwest exposure (Eagar 1978).

3.6 Conclusions

Similar to previous studies (Witter and Ragenovich 1986; Busing and Clebsch 1988; Busing et al. 1988; Dull et al. 1988; Nicholas et al. 1992a) that have reported high levels of overstory fir mortality, 68.2% of standing fir basal area is dead over the five mountains of this study. Despite catastrophic mortality, historical patterns of fir dominance at higher elevations and increased importance of spruce and hardwoods at lower elevations are still maintained. Although other site variables influence the abundances of overstory species, especially at the stand level, elevation is the best predictor of large scale patterns. Over the short term, mean overstory densities of live fir increase with time since adelgid infestation. The factors that control the proportion of standing fir that are dead, fir mortality, treefall, and recruitment, are primarily dependent on time since adelgid infestation. The cumulative effect of these three factors results in an increase in the proportion of standing dead fir over time during the early

stages of infestation, followed by a decrease as dead trees fall and young fir reach the overstory.

Chapter IV

Understory Responses to Overstory Change

4.1 Abstract

The understory community of the southern Appalachian spruce-fir forests is changing following catastrophic mortality of adult Fraser fir (*Abies fraseri* (Pursh) Poir.) from the balsam woolly adelgid (*Adelges piceae* Ratz.), an exotic aphid-like insect. Widespread death of the formerly dominant fir has led to concerns about the ability of young fir to grow to maturity and reproduce under altered environmental conditions. To study understory changes and potential threats to fir survival, thirty-six permanent plots were established on five mountains in the Great Smoky Mountains in 1990 and 1991. The presence of a live fir overstory is the most important predictor of densities of the smallest size seedlings. As the last stands of with a mature fir overstory die, fir regeneration will likely become more patchy in space and time. Densities of red spruce (*Picea rubens* Sarg.) seedlings and small shrubs are much higher in plots with mixed species canopies whose fir component is mostly dead, most likely in response to increased levels of insolation. Other changes in dead fir stands include increases in herb and sub-shrub coverage, such as *Rubus canadensis* L., and decreases in bryophyte coverage. Woody seedlings are uncorrelated or positively associated with fir seedling densities; however, spruce and hardwood saplings, large shrubs, and herbs are negatively associated with fir seedlings, perhaps suggesting inhibitory relationships with fir. In the near future, increased densities of non-fir species will mature and will likely begin excluding poorly regenerating small fir seedlings, especially at lower elevations where fir is less abundant.

4.2 Introduction

The southern Appalachian spruce-fir forests, relicts of the last glaciation, occur in an island-like distribution at the peaks of the seven highest mountain areas in North Carolina, Tennessee, and southwestern Virginia (Oosting and Billings 1951; Ramseur 1960; Delcourt and Delcourt 1984). The endemic Fraser fir (*Abies fraseri* (Pursh) Poir.) and red spruce (*Picea rubens* Sarg.) (nomenclature follows Radford et al. 1968) dominate the canopy at elevations of about 1675-1890 m, above which fir is usually the sole dominant (Whittaker 1956). Hardwoods are much less important overstory components in spruce-fir forests (Whittaker 1956; Ramseur 1960).

Despite the few overstory taxa, the understory is dense and often consists of five layers: 1) bryophytes, 2) low herbs, such as *Oxalis acetosella* L., 3) ferns, 4) low shrubs, such as *Vaccinium erythrocarpum* Michx., and 5) high shrubs, especially *Viburnum alnifolium* Marsh. (Whittaker 1956; Crandall 1958; Ramseur 1960; Boner 1979). Evergreen shrubs, such as *Rhododendron* spp., *Vaccinium corymbosum* L., and *Kalmia latifolia* L., grow on more xeric ridges. (Korstian 1937; Oosting and Billings 1951). Understory deciduous tree species, such as mountain maple (*Acer spicatum* Lam.), fire cherry (*Prunus pensylvanica* L. f.), and young yellow birch (*Betula lutea* Michx. f.), become more numerous with decreasing elevation and in sheltered draws. Shade tolerant spruce and fir seedlings and saplings are abundant and suppressed individuals can survive in the understory for fifty years or more (Oosting and Billings 1951).

In 1957, the balsam woolly adelgid (*Adelges piceae* Ratz.), an exotic pest of true fir, was first detected in the southern Appalachians and has since spread throughout the spruce-fir forests, killing enormous numbers of mature Fraser fir (Speers 1958). Smaller fir with smooth

bark are impervious to lethal stem infestation (Eagar 1978). The understory plant community is being changed profoundly by the opening of the canopy. Certain shrubs, notably *Vaccinium erythrocarpum* and *Viburnum alnifolium*, are decreasing in abundance in the understory with increasing number of years since canopy opening, while some deciduous tree taxa and *Rubus canadensis* L. are increasing (Boner 1979; DeSelm and Boner 1984; Pauley 1989; Pauley and Clebsch 1990). The species composition of the herb layer has changed and moss cover has decreased (Boner 1979). Several rare, endemic, or widely disjunct vascular plants and bryophytes occur in the spruce-fir forest understory (White and Renfro 1984; Smith 1984). Since little is known about the autecology of many of these species, accurate predictions of future abundances in the newly altered environment are not possible. Smith (1984), however, estimates that nearly half of the 204 known bryophyte species that occur in spruce-fir forests may be adversely impacted by the changes wrought by the adelgid.

In this chapter, I will discuss the distribution of woody seedlings and saplings, including shrub taxa, and identify environmental factors and differences in overstory composition that influence those distributions. I will address the following questions: 1) how understory fir, spruce, hardwood, and shrub densities vary among mountains suffering major canopy mortality at different times and among overstories composed of different amounts of live and dead overstory Fraser fir; 2) how densities of different size classes of understory fir vary with densities of understory spruce, hardwoods, and shrubs; 3) how understory densities change with elevation, time since death of canopy fir, and aspect; and 4) how fir understory densities vary by different ground cover types and how ground cover changes under different canopy compositions.

4.3 Methods

4.3.1 Study site and data collection

The study was initiated and data collected by Paul Durr, a former biological technician with the Uplands Research Laboratory, Great Smoky Mountains National Park. The study site encompasses five peaks in the Great Smoky Mountains National Park (GSMNP), from northeast to southwest: Mount Sterling (1781 m elevation), Mount Guyot (2019 m), Mount LeConte (2010 m), Mount Collins (1887 m), and Clingmans Dome (2025 m) These five were chosen because as a group they represent nearly the entire range of Fraser fir in the park. None of the study areas had been logged or burned and therefore supported old-growth stands of spruce and fir prior to infestation (Pyle 1984; Pyle and Schafale 1988). Mt. Sterling was the first mountain to be infested by the adelgid, which subsequently spread westward throughout the Park. Major fir mortality occurred at the summit of Mt. Sterling in 1970-1972, on Mt. Guyot in 1980-1982, on Mt. LeConte in 1982-1984, on Mt. Collins in 1985-1987, and on Clingmans Dome in 1990-1992 (C. Eagar personal communication). The median values of these intervals were used in estimating the number of years since major mortality in the statistical analyses below. Five plots on Clingmans Dome and Mt. Collins were originally established in 1985 for the National Acid Precipitation Assessment Program and used by Nicholas et al. (1992a, b). Clingmans Dome and Mt. Collins were sampled in 1990; Mt. LeConte, Mt. Guyot, and Mt. Sterling were sampled in 1991.

Thirty-six 400 m^2 (20 x 20 m) permanent plots, corrected for slope, were established within 100 m elevation of the peak summits. Prior to vegetation measurement, elevation, aspect, percent slope, landform, slope position, and microrelief were recorded for each permanent plot. Before use in statistical analysis, site aspect in degrees was transformed to a

linear scale (Beers et al. 1966). Each mountain was to have two replicate plots in each of four stand types:

- pure live fir (PLF) with ≥65% overstory basal area in fir and ≥65% of those trees living
- pure dead fir (PDF) with ≥65% of overstory basal area in fir and ≥65% of those trees dead
- mixed live fir (MLF) with ≤35% of overstory basal area in fir, ≥65% of which is live, mixed with spruce and/or hardwoods
- mixed dead fir (MDF) with ≤35% of overstory basal area in fir, ≥65% of which is dead, mixed with spruce and/or hardwoods.

One PLF plot from Clingmans Dome, one PLF plot on Mount Sterling, one PDF plot from Mount Sterling, and one MLF plot on Mount Guyot were never established because a second replicate of the stand type could not be found on those peaks.

Saplings and large woody shrubs, ≥1.37 m tall and <5 cm dbh, were tallied in 16 2 × 2 m quadrats, four in each of four 2 × 10 m strips. Each strip was randomly located in one of the 10 × 10 m plot quarters. Suffrutescent sub-shrubs, including *Rubus* and *Hydrangea*, were not included. Nested randomly in each 2 × 2 m quadrat was a 1 × 1 m subplot, for a total of 16 subplots per plot. In these subplots, percent ground cover in nine types (bare soil, twig/leaf litter, bare rock, bole, bryophytes/lichen, aerial woody debris, ground woody debris, stream/seep, and herb/sub-shrub) was estimated. Since these cover types often overlay each other and summation of cover types may result in values over 100%, cover percentages were scaled to total 100% to enable plot comparisons. Tree seedling and small shrub occurrence by species and size classes (unbranched seedlings, branched seedlings ≤ 0.25 m tall, 0.26 m-1.0 m, 1.01 m-1.36 m) was recorded. Fir were classed as unbranched if they had no lateral branches and bud scars from annual growth were observed on the stem.

4.3.2 Data analysis

I tested sapling sized (≥ 1.37 m tall and < 5 cm dbh) fir, spruce, combined hardwoods, and combined shrubs among the five mountains and the four stand types using a two-way factorial MANOVA. I performed another two-way factorial MANOVA to investigate variation in spruce and hardwood seedlings, small shrubs (< 1.37 m tall), and fir seedlings divided into size classes. Germinal fir were excluded from the analysis because the plots were sampled over two years and Fraser fir produce large seed crops every 2 - 4 years (USDA Forest Service 1974). For comparative purposes, germinal seedlings of other species were also omitted. I performed a three-way factorial MANOVA of fir (by size classes), spruce, and hardwood seedling and small shrub (< 1.37 m tall) counts in the 1 × 1 m subplots on percent cover of herbs, twig/leaf litter, and bryophytes. For the MANOVA, percent cover was divided into four 25% increment classes for each ground cover type. Reported significant differences among means were tested using Ryan's Q multiple comparisons tests following a MANOVA (Day and Quinn 1989).

For regression analyses, densities of understory species were log-transformed following use of the Box-Cox procedure and examination of the residuals (Sokal and Rohlf 1995). I performed a multivariate regression of understory fir in size classes on understory spruce, hardwoods, and shrubs. I used understory fir, spruce, hardwood, and shrub densities as dependent variables and several environmental and overstory variables as independent variables.

All statistical tests were conducted using SAS (SAS Institute 1989).

4.4 Results

Most shrubs ≥ 1.37 m tall were *Viburnum alnifolium*. Although no significant differences were found among the five mountains, the densities of shrubs ≥ 1.37 m tall on Clingmans Dome and Mt. Collins were greater than those on the other three mountains (Fig. 4.1). There was also a trend for increasing densities of fir saplings on the earlier infested mountains. No significant differences were found among the four stand types, but mean fir sapling densities were slightly greater in the PLF and PDF stands (Fig. 4.2).

Densities of unbranched fir seedlings were significantly greater on Mt. Guyot; densities of 1.01 m -1.36 m tall fir were significantly greater on Mt. Collins than on the three eastern mountains (Fig. 4.3). The high mean densities of unbranched fir seedlings on Mt. Guyot were the result of extremely high densities, exceeding 100,000 stems/ha, in the two PLF plots. Small shrub densities, mostly *Vaccinium erythrocarpum*, were significantly greater on Mt. Collins than on Mt. LeConte and Mt. Sterling. Fir densities in the two smallest size classes were significantly much greater in the PLF stands than in other stand types (Fig. 4.4).

Equations for the two smallest fir size classes, in the regression of fir seedling densities on densities of other understory taxa, had the largest R^2 values; spruce saplings and hardwood saplings and seedlings were significant regressor variables for both of these size classes (Table 4.1). Regression coefficients for sapling-sized independent variables were negative while those of seedlings are positive.

The three ground cover types that had the highest percent coverage over all the 1 × 1 m subplots were herb/sub-shrub (including *Rubus*), twig/leaf litter, and bryophytes. Although the percent cover of these ground cover types did not vary significantly by mountain, mean herb/sub-shrub coverage was greater and mean twig/leaf litter coverage was lower in PDF and MDF stands (Table 4.2). Bryophyte coverage was greatest in PLF plots and least in PDF plots.

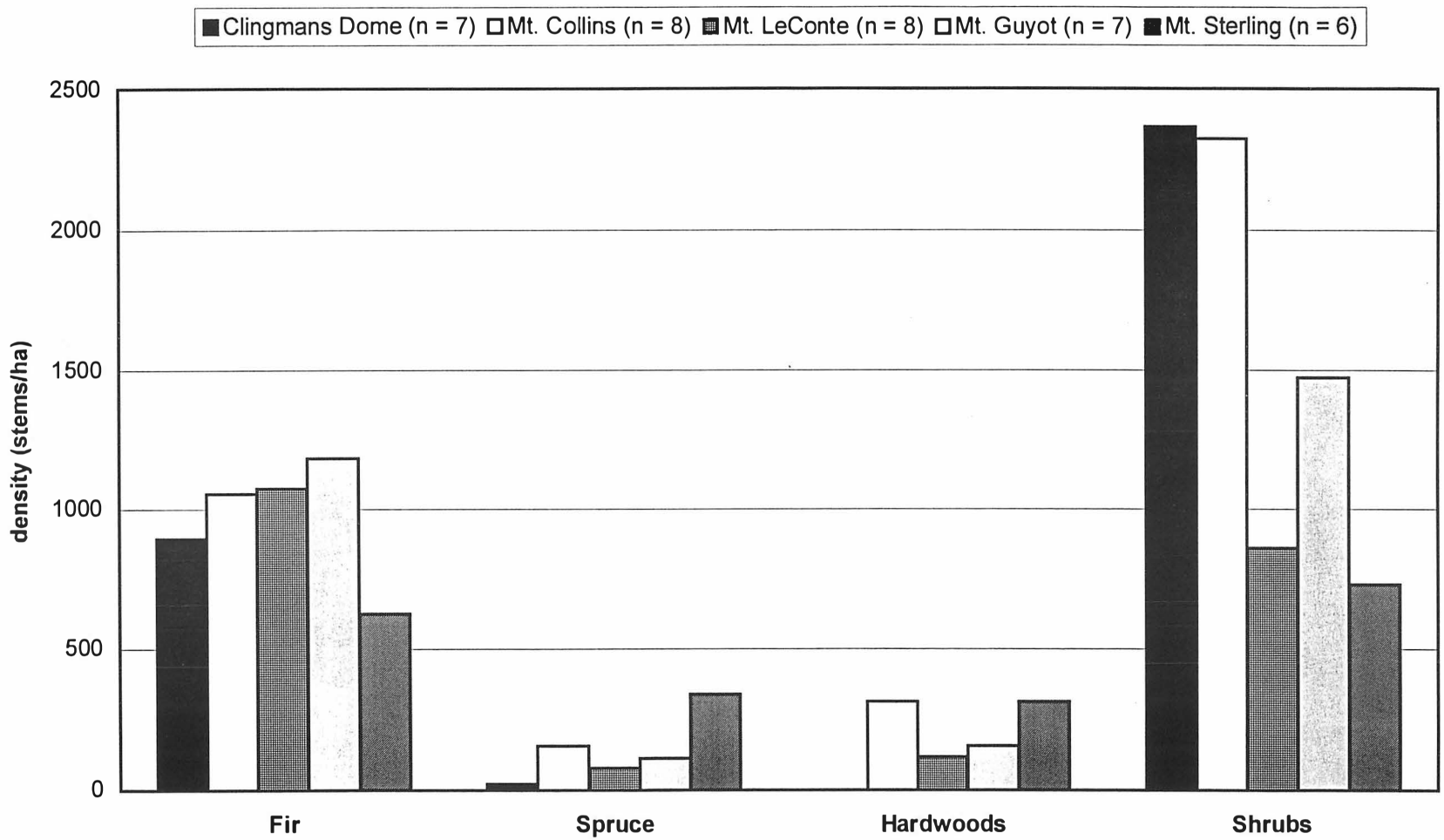

Figure 4.1. Live fir, spruce, and hardwood sapling and large shrub (≥ 1.37 m tall and < 5 cm dbh) densities (stems/ha) for five mountains in GSMNP. Sample size (n) is the number of permanent plots. No significant differences were found among mountains with MANOVA (F = 0.94, 16 df; P = 0.53).

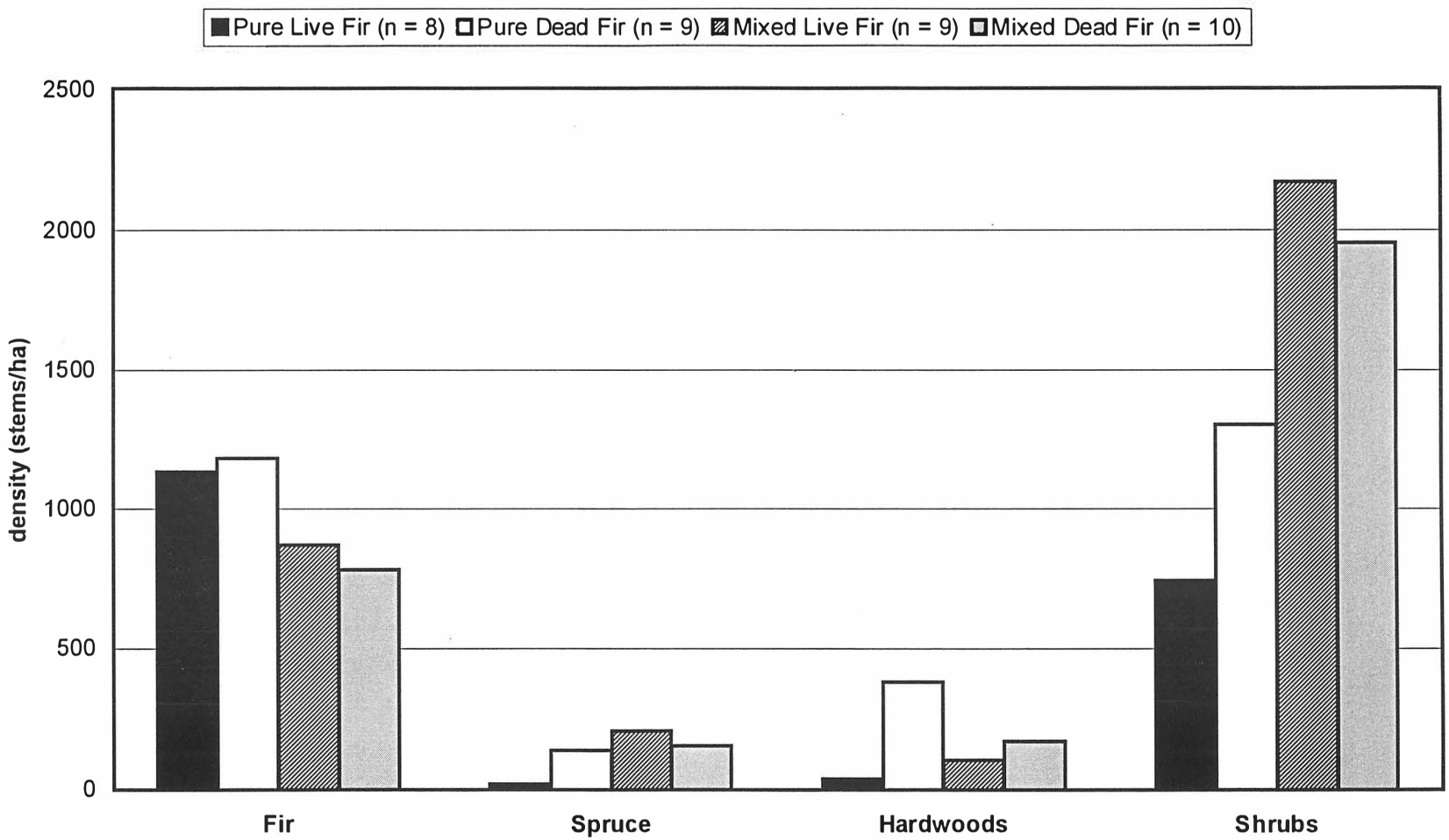

Figure 4.2. Live fir, spruce, and hardwood sapling and large shrub (≥ 1.37 m tall and <5 cm dbh) densities (stems/ha) by stand type for five mountains in GSMNP. Sample size (n) is the number of permanent plots. No significant differences were found among stand types with MANOVA (F = 0.82, 12 df; P = 0.63).

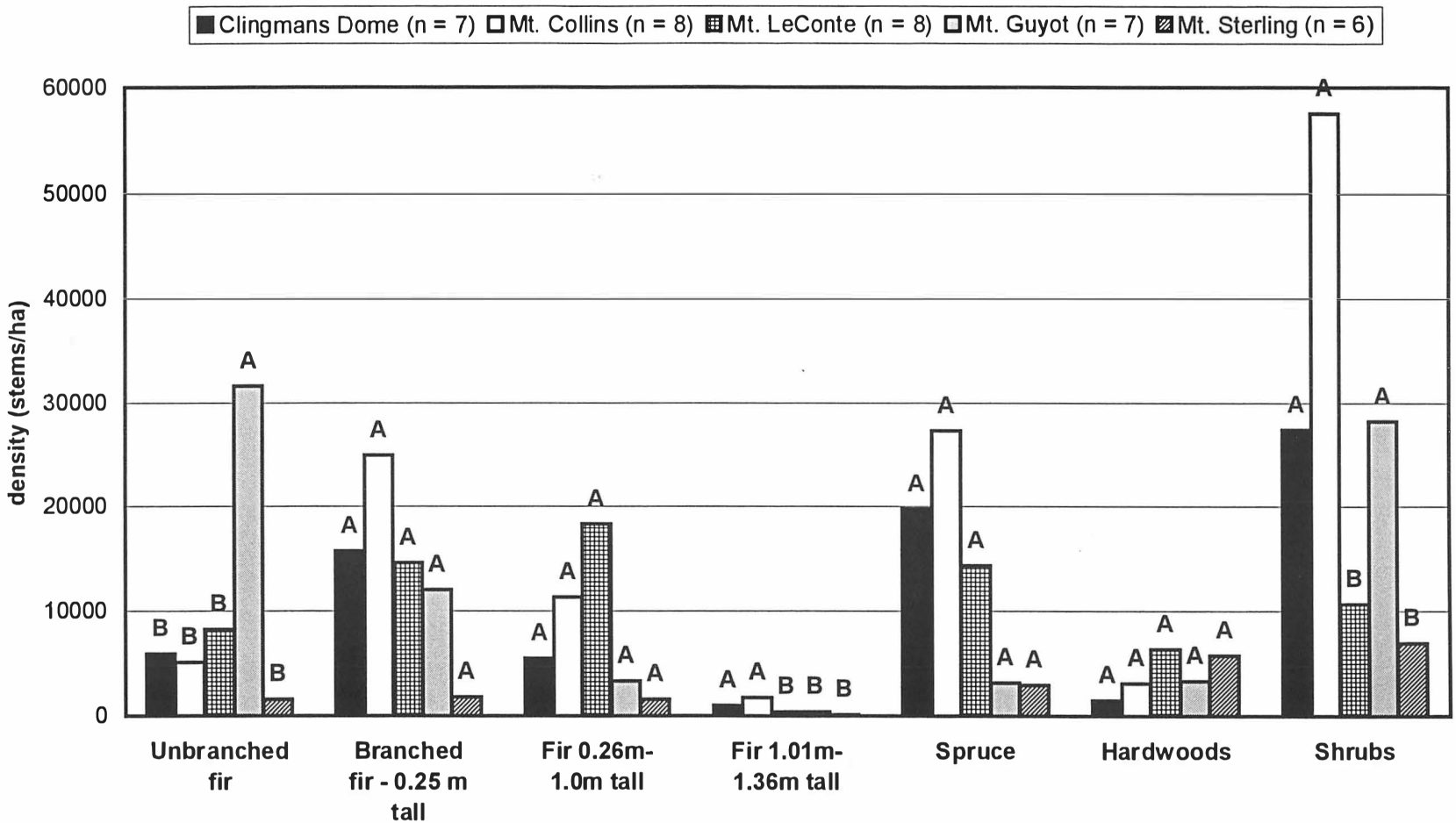

Figure 4.3. Live fir, spruce, and hardwood seedling and small shrub (< 1.37 m tall) densities (stems/ha) for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means with the same letter are not significantly different ($\alpha = 0.1$) by Ryan's Q multiple range tests following a significant MANOVA ($F = 2.32$, 28 df; $P = 0.0084$).

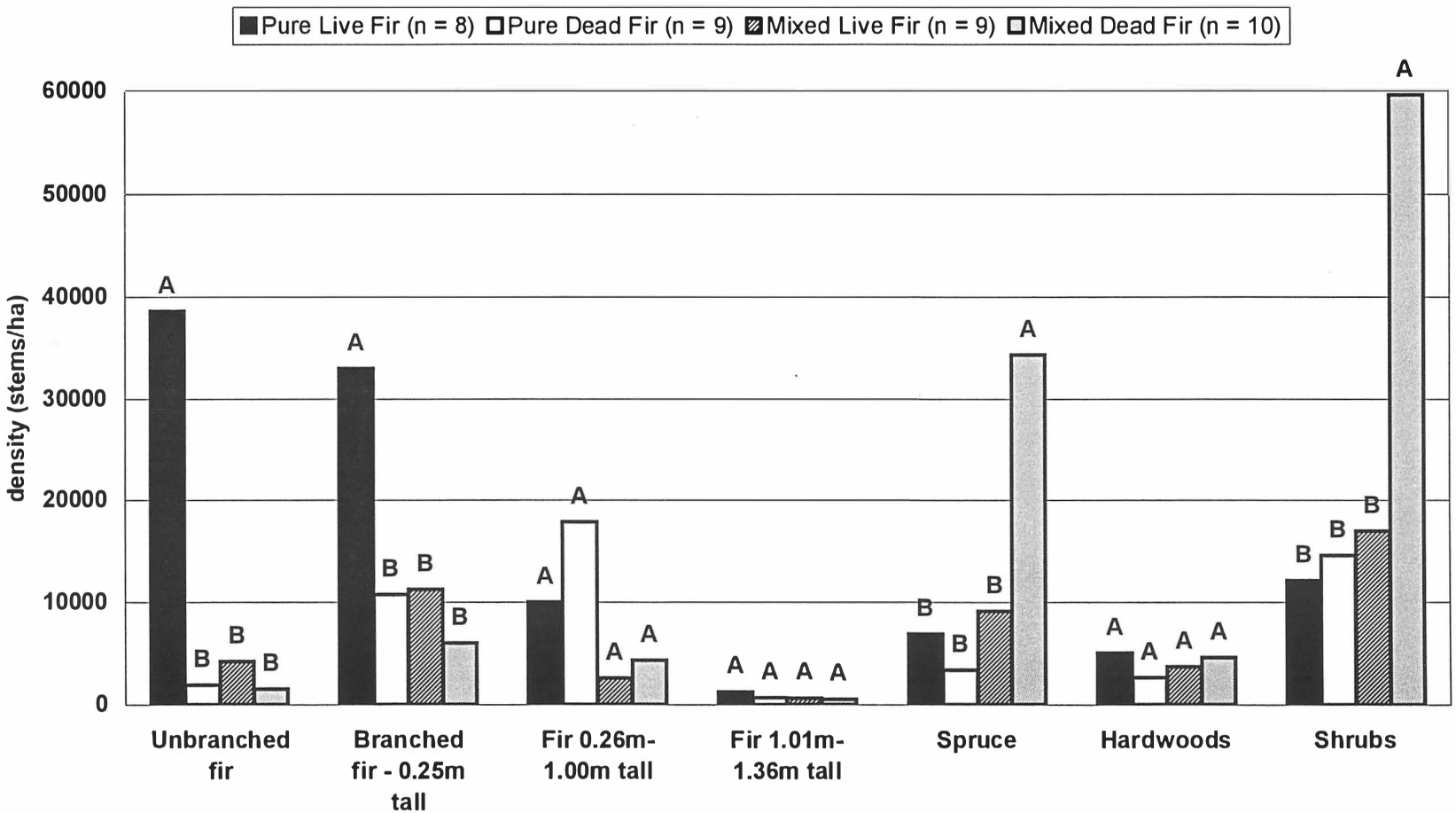

Figure 4.4. Live fir, spruce, and hardwood seedling and small shrub (< 1.37 m tall) densities (stems/ha) by stand type for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means with the same letter are not significantly different ($\alpha = 0.1$) by Ryan's Q multiple range tests following a significant MANOVA ($F = 3.52$, 21 df; $P = 0.0009$).

Table 4.1. Multivariate regression of understory fir in size classes on understory spruce, hardwoods, and shrubs for five locations in GSMNP. The model was fit using stepwise independent variable selection with $\alpha = 0.15$ as the criterion for entering or leaving the model. Each fit model has an overall significance value of $P \leq 0.05$.

	Intercept	Spruce ≥ 1.37 m tall	Hardwoods ≥ 1.37 m tall	Shrubs ≥ 1.37 m tall	Spruce < 1.37 m tall	Hardwoods < 1.37 m tall	Shrubs < 1.37 m tall
Unbranched R^2 =0.462	4.04	-0.72 r^2 =0.188	-0.40 r^2 = 0.076	-	-	0.64 r^2 = 0.198	-
≤ 0.25 m tall R^2 = 0.547	1.64	-0.38 r^2 = 0.050	-0.30 r^2 = 0.046	-0.24 r^2 = 0.109	-	0.39 r^2 = 0.058	0.62 r^2 = 0.284
0.26 m - 1.00 m tall R^2 = 0.167	2.55	-	-	-	-	-	0.46 r^2 = 0.167
1.01 m - 1.36 m tall R^2 = 0.179	0.37	-	-	-	0.36 r^2 = 0.179	-	-
≥ 1.37 m tall R^2 = 0.168	5.62	-	-	-0.19 r^2 = 0.083	0.16 r^2 = 0.085	-	-

Table 4.2. Mean percent cover (± 95% confidence level) for herbs, twig/leaf litter, bryophytes in four overstory stand types for five locations in GSMNP.

	Pure Live Fir (n = 128)[1]	Mixed Live Fir (n = 144)	Pure Dead Fir (n = 144)	Mixed Dead Fir (n = 160)
Herbs	38.3 ± 5.3	48.2 ± 5.1	73.9 ± 4.4	58.0 ± 4.5
Twig/Leaf Litter	27.3 ± 4.1	27.0 ± 4.1	10.1 ± 3.0	18.1 ± 3.0
Bryophytes	26.6 ± 3.4	16.3 ± 3.1	5.8 ± 1.4	16.3 ± 2.7

[1] Sample size (n) is the number of 1 × 1 m subplots.

Twig/leaf litter and bryophyte cover classes were significant factors in the MANOVA of seedling and small shrub counts in the 1 × 1 m subplots (Fig 4.5). Since the percent coverages of different ground cover types are not statistically independent, a significant interaction between these two cover types was detected.

Densities of the smallest and the largest fir seedling classes are slightly negatively associated with the number of years since major mortality occurred at the summits of the mountains (Table 4.3). Large shrub densities are also negatively associated with years since major mortality. The two youngest seedling classes correspond strongly with higher live overstory fir basal areas and negatively with higher live hardwood basal areas. Significant positive coefficients were obtained for understory spruce regressed on overstory spruce, but not for understory hardwoods on overstory hardwoods. Percent slope was included in the multivariate regression, but was omitted from Table 4.3 since it was not significant for any understory variable. A series of univariate analysis of covariance tests of understory densities regressed on environmental and overstory variables in four stand types did not reveal any significant differences in understory-site relationships under different overstory stand conditions.

4.5 Discussion

In Chapter 3, the importance of time since major infestation in influencing patterns of overstory fir distribution was demonstrated. Live overstory fir densities and proportions of dead fir were different among mountains that suffered major mortality at different times. Since understory fir and other species are not directly affected by the balsam woolly adelgid, the mountain chronosequence effect is less visible.

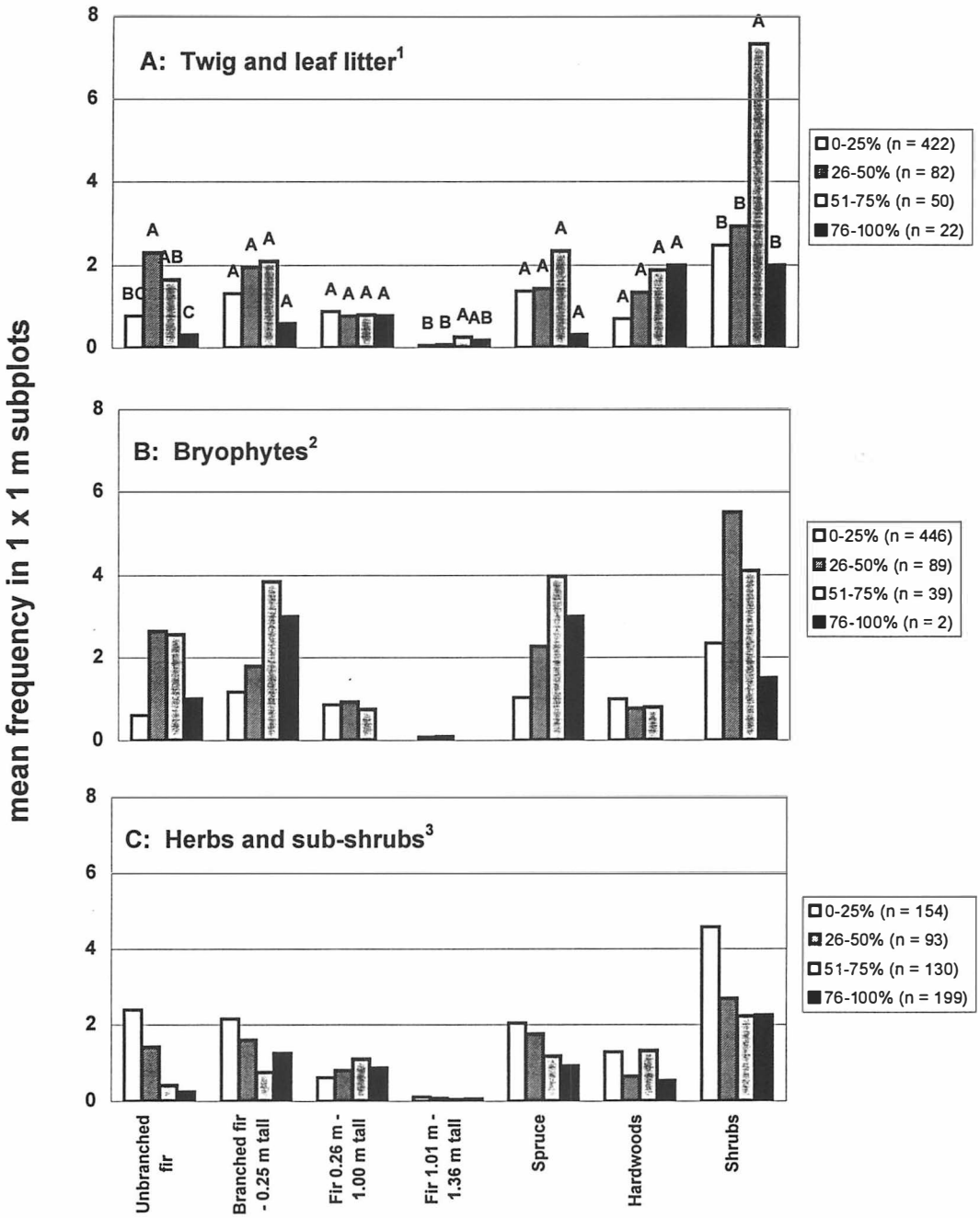

Figure 4.5. Fir (in 4 size classes), spruce, and hardwood seedlings and shrub species < 1.37 m tall for five locations in GSMNP. Mean frequency by percentage cover of three ground cover types. Sample size (n) is the number of 1 x 1 m subplots.

[1] F = 2.151, 24 df; P = 0.0010. Means with the same letter are not significantly different ($\alpha = 0.1$) by Ryan's Q multiple comparisons tests.

[2] F = 1.911, 24 df; P = 0.0051. No means were significantly different ($\alpha = 0.1$) by Ryan's Q multiple comparisons tests.

[3] F = 0.9083, 24 df; P = 0.5912.

Table 4.3. Multivariate regression of understory fir (in size classes), spruce, hardwoods, and shrubs on elevation, years since major mortality (YSMM), transformed aspect, and overstory fir, spruce, and hardwood basal area for five areas in GSMNP. Stepwise independent variable selection was used with $\alpha = 0.15$ as the criterion. Each fit model has an overall significance value of $P \leq 0.05$. Model R^2 is given for each dependent variable. Percent slope was included in the model, but was not significant; no independent variables were significant for fir 0.26 m - 1.0 m tall.

	Intercept	Elevation	YSMM	Aspect	Fir basal area	Spruce basal area	Hardwood basal area
Unbranched fir $R^2 = 0.483$	6.16	-	-0.15 $r^2 = 0.039$	-	0.15 $r^2 = 0.308$	-	-0.14 $r^2 = 0.136$
Fir ≤ 0.25 m $R^2 = 0.342$	7.05	-	-	-	0.10 $r^2 = 0.131$	-	-0.23 $r^2 = 0.210$
Fir 1.01 m - 1.36 m $R^2 = 0.157$	31.44	-0.01 $r^2 = 0.066$	-0.27 $r^2 = 0.091$	-	-	-	-
Fir ≥ 1.37 m $R^2 = 0.134$	4.69	-	-	1.20 $r^2 = 0.134$	-	-	-

Table 4.3. cont'd

	Intercept	Elevation	YSMM	Aspect	Fir basal area	Spruce basal area	Hardwood basal area
Spruce < 1.36 m $R^2 = 0.421$	3.89	-	-	-	0.07 $r^2 = 0.045$	0.12 $r^2 = 0.299$	-0.14 $r^2 = 0.078$
Spruce ≥ 1.37 m $R^2 = 0.232$	-0.06	-	0.13 $r^2 = 0.097$	-	-	0.06 $r^2 = 0.136$	-
Hardwoods < 1.37 m $R^2 = 0.093$	5.79	-	-	-	0.07 $r^2 = 0.093$	-	-
Hardwoods ≥ 1.37 m $R^2 = 0.223$	32.80	-0.02 $r^2 = 0.223$	-	-	-	-	-
Shrubs < 1.37 m $R^2 = 0.172$	9.41	-	-	-	-	-	-0.19 $r^2 = 0.172$
Shrubs ≥ 1.37 m $R^2 = 0.294$	7.15	-	-0.26 $r^2 = 0.181$	-	-0.09 $r^2 = 0.113$	-	-

4.5.1 **Fir saplings**

Although not statistically significant, there was a trend of increasing numbers of Fraser fir saplings and decreasing numbers of the largest fir seedling class (1.01 m -1.36 m tall) on the earlier infested mountains (Figs. 4.1 and 4.3); the regression of the largest seedling class on the number of years since major mortality was significant (Table 4.3). The increase in sapling densities and decrease in large seedling densities as time since infestation increases is similar to the findings of Witter (1988) on Mt. Mitchell where fir less than 244 cm tall decreased and fir > 244 cm tall increased over a 20 yr period. Witter's interpretation that the smaller fir are decreasing as a result of recruitment to the overstory in response to increased light levels is probably valid for these data as well.

The proportion of dead canopy fir had little effect on the densities of saplings and large shrubs. Most individuals ≥ 1.37 m tall have germinated and grown under pre-adelgid conditions. Accordingly, densities of fir saplings in PLF and PDF plots were nearly the same and greater than densities in MLF and MDF plots (Fig. 4.2). In other words, survivorship of fir saplings has not been noticeably affected by canopy opening or the adelgid. Over the short term, however, it would be expected that accelerated recruitment from the seedling layer in impacted stands would increase fir sapling densities relative to slower rates of recruitment in any relatively intact stands that may still remain. It is possible that recruitment from seedling to sapling size may be masked by recruitment from sapling to overstory size (Fig. 3.5 and c.f. Chapter 5) or by increased sapling mortality in impacted stands.

4.5.2 **Fir seedlings**

The effects of the death of adult fir on distribution of the two smallest seedling classes are clearly demonstrated by two results: 1) significantly higher densities in PLF stands

compared with those in PDF stands, which have been reduced to levels comparable to mixed fir stands (Fig. 4.3) and 2) the importance of the basal area of overstory fir in the regression of understory on overstory and site variables (Table 4.3). In addition, the relative densities of unbranched seedlings by mountain and by stand type correspond fairly well with the basal areas and densities of live overstory fir (compare Figs. 4.3 and 4.4 and Figs. 3.3 - 3.6). This correlation of small fir seedlings with an intact canopy of adult fir suggests that lower small seedling densities are in part the result of insufficient regeneration in sites where the majority of adult fir are dead. The larger size classes did not show the same dependence on current overstory fir since they are the advance regeneration of a dramatically different, pre-adelgid overstory fir population. In sites where regeneration is limited, future reproduction will be dependent on the growth to maturity of larger seedlings and saplings.

The dependency of small seedling densities on current overstory abundance also suggests a large proportion of seedlings germinate close to their parents. Sullivan and Peterson (1994) have found that fir seed dispersal is limited. Since infestation and fir death are also spatially and temporally clumped phenomena (Eagar 1978), the implication is that future fir regeneration will be more patchy in space and time than the advance regeneration of pre-adelgid fir.

Although overstory density and basal area in the permanent plots increased on the earlier infested mountains (Figs. 3.3 and 3.5), time since major mortality had a negative regression coefficient in the equation for unbranched seedlings. This may reflect decreased production of viable seed in individual fir on the earlier infested mountains. Surviving members of the original overstory fir populations on those peaks have endured potentially weakening environmental changes, such as warmer and drier conditions than prior to the adelgid, longer than old fir on the more western peaks. They may have been infested for a

longer period of time on the average, with corresponding reductions in cone and viable seed production (Fedde 1973a, b). Overstory fir on the earlier infested mountains are younger and smaller on average, and most likely produce fewer cones (c.f. Chapter 5).

In addition to regeneration reductions, another factor may partially explain the lower densities of small seedlings in stands dominated by dead fir and the inverse relationship of small fir with time since major mortality. In stands with a more open canopy, rates of fir seedling growth may be higher. The (non-significant) higher densities of 0.26 m - 1.00 m tall fir in PDF stands may be an indication of recruitment to the larger seedling classes from the smaller. The lack of a significant regression of the larger fir seedling classes on years since major mortality and the absence of significantly higher densities of larger fir seedlings on earlier infested mountains suggests that this factor is less important than the death of reproducing fir. Growth rates of understory fir will be discussed more in depth in Chapter 5.

From 1985 to 1989, Nicholas et al. (1992b) sampled plots stratified by elevation on Clingmans Dome and Mt. Collins, using the same understory size classes as this study. Mean fir seedling densities for 1830 m elevation plots were 23,828 stems/ha with 82% of fir seedlings ≤ 0.25 m tall. Seven plots in this study were 1830 ± 50 m elevation on Clingmans Dome and Mt. Collins. The mean fir seedling density for these plots was 48,929 stems/ha (± 57,275 stems/ha 95% confidence level) with 70% ≤ 0.25 m tall. Mean fir seedling density for the Nicholas et al. (1992b) 1980 m plots was 21,124 stems/ha with 83% ≤ 0.25 m tall. Six plots on Clingmans Dome and Mt. Collins in this study were had an elevation of 1980 ± 50 m ; the mean seedling density for these plots was 19,792 stems/ha (± 14,807 stems/ha 95% confidence level) with 68% ≤ 0.25 m tall. In a 1988 study on Mount Collins at elevations of 1760 - 1830 m, Pauley and Clebsch (1990) found an average seedling density of 33,000 stems/ha, with 87% of seedlings ≤ 0.25 m. Two plots in this study on Mt. Collins are within

this elevation range. In these plots, the mean fir seedling density was 27,500 stems/ha (± 6125 stems/ha 95% confidence level) with only 60% ≤ 0.25 m tall. The small sample sizes of plots in this study at elevations comparable to those of Nicholas et al. (1992b) and Pauley and Clebsch (1990) and the nonrandom method of plot placement preclude direct comparisons of fir seedling densities with the two earlier studies. The consistently lower percentages of seedlings ≤ 0.25 m tall in this study, however, may also suggest that abundances of small seedlings are decreasing.

4.5.3 Understory spruce, hardwoods, and shrubs

Contrary to previous research (Boner 1979; DeSelm and Boner 1984) demonstrating changes in other understory vegetation after canopy opening, the number of years since major mortality is a significant variable only for spruce saplings and large shrubs (Table 4.3). Failure to detect dependencies of understory species on time is in large part the result of the plot establishment regime. Purposely selecting a mixture of devastated and intact plots on each mountain means that several of the plots suffered fir death at times that vary considerably from the rough estimates available for the mountain as a whole.

The positive relationship between spruce saplings and time is most likely a response to greater levels of light in stands that have suffered canopy fir death at earlier times. Since red spruce tends to be more abundant than fir on drier sites, such as ridgetops (Whittaker 1956), it is possible that young spruce will have higher rates of growth and survivorship than young fir in some adelgid killed stands. Large shrubs exhibit a relatively strong negative relationship with time since mortality (Table 4.3). Average *Viburnum* densities are 2277 stems/ha on Clingmans Dome declining to 871 stems/ha on Mt. Guyot and 0 stems/ha on Mt. Sterling. Boner (1979) also concluded that densities of *Viburnum* decreased with time since initial fir

death. He reported mean *Viburnum* densities of 1122 stems/ha in uninfested stands and 105 stems/ha in stands that had suffered initial fir death 16-20 yr previously. This suggests that *Viburnum*, which dominates the large shrub category, is a shade-tolerant species which is less tolerant of post-adelgid environmental conditions.

Shrubs, hardwood seedlings, and spruce seedlings do not show differences in abundance between PLF and PDF stands. Since spruce seedlings and small shrubs show a marked increase in MDF stands relative to MLF stands, failure of these other species to increase in PDF stands may be caused by slow or inadequate seed dispersal to these sites. Another possibility is that these species are unable to compete well with advance regeneration of fir.

4.5.4 Fir correlations with woody plants

The regression of fir on other woody plants (Table 4.1) provided no evidence of negative interactions between understory fir and spruce or hardwood seedlings or small shrubs. It might be expected that the competitive relationships between fir and the other species would change under different canopy conditions. I found no evidence of this in the analysis-of-covariance tests among the four stand types. Since there were only 8-10 plots per stand type, one reason may be inadequate sample sizes. Another reason is that the majority of the taxa, including spruce, yellow birch, mountain ash (*Sorbus americana* Marsh.), *Viburnum*, and *Vaccinium erythrocarpum*, are moderately shade tolerant and may require more time for a sizable response to increased light levels than faster growing intolerant species (Spurr and Barnes 1973; Erdmann 1990). Seedling counts of canopy gap species, such as fire cherry, are not markedly higher on earlier infested mountains or PDF or MDF stands.

The positive regression coefficients of spruce and hardwood seedlings and small shrubs indicate that fir, spruce, and hardwood seedlings all tend to favor similar sites, such as decaying boles, bryophyte-covered surfaces, or treefall produced root mounds (Beck 1990; Blum 1990; Erdmann 1990; Pauley and Clebsch 1990; Smallidge and Leopold 1994). Spruce and hardwood saplings may inhibit smaller fir seedlings, as is indicated by negative regression coefficients for the two smallest fir size classes (Table 4.1). This also applies to large shrubs for fir $\leq$ 0.25 m tall. While spruce and hardwood seedlings do not inhibit fir seedling establishment or survivorship, their large numbers in MDF plots present the possibility that when they reach sapling size, they will dominate the understory in spruce-fir-hardwood stands, leading to the elimination of fir from the mixed stands more common at lower elevations, especially if fir regeneration is patchy or episodic.

4.5.5 Variation in ground cover types and understory correlations with site variables

Greater percent cover of herbs in PDF and MDF plots and the much lower percent cover of bryophytes in the PDF plots relative to the PLF plots (Table 4.2) support the findings of other researchers (Boner 1979; DeSelm and Boner 1984) that the spruce-fir forests are becoming drier and more insolated. One result is that densities of *Rubus* species have increased with canopy opening (Boner 1979; DeSelm and Boner 1984); Pauley (1989) suggested that *Rubus* inhibits the establishment of Fraser fir seedlings. Unfortunately, in this study, densities of *Rubus* canes were not sampled, but percentage cover was estimated and reported in combination with fern, *Oxalis*, and other herbaceous plant coverage. Combining these taxa in percent cover of herbs obscures the ecological relationships that different herbaceous taxa have with understory fir, spruce, hardwoods, and shrubs. This is at least

partially responsible for the failure of the MANOVA to detect differences in understory densities among herb cover classes (Fig. 4.5C). The trends for higher counts of small shrubs, spruce seedlings, and the two smallest fir seedling classes in I × 1 m subplots with less herbaceous cover, however, suggests that herbaceous vegetation may competitively exclude the woody taxa, or vice versa. *Rubus*, *Vaccinium*, fir seedlings, and ferns often form dense, nearly monospecific patches. The understory composition following the death of canopy fir from adelgid infestation resembles changes observed in fir forest blowdowns. Crandall (1958) presented data comparing the understory of a fir blowdown on Clingmans Dome with the understory of a nearby intact stand. She observed that in the open area, moss coverage was 0.4%, herb coverage was 57.4%, and *Rubus* density was 474 stems/100 m^2 ; in the intact stand, moss coverage was 38.1%, herb coverage was 7.9%, and *Rubus* was not present.

Observed differences in tree seedling and small shrub densities among twig/leaf litter and bryophyte cover classes are probably the product of the distribution of ground cover types and woody plants among stand types (Table 4.2). Smaller fir seedlings tend to be more abundant in medium twig/leaf litter coverages. Low twig/leaf litter probably indicates that few live, reproducing fir or spruce exist in the canopy, since twig/leaf litter is more abundant in the fir and spruce dominated PLF and MLF stands. Crandall (1958) and I have observed that areas directly under dense stands of small overstory, sapling, and large seedling fir are often almost entirely covered with thick leaf and twig litter. These sites are probably too shaded for the growth of small seedlings. The higher counts of the two smallest fir seedling classes in subplots with higher bryophyte cover is most likely the result of fir seedlings and bryophytes both preferring intact (PLF) fir stands (note that only two 1 × 1 m subplots had 76-100% bryophyte cover) (Fig. 4.5B). Pauley and Clebsch (1990) also found that fir seedlings occur more often on bryophyte covered surfaces than in sites without bryophytes.

Given the prominent role that the elevation gradient plays in determining overstory and understory distributions (Cain 1935; Oosting and Billings 1951; Whittaker 1956; Boner 1979; Nicholas et al. 1992a and b; Chapter 3), it is surprising that elevation is a significant variable for only 1.01 m - 1.36 m tall fir seedlings and hardwood saplings. One possible explanation is that the sampling regime of four stand types may have obscured the elevational response. Another possible cause may be that the impact of the adelgid has increased seedling density variation along the elevational gradient by eliminating adult fir in patches and by favoring the growth of shade-intolerant vegetation in devastated stands.

In summary, several possibilities may arise in the next few decades. Since the decrease in small fir seedling densities in stands dominated by dead fir relative to predominantly live fir stands is likely the result of decreases in reproduction, densities of smaller fir seedlings can be expected to decline in the short term as more adult fir die over time. Sapling fir densities, however, tend to increase with time since major canopy mortality over the short term and probably result in temporarily increased recruitment to the overstory. Since adelgid infestation and mortality are patchy phenomena (Eagar 1978) and fir seed dispersal appears limited, future fir reproduction will probably become more spatially and temporally clumped. Although seedlings and small shrubs do not show evidence of direct competition with understory fir, saplings and large shrubs do. Increases in herb/sub-shrub cover and decreases in bryophyte cover in stands dominated by dead fir are most likely the result of greater insolation. If so, the warmer and drier conditions that now occur since infestation will likely favor higher densities of spruce and hardwood saplings. There is also some evidence in this study and in the literature that increases in herbaceous vegetation cover, especially *Rubus*, inhibit small fir seedlings. As a result, fragmented populations of fir may become excluded within a few generations from mixed stands that were common at lower elevations.

4.6 Conclusions

The species abundances of the spruce-fir forest understory have changed following the decimation of adult fir and subsequent canopy opening, as other studies have shown (Boner 1979; DeSelm and Boner 1984; Pauley 1989; Pauley and Clebsch 1990). Previous studies have reported vigorous fir regeneration (Boner 1979; Witter and Ragenovich 1986; Nicholas et al. 1992b). In this study, however, densities of fir seedlings ≤ 0.25 m tall are significantly greater in stands dominated by live fir than in dead fir stands and are positively associated with live fir basal area. Densities of spruce seedlings and small shrubs, mostly *Vaccinium erythrocarpum*, are significantly greater in mixed spruce-fir-hardwood stands that have experienced canopy opening. Coefficients of a regression of fir seedlings on spruce seedlings, hardwood seedlings, and shrubs were positive or non-significant. Similar to changes in fir blowdowns prior to adelgid infestation (Crandall 1958), mean percent cover of herbs/sub-shrubs is greater in stands whose fir component is mostly dead. Mean percent cover of bryophytes is greatest in stands dominated by live fir and lowest in stands dominated by dead fir.

Chapter V

Size and age class distributions of overstory and understory Fraser fir

5.1 Abstract

Fraser fir (*Abies fraseri* (Pursh) Poir.) is a southern Appalachian endemic species that has suffered catastrophic mortality throughout most of its entire native range from the depredations of an exotic insect, the balsam woolly adelgid (*Adelges piceae* Ratz.). The adelgid infests fir over about 4 cm dbh, killing them in 2 - 7 years. To study the impacts of infestation on the size and age distributions of Fraser fir, thirty-six 400 m^2 permanent plots were established near the summits of five mountains suffering major mortality at different times in the Great Smoky Mountains. I found that on mountains where the forest canopy has been open longer due to fir death, understory fir are growing more rapidly and are reentering the overstory. Overstory size distributions on earlier infested mountains have fewer large fir and relatively higher densities of smaller fir as the result of selective mortality of larger fir and increased recruitment from the understory. The unimodal shape of the understory age class distributions remains mostly unchanged over the five mountains and is most likely caused in part by naturally episodic seed crop production. Densities of 0 - 10 yr old fir seedlings were much lower in stands dominated by dead fir than in mostly intact fir stands. Unless sufficiently large seed crops are produced by the emerging second generation of adult fir, the failure to replenish the seedling pool may threaten the stability of future fir populations. Although attempts to model adelgid-induced cycles in fir populations using sine wave models were unsuccessful, the models did detect cyclic trends that I attributed to patterns of reproduction and growth.

5.2 Introduction

Fraser fir (*Abies fraseri* (Pursh) Poir.) is endemic to the southern Appalachian fir and spruce-fir forests that occur in a disjunct distribution on seven high mountain areas in North Carolina, Tennessee, and southwestern Virginia and only occupy a total of about 26,600 ha (Dull et al. 1988). Fraser fir is the canopy dominant species above about 1890 m elevation; from 1675 m - 1890 m, red spruce (*Picea rubens* Sarg.) is codominant (Whittaker 1956). Fraser fir probably originated from monospecific fir populations extending along the Appalachians in a continuous chain during the Pleistocene and exhibiting north to south clinal variation (Robinson and Thor 1969; Thor and Barnett 1974). With climate warming, southern fir populations retreated upslope and became genetically isolated from northern Appalachian fir. In part because of glacial relict origin, southern Appalachian spruce-fir forests are rich in many rare, disjunct, and endemic species (Delcourt and Delcourt 1984; White and Renfro 1984).

In 1957, the balsam woolly adelgid (*Adelges piceae* Ratz.), an exotic, aphid-like insect, was found on Mt. Mitchell, North Carolina (Speers 1958). The adelgid feeds in the bark fissures of adult fir and injects salivary compounds that cause the host tree to produce heavily lignified tracheids that reduce sapwood conductance (Puritch 1971; Hollingsworth *et al.* 1991). Infested Fraser fir usually die in two to seven years (Amman and Speers 1965; Eagar 1984). From Mt. Mitchell, the adelgid quickly spread throughout the southern Appalachians, resulting in catastrophic mortality of adult Fraser fir. Dull et al. (1988) reported that the percentage of standing dead Fraser fir ranges from 44% on Roan Mountain, Tennessee, to over 90% in parts of the Great Smoky Mountains. Nicholas et al. (1992a) compared their 1989 data with data from Oosting and Billings (1951) collected in 1946 and found that, depending on elevation, the 1989 values for live fir basal area were only 8 - 62% of the 1946 values. The USDI Fish and

Wildlife Service (1993) listed Fraser fir as a Category 2 species, but under recent revisions of federal listing procedures, Fraser fir is not a candidate species (USDI Fish and Wildlife Service 1996).

This chapter will investigate the size and age distributions of overstory and understory Fraser fir. Size and age distributions have often been used to analyze the mortality, disturbance history, and successional status of tree populations. Although size distributions have received more attention in the past, especially in commercial forest management, both approaches yield useful but different information about stand dynamics. The age structure of a stand reveals more about stand history and successional status than does size (Hett and Loucks 1976; Whipple and Dix 1979; Shea 1985). Size structure is more sensitive to environmental variation and is a better indicator of reproductive output (Knowles and Grant 1983; Shea 1985). Age curves have been used to approximate survivorship curves under the assumption that every cohort has been subjected to the same age-specific mortality and reproduction rates. Since this is not the case with Fraser fir, the size and age distributions presented here are descriptions of present conditions and make no assumptions about survivorship probabilities.

This study encompasses five mountains that have suffered major mortality at different times, providing the opportunity to study Fraser fir populations in different stages of infestation and recovery. Specific questions addressed in this chapter are: 1) how mean understory and overstory fir age varies by mountain; 2) how the average age and size of cone-producing fir change by mountain; 3) how overstory size and age distributions change by mountain; 4) how understory age distributions vary by mountain and by overstory canopy composition; and 5) whether or not cyclic patterns exist in fir populations and, if so, whether or not they are induced by the adelgid.

5.3 Methods

5.3.1 Study site and data collection

The study was initiated and data collected by Paul Durr, a former biological technician with the Great Smoky Mountains National Park. The study sites were five peaks in the Great Smoky Mountains National Park (GSMNP), from northeast to southwest: Mount Sterling (1781 m elevation), Mount Guyot (2019 m), Mount LeConte (2010 m), Mount Collins (1887 m), and Clingmans Dome (2025 m). These five were chosen because as a group they encompass nearly the entire range of Fraser fir in the park. Areas that had been logged or burned were avoided when placing the permanent plots. Mt. Sterling was the first mountain to be infested by the adelgid, suffering widespread fir death in 1970-1972 (Ciesla et al. 1963; C. Eagar, personal communication). From there, the adelgid spread westward throughout the Park. Clingmans Dome was infested last and experienced major fir mortality in 1990-1992 (C. Eagar, personal communication). Clingmans Dome and Mt. Collins were sampled in 1990; Mt. LeConte, Mt. Guyot, and Mt. Sterling were sampled in 1991.

Thirty-six 400 m^2 (20 × 20 m) permanent plots, corrected for slope, were established from the summits to 100 m elevation below the summits of the five mountains. Each mountain was to have two replicate plots in each of four stand types:

- pure live fir (PLF) with ≥65% overstory basal area in fir and ≥65% of those trees living
- pure dead fir (PDF) with ≥65% of overstory basal area in fir and ≥65% of those trees dead
- mixed live fir (MLF) with ≤35% of overstory basal area in fir, ≥65% of which is live, mixed with spruce and/or hardwoods
- mixed dead fir (MDF) with ≤35% of overstory basal area in fir, ≥65% of which is dead, mixed with spruce and/or hardwoods.

One PLF plot from Clingmans Dome, one PLF plot on Mount Sterling, one PDF plot from Mount Sterling, and one MLF plot on Mount Guyot were never established because a second replicate of the stand type could not be found on those peaks.

Diameter at breast height (dbh) (1.37 m above the ground) to the nearest millimeter was measured for all live and dead overstory (≥ 5 cm dbh) trees. Each overstory stem was mapped and the crown position (dominant, codominant, intermediate, and overtopped) of each tree was estimated. Six randomly selected dominant or codominant live fir in the PLF and MLF stand types were cored for age using an increment borer.

Saplings and woody shrubs (≥ 1.37 m tall and < 5 cm dbh) were tallied by species in sixteen 2 × 2 m quadrats, four in each of four 2 × 10 m strips. Each strip was randomly located in one of the 10 × 10 m plot quarters. Nested randomly in each of the 2 × 2 m quadrats was a 1 × 1 m subplot where tree seedlings were tallied by species and size class. The five seedling size classes were: germinal, unbranched, branched but less than 0.25 m tall, 0.26-1.00 m tall, and 1.01-1.37 m tall. Fir seedling and sapling age profiles were determined by destructive sampling outside but as close as possible to the permanent plots. Five live individuals from the four largest seedling size classes (unbranched, ≤ 0.25 m tall, 0.26-1.00 m tall, 1.01-1.36 m tall) and five saplings (≥ 1.37 m tall but < 5 cm dbh) were cut at ground level and cross-sections of the stems were taken to the laboratory for age determination. Understory age data were collected in all four stand types.

5.3.2 Data analysis

The size structure of the adult Fraser fir populations on each of the mountains was described using 1 cm dbh classes. A power function model,

$$y = y_0 x^{-b} \qquad \text{(equation 1)}$$

where y is the density of trees of dbh x and -b is the mortality rate, was fit to a density-dbh plot of the data for each mountain. Another widely used model, the negative exponential distribution, was not used because, unlike the power function, the model assumes that the probability of individual mortality remains constant with tree size (Hett and Loucks 1976). This is not the case with Fraser fir, since lethal stem infestation by the adelgid occurs in fissures in the bark of larger trees (Eagar 1984).

To investigate the possibility of an adelgid-caused wave pattern in overstory fir, a linearly damped sine wave was superimposed on the power function model. The sine wave model,

$$y = y_0 x^{-b} + (cx + h) \sin (fx + g + \pi/2) \qquad \text{(equation 2)}$$

has two additional components: the linear damping expression ($cx + h$) and the sine wave function (sin ($fx + g + \pi/2$)). The cumulative proportions of overstory fir densities in size classes were calculated for each mountain and plotted.

Understory fir were categorized into 5 yr age classes and the power function model (equation 1), with x representing the age class midpoint, was fit to a density-age class plot of the data on each mountain. Since Fraser fir produces prolific seed crops every 2 - 4 years (USDA Forest Service 1974), the 0-5 yr age class was omitted when fitting models. Since equal numbers of understory stems were aged in each size class, the age class densities were weighted according to the density of stems sampled in a given size class, on a given mountain. The sine wave model (equation 2) was also fit to the understory age-class distributions on each mountain. The cumulative proportions of understory fir densities in age classes were calculated for each mountain and plotted. Understory age class distributions and cumulative proportion distributions were constructed for the four stand types with understory densities in

each age class weighted by the densities of stems in that age class sampled in each of the four stand types.

All model fitting and statistical testing was performed using SAS (SAS Institute 1989).

5.4 Results

Mean age of dominant and codominant overstory fir (≥ 5 cm dbh) on each mountain decreases from west, the later infested mountains, to east, the earlier infested mountains (Fig. 5.1). Overstory dominant and codominant fir on Mt. Collins and Clingmans Dome are significantly older than fir on Mt. Guyot and Mt. Sterling. Understory fir in three size classes, unbranched, 1.01 m - 1.36 m tall, and 1.37 m tall - 4.9 cm dbh, also exhibit this trend (Fig. 5.1).

The distributions of dominant and codominant fir in 10 yr age classes are increasingly skewed to younger age classes on the mountains that were infested earlier (Fig. 5.2). On Mt. Guyot and Mt. Sterling, the majority of the canopy dominants are clustered in only three age classes. Mt. Collins has an overstory age class distribution markedly different than those from the other mountains, having no dominant or codominant individuals younger than 60 yr.

Cone-bearing fir were found only on Mt. LeConte, Mt. Guyot, and Mt. Sterling because of differences in sampling years (Table 5.1). The mean dbh of cone-bearing fir was greater than the mean dbh of fir without cones on all three mountains (Table 5.1A). Although cone-bearing fir were largest on Mt. Sterling, these fir were also significantly (95% confidence intervals did not overlap) younger on average than fir on Mt. LeConte and Mt. Guyot (Table 5.1B). The mean ages of fir with and without cones were not significantly different on Mt. Guyot and Mt. Sterling. Cone-bearing fir on Mt. Sterling were in fact younger on average than coneless fir.

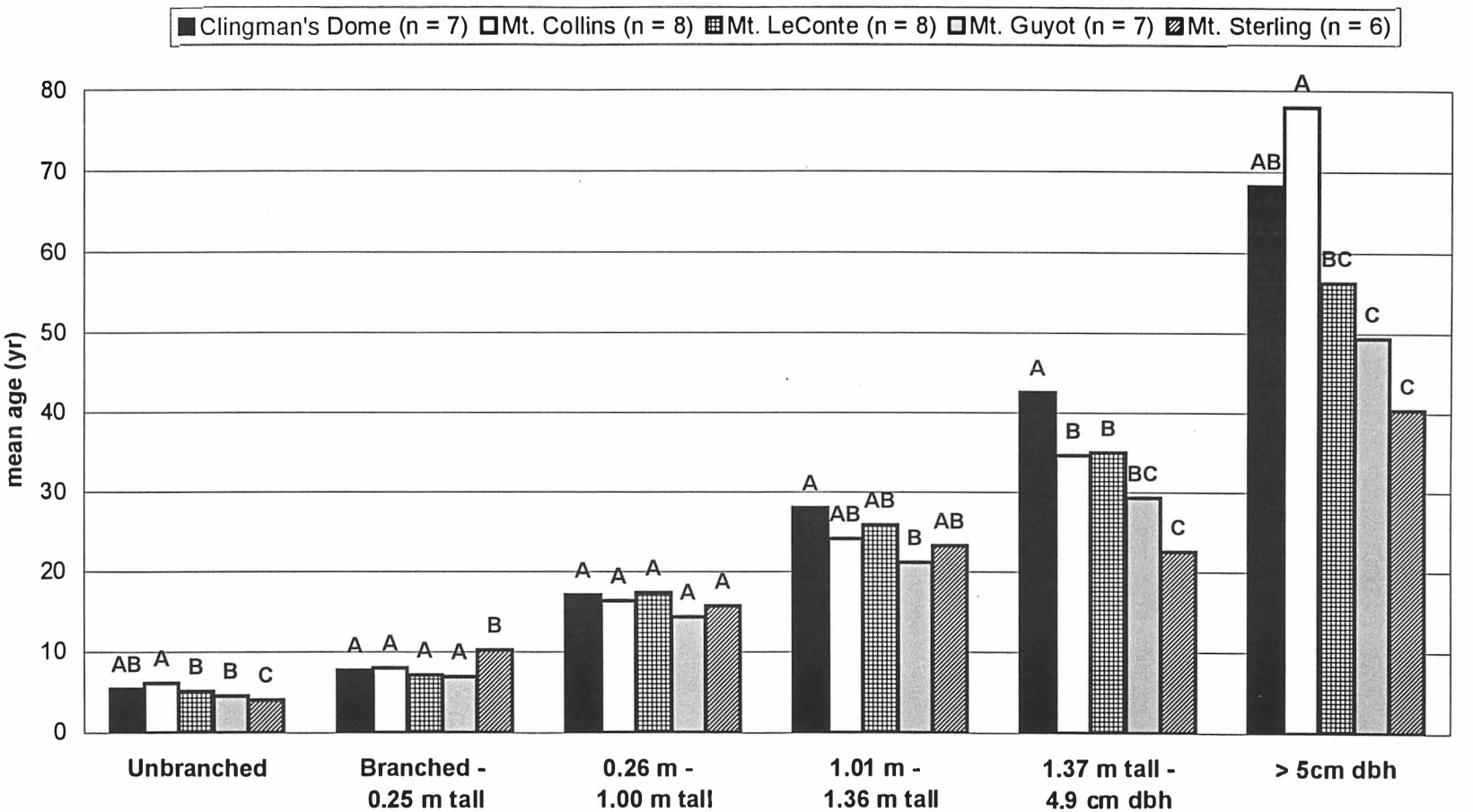

Figure 5.1. Mean age of Fraser fir in six size classes for five locations in GSMNP. Sample size (n) is the number of permanent plots. Means in the same size class with the same letter are not significantly different ($\alpha = 0.05$) by Ryan's Q multiple comparisons tests following a significant MANOVA ($F = 10.42$, 4 df; $P < 0.0001$).

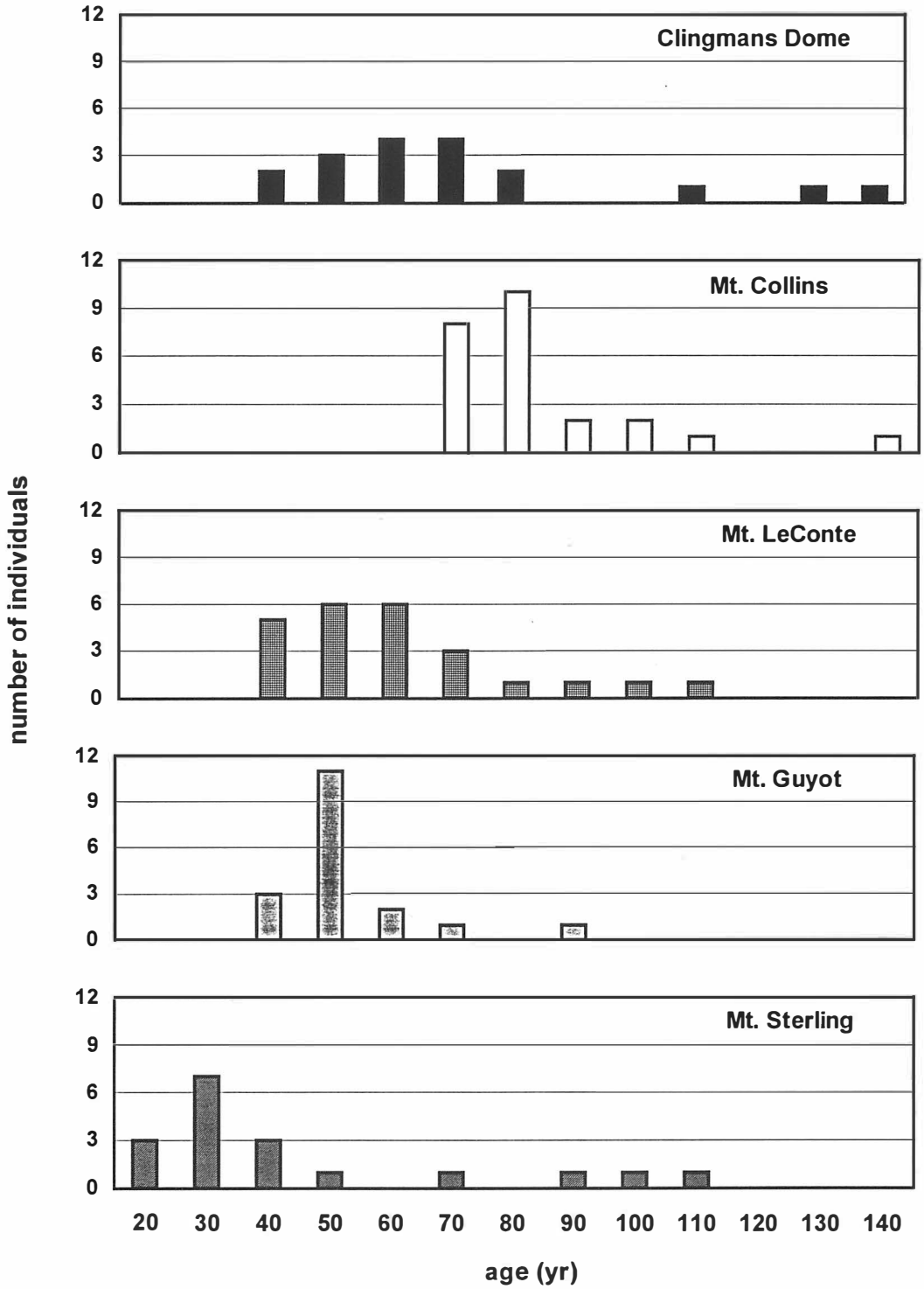

Figure 5.2. Number of dominant and codominant overstory fir in 10 yr age classes for five locations in GSMNP.

Table 5.1. Mean dbh and age of cone-bearing fir for five locations in GSMNP. No cones were found on fir on Clingmans Dome or Mt. Collins; these mountains were sampled in 1990 while the other three were sampled in 1991.

		Mt. LeConte	Mt. Guyot	Mt. Sterling
A. Mean dbh (cm) and 95% confidence interval (in parentheses) of cone-bearing fir and fir without cones.				
Fir with cones	**n**[1]	75	130	11
	DBH (cm)	16.2 (15.2-17.3)	15.3 (14.8-15.9)	18.4 (15.7-21.0)
Fir without cones	**n**	280	199	61
	DBH (cm)	9.2 (8.8-9.7)	9.5 (9.0-10.0)	9.2 (8.0-10.4)
B. Mean age (yr) and dbh (cm) with 95% confidence interval (in parentheses) of cone-bearing fir and fir without cones cored for age.				
Fir with cones	**n**	20	17	7
	Age (yr)	58.9 (50.8-67.1)	49.5 (44.3-54.6)	30.9 (18.3-43.4)
	DBH (cm)	20.2 (18.9-21.6)	19.6 (18.2-21.0)	21.2 (19.3-23.2)
Fir without cones	**n**	4	1	11
	Age (yr)	43.0 (37.6-48.4)	47.0	46.4 (27.0-65.7)
	DBH (cm)	16.8 (14.1-19.5)	19.0	12.8 (9.1-16.5)

[1] Sample size (n) is the number of trees.

5.4.1 Overstory Size Class Distributions

Density distributions of overstory Fraser fir in 1 cm dbh size classes follow the inverse J-shaped distribution typical of uneven-aged, old growth conifer stands (Fig. 5.3) (Leak 1965; Hett and Loucks 1976; Whipple and Dix 1979; Parker and Peet 1984; Ågren and Zackrisson 1990). The dbh exponent, $-b$, in the power function equation (equation 1) is the size-specific depletion rate. The exception to the inverse-J distribution is Mt. Collins, where the size class distribution is nearly uniform or perhaps bimodal, with slight peaks in the observed densities at 5-7 cm dbh and 23-26 cm dbh. Fir larger than 25 cm dbh are rarer on Mt. LeConte and Mt. Guyot than on Clingmans Dome and Mt. Collins; few fir on Mt. Sterling are larger than 20 cm dbh. Superimposing a sine wave (equation 2) on the power function predictions improved the fit of the predicted curve for all of the mountains by 0.6% - 4.5% as measured by increased regression sums-of-squares (Fig. 5.4). The wavelength, λ, of the predicted curve was calculated for each distribution:

$$\lambda = 2\pi/f \qquad \text{(equation 3)}$$

where f is from the sine wave term of equation (2). As a result of the nearly uniform size class distribution of stems on Mt. Collins, the cumulative distribution for that peak resembles a constant linear decrease (Fig. 5.5). Mt. Sterling, Mt. Guyot, and Mt. LeConte do not have the low densities of large fir that Clingmans Dome exhibits. Two-sample Kolmogorov-Smirnov tests showed that the cumulative distributions for Clingmans Dome and Mt. Collins differed significantly ($P < 0.05$) from those of the other three mountains and each other.

5.4.2 Understory Age Class Distributions

In the density distributions of understory stems in 5 yr age classes, with the exception of Mt. Guyot, the weighted densities of the 0-5 yr age classes are lower than the 6-10 yr age

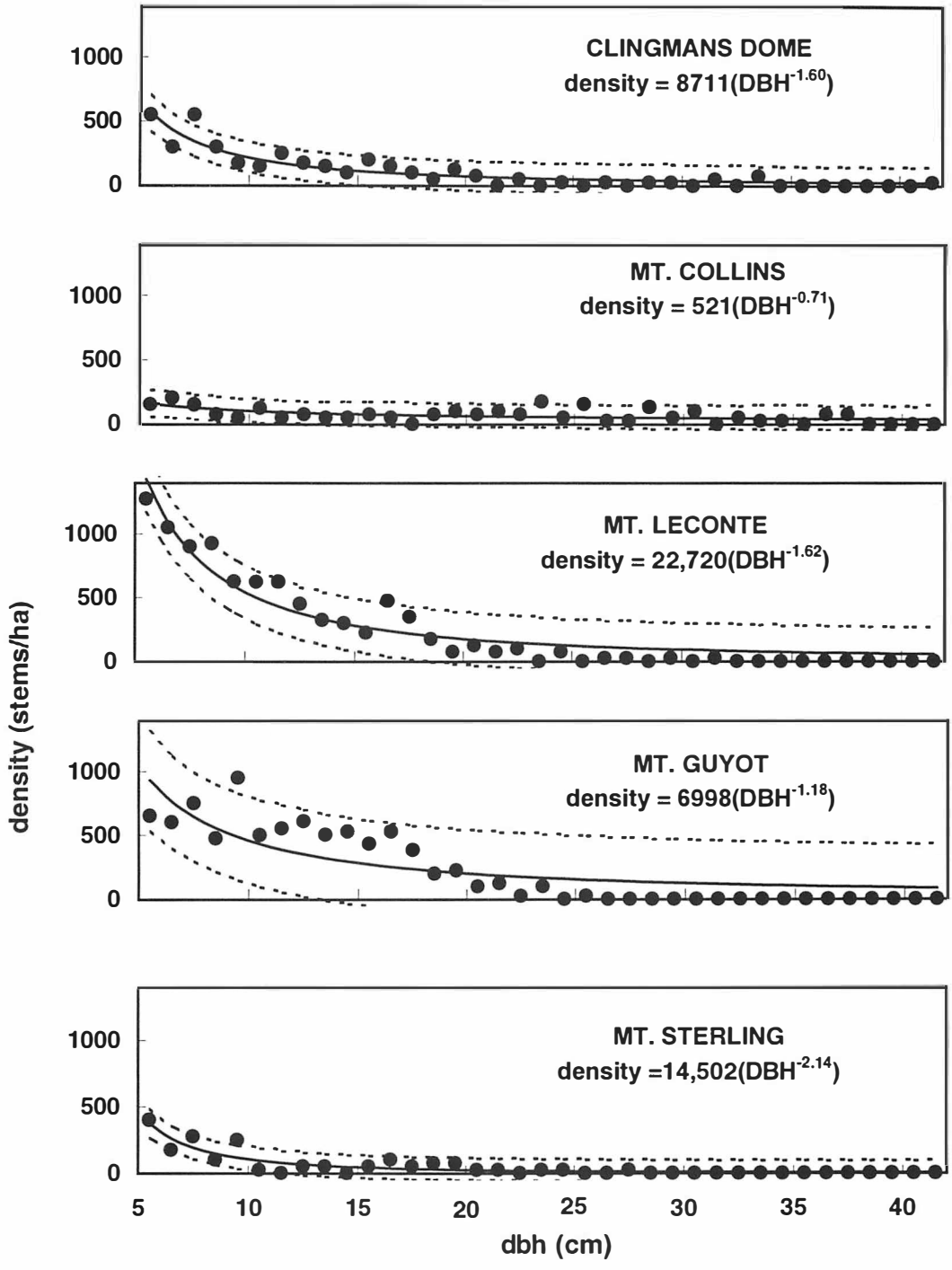

Figure 5.3. Densities of overstory fir in 1 cm dbh size classes for five locations in GSMNP (dots)— power function model. Solid lines are predictions of the power function equation; dashed lines are 95% confidence limits.

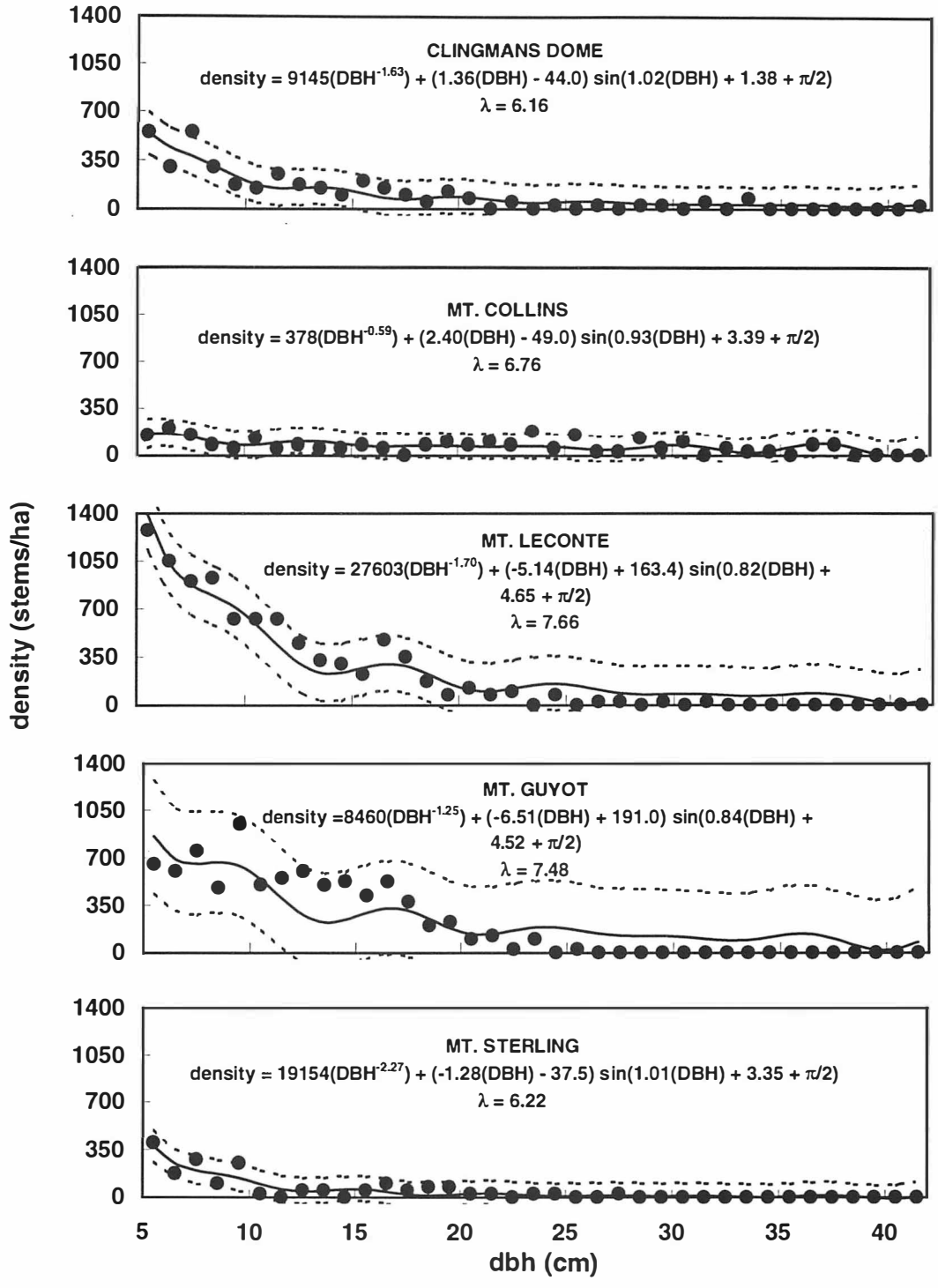

Figure 5.4. Densities of overstory fir in 1 cm dbh size classes for five locations in GSMNP (dots)—sine wave model. Solid lines are predictions of the sine wave equation; dashed lines are 95% confidence limits.

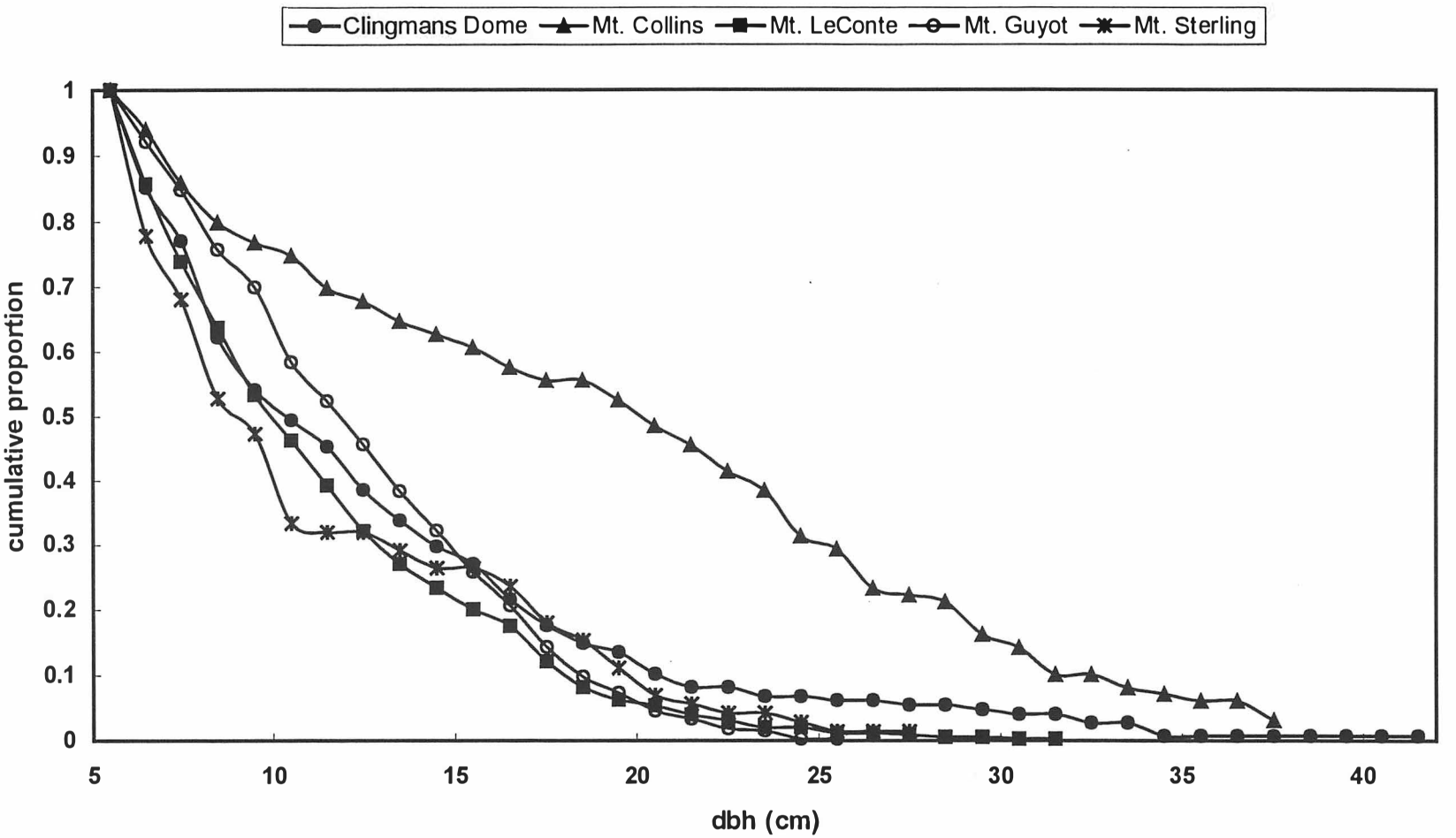

Figure 5.5. Cumulative proportion distributions of overstory fir in 1 cm dbh size classes for five locations in GSMNP. Clingmans Dome and Mt. Collins distributions are significantly different ($\alpha = 0.05$) from all other distributions by Kolmogorov-Smirnov tests.

classes (Fig. 5.6). Mt. Sterling is notable for the very low weighted counts of understory stems in the 6-10 yr age class. Mt. Sterling has only negligible numbers of understory fir older than 25 years; Mt. Guyot and Mt. Collins have very few understory fir older than 40 years. The sine wave model was also fit to the understory age distributions and the resulting wave lengths for each peak ranged from 6.35 yr to 6.41 years. Two sample Kolmogorov-Smirnov tests of the cumulative age distributions for understory Fraser fir did not find any significant differences among the five cumulative distributions (Fig. 5.7).

The shapes of the weighted density distributions of understory fir in 5 yr age classes by stand type are also unimodal (Fig. 5.8). Densities of 0 - 10 yr old seedlings in PLF stands are much greater than those in the other three stand types. In PDF stands, 0 - 5 yr old fir densities are comparable to those in mixed fir stands, while 6 - 10 yr old seedling abundances, while still much lower than in PLF stands, are more than 50% greater than those in mixed stands. Mixed fir stand types appear to have slightly more very old (> 50 yr) suppressed understory fir. Two sample Kolmogorov-Smirnov tests of the cumulative distributions did not find any significant differences ($\alpha = 0.05$) among the cumulative proportion distributions of the four stand types (Fig. 5.9).

5.5 Discussion

5.5.1 Mean ages of overstory and understory fir

Severe mortality of the canopy Fraser fir has resulted in increased insolation to the forest floor. Some species have increased in abundance, most likely in response to improved growing conditions (Crandall 1958; Boner 1979; DeSelm and Boner, 1984; Pauley 1989; Pauley and Clebsch 1990; Witter and Ragenovich 1986; Nicholas et al. 1992b; Chapter 4). The trend that understory fir of a given size are younger on earlier infested mountains suggests that

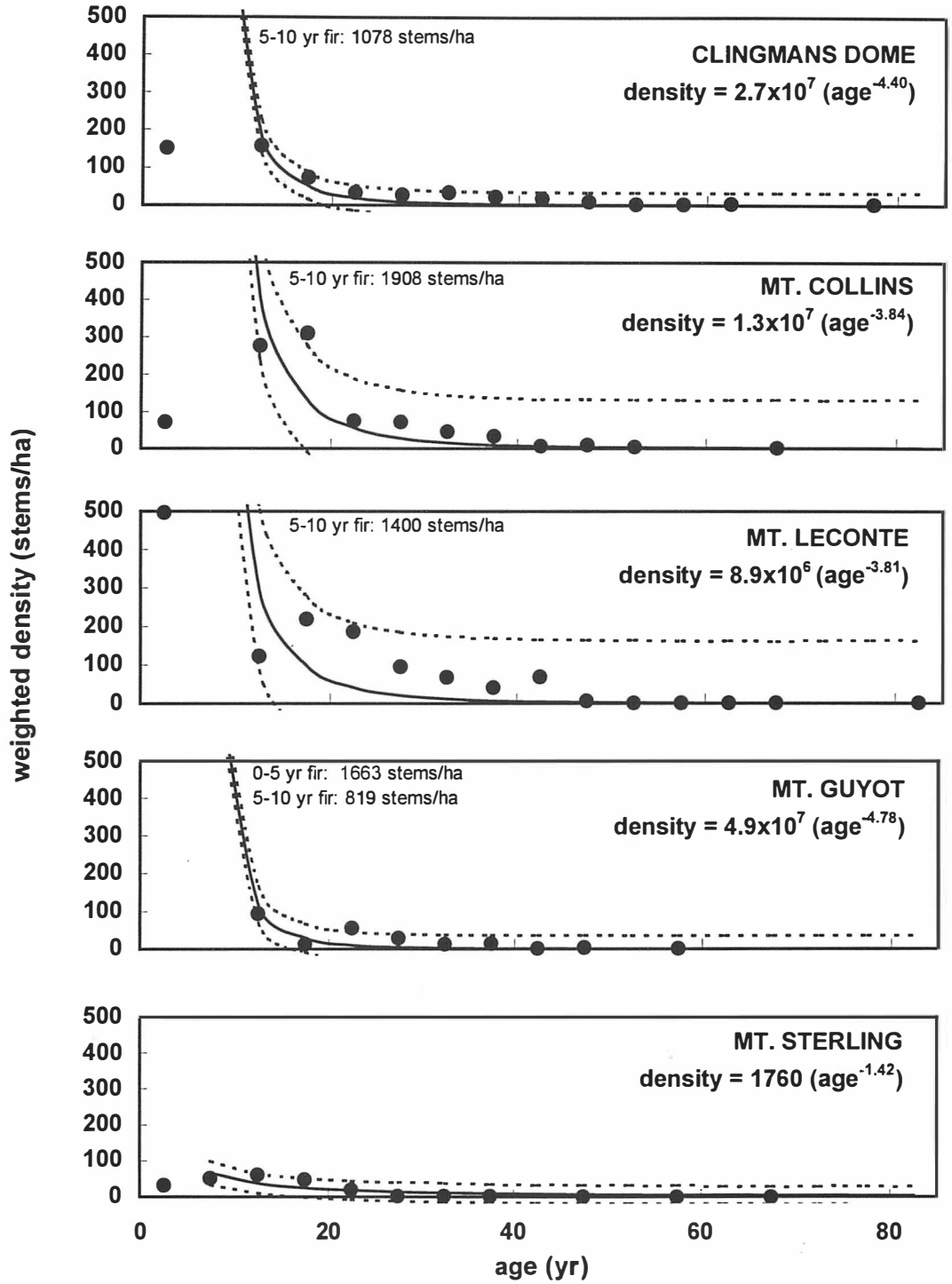

Figure 5.6. Densities of understory fir in 5 yr age classes for five locations in GSMNP (dots). Solid lines are predictions of the power function equation; dashed lines are 95% confidence limits. Note that 0 - 5 yr fir densities were not included in the power function model.

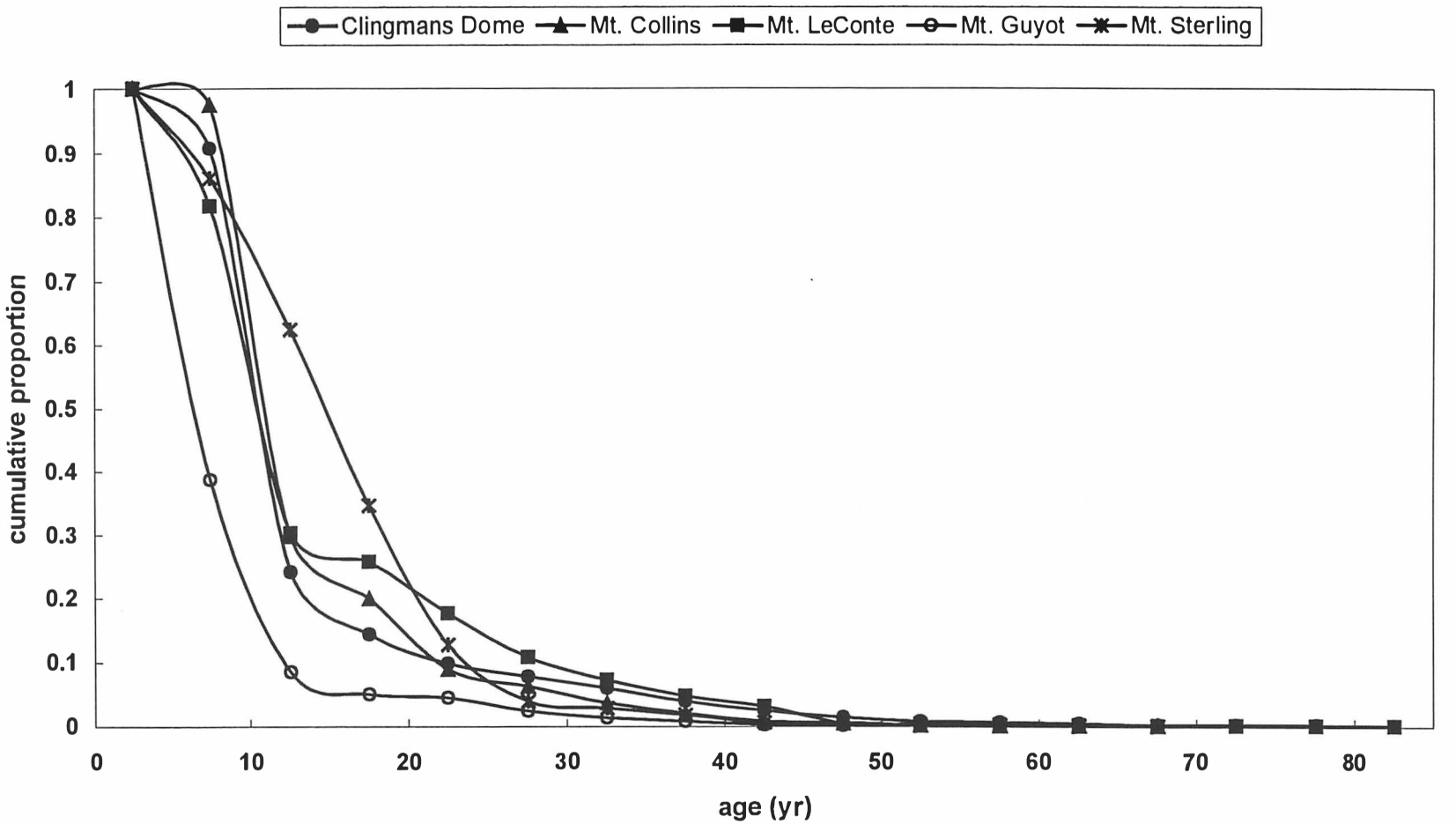

Figure 5.7. Cumulative proportion distributions of understory fir in 5 yr age classes for five locations in GSMNP. No distributions are significantly different ($\alpha = 0.05$) by Kolmogorov-Smirnov tests.

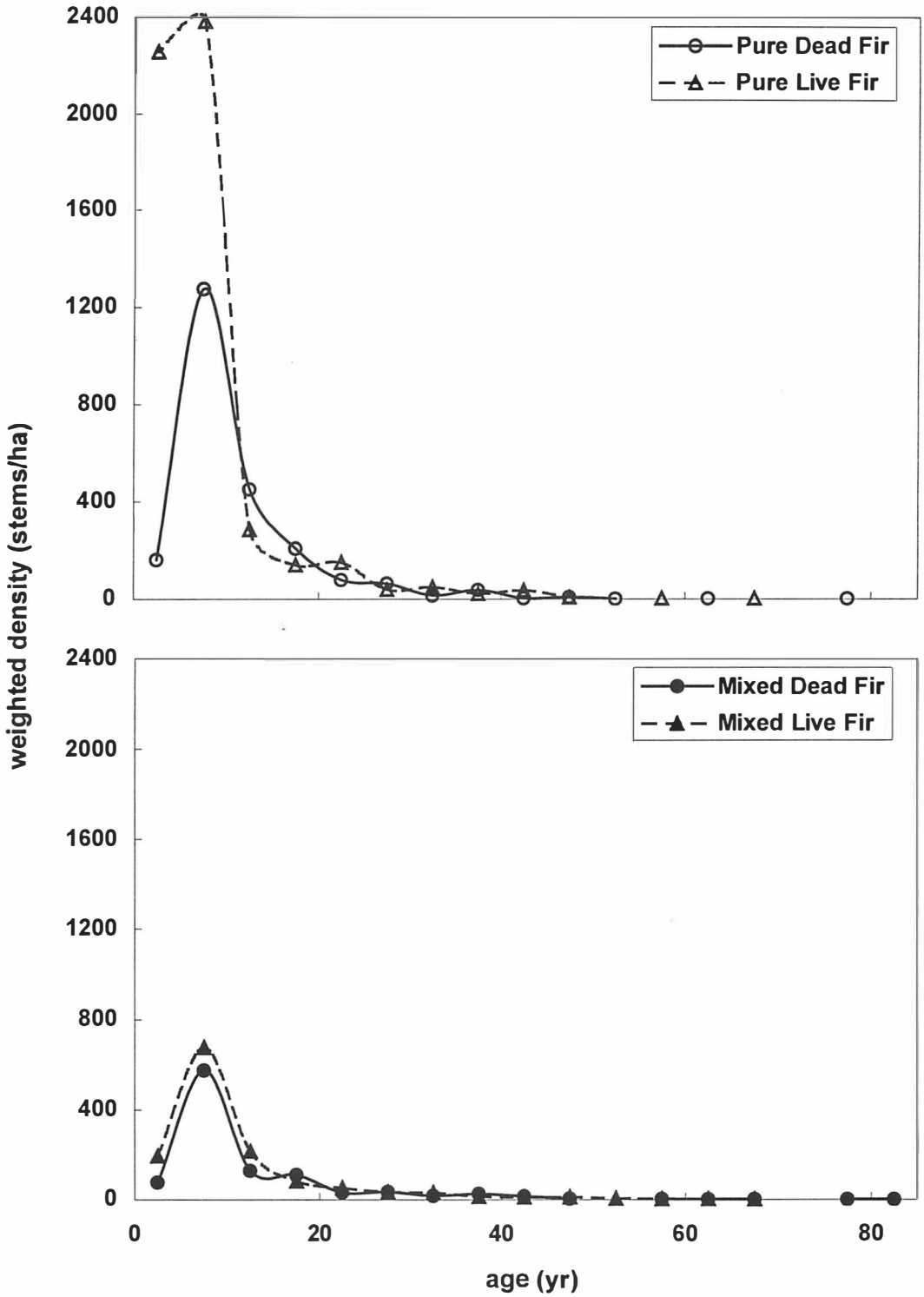

Figure 5.8. Densities of understory fir in 5 yr age classes by stand type for five locations in GSMNP.

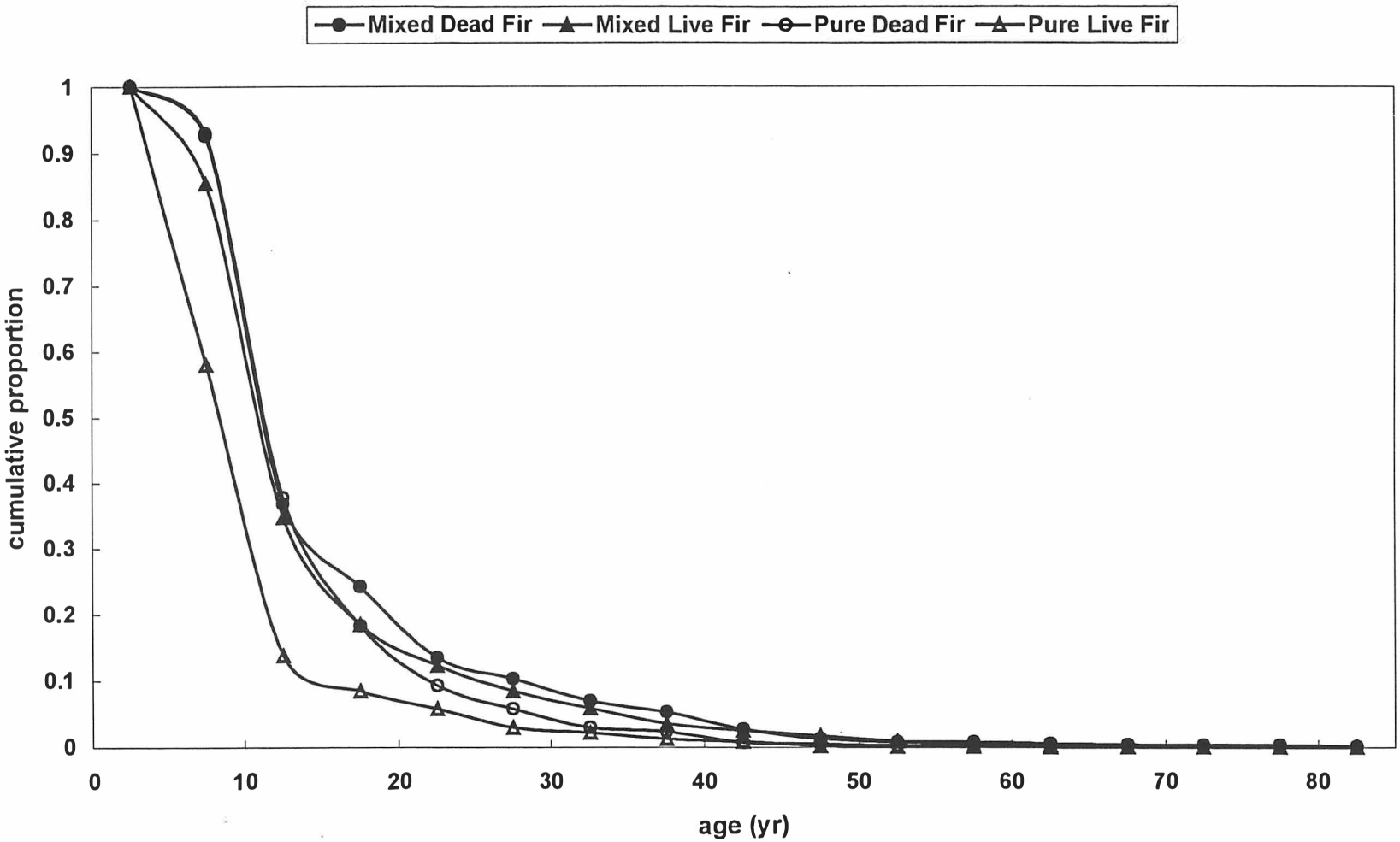

Figure 5.9. Cumulative proportion distributions of understory fir in 5 yr age classes by stand type for five locations in GSMNP. No distributions are significantly different ($\alpha = 0.05$) by Kolmogorov-Smirnov tests.

increased canopy openness has also caused understory fir to grow faster. This may account in part for recently observed low densities of small fir seedlings (Nicholas et al. 1992b; Chapter 4) as young fir grow rapidly into the larger size classes. Competition with invasive, shade-intolerant species, especially *Rubus*, however, has been found to reduce understory fir populations (Witter and Ragenovich 1986; Pauley 1989; Pauley and Clebsch 1990). Survival of the present, healthy understory is not assured.

Ultimately, maintenance of understory fir densities sufficient to regenerate historical abundances of adult fir depends on the ability of second generation and surviving canopy fir to produce enough viable seed. With a combination of selective mortality of older and larger fir and canopy capture by younger individuals, the mean age of dominant and codominant fir would be expected to decrease and the age class distribution to become skewed towards younger individuals. Comparison of the mountains earlier infested by the adelgid, which have had more time for recruitment and growth of suppressed stems, with the later infested mountains show these trends (Fig. 5.1 and 5.2). Since cone production tends to occur at younger ages on earlier infested mountains, the mean dbhs of cone-bearing fir are generally larger than mean dbhs of fir without cones, and mean ages of cone-bearing and coneless fir do not differ significantly on two of the three mountains, it appears that size is more important than age in determining whether or not fir will reproduce. Since Fraser fir in Christmas tree seed orchards produce viable seed when they are only 8-10 yr old and 1.8 - 3 m tall (J.B. Jett, personal communication), further decreases in age of maturity are possible, given the proper environmental conditions. One long-term result of faster growing fir understories and fir overstories that mature more rapidly will be an increase in the rates of fir regeneration and reinfestation.

Although understory fir may be growing faster and thus maintain a fair level of reproductive potential following the death of the first generation adults, adelgid infestation is dependent on the size, not age, of the tree. The question remains whether this potential can be realized before second generation fir are killed. Fraser fir produces large cone crops across its native range every 2 - 4 years and few in intervening years (USDA Forest Service 1974). The factors that determine large seed years remain largely unknown. The presence of cones on several Mt. LeConte, Mt. Guyot, and Mt. Sterling fir (sampled in 1991) and none on Clingmans Dome and Mt. Collins fir (sampled in 1990), indicate that 1991 was a large seed year. Other recent years of prolific seed production were 1987 and 1994 (Nicholas et al. 1992b; J.B. Jett, personal communication). Additional factors that influence seed production include adelgid infestation, seed predation, and increased canopy openness in stands that have suffered major fir mortality. Cone production and seed viability decrease in infested Fraser fir while the incidence of seed predation by the seed chalcid *Megastigmus specularis* Walley increases (Fedde 1973a, b). Production of female cones in Fraser fir, however, increases in open-grown individuals or on parts of the tree more exposed to sunlight (J.B. Jett, personal communication).

5.5.2 Overstory size and age class distributions

Mortality of infested fir and recruitment of young fir into the overstory are largely responsible for determining the shapes of the size class distributions for the five mountains. Since adelgid-caused mortality and subsequent release and recruitment were initiated at different times on the mountains, these processes have led to changes in the size distribution of overstory Fraser fir. One change is the loss of large fir caused by the selective mortality of larger individuals. The significant differences between the cumulative distributions for

Clingmans Dome and Mt. Collins, and the other three mountains probably derive primarily from the survival of small numbers of large fir. If these survivors die in turn, the distributions will more closely resemble those of the other three peaks.

Recruitment on the earlier infested mountains is the most likely cause for increased densities of fir in the smaller size classes. In the cumulative distribution graph, this appears as a steeper decline in the first part of the curve. On Mt. Sterling, 5-6 cm dbh fir density is nearly two-thirds that of Clingmans Dome, whose higher elevation summit was probably more dominated by fir before the adelgid. Also, since Mt. Sterling has had about 10 years of post-mortality recruitment longer than Mt. Guyot, the next mountain to the west, more of its fir population is concentrated in the smaller dbh classes than any other mountain. Assuming that a chronosequence view of the five mountains is valid, over time the cumulative size distribution of overstory fir in a given location will become steeper in the smaller dbh classes.

The 10 yr age class distributions of dominant and codominant fir also reflect the effects of the selective mortality of large fir and recruitment of younger fir. Although even Mt. Sterling has a few old fir (> 70 yr) surviving, these individuals are smaller on average than fir of a comparable age on Clingmans Dome and Mt. Collins. This observation emphasizes the poor correlation between age and size in old-growth Fraser fir (Oosting and Billings 1951) or any shade-tolerant species.

The processes of adelgid infestation, fir mortality, and recruitment do not operate uniformly over large areas (Eagar 1978), resulting in differences in the size class distributions among stands on a mountain. The 95% confidence intervals are substantially wider for the power curve and sine wave model fits for size class distributions on Mt. Guyot and Mt. LeConte than for Mt. Collins and Clingmans Dome. Assuming that the models adequately mimic historical size class distributions, these departures from ideal model conditions are most

easily explained by the patchy nature of adelgid outbreaks in Fraser fir stands (Eagar 1978). The size class distributions presented in Figs. 5.4 and 5.5 represent a pooling of stands in different stages of infestation and recovery. Mortality and recruitment would be expected to occur at different rates in patches with different initial overstory species compositions, with different environmental conditions, and suffering major canopy fir death at different times. As these processes operate over time, variation in size distributions increases among the stands on a given mountain. The 95% confidence intervals on Mt. Sterling, however, are as narrow as those for Clingmans Dome and Mt. Collins. This may be because nearly all of the large, pre-infestation fir have been killed, reducing the patchiness in size distributions, or because of the fewer number of plots on Mt. Sterling.

5.5.3 Understory age class distributions

The age class distributions of understory Fraser fir seem to show no time-dependent trends among the five mountains. It would be expected that old understory fir would be fewer on earlier infested peaks because of release and recruitment into the overstory with canopy opening. The data from Mt. Sterling agree with this prediction, but understory individuals older than 30 years persist on all other mountains. The sampling design on each mountain is a nonrandom selection of stands with some having fairly intact canopies. In the more intact stands, some understory individuals are probably still suppressed. Another possible explanation is that old, suppressed fir either require several years after release to enter the overstory or have been suppressed for so long that they are incapable of substantial growth responses following greater insolation, especially if these individuals have suffered heavy but nonlethal infestations of nodes and bud bases.

Unimodal age structures in young woody plants have been found to be characteristic of episodically regenerating populations (Leak 1975; Smallidge and Leopold 1994). Since fir produces "bumper crops" of seeds at 2 - 4 year intervals (USDA Forest Service 1974), this explains in part, at least, the dearth of seedlings in the 0-5 yr age class on all but Mt. Guyot. Nicholas et al. (1992b), however, report that for their plots on Clingmans Dome and Mt. Collins, 1987 was a year of heavy seedfall. Germinal densities in 1988 were 10,277 stems/ha at 1980 m elevation and 1389 stems/ha at 1830 m elevation (Nicholas et al. 1992b). The seedlings from that crop would be 2 years old when the two mountains were sampled in 1990 for this study. Although there is no data on Fraser fir seedling mortality rates, comparing 0-5 yr age class densities of 151 stems/ha on Clingmans Dome (with plot elevations of 1925 m to 1980 m) and 73 stems/ha on Mt. Collins (plot elevations of 1810 m to 1880 m) (Fig. 5.6) with the 1988 germinal densities above indicates that mortality of young seedlings is high. Is this normal? There are no comparable pre-adelgid data, but Nicholas et al. (1992b) reported that 1-4 yr old fir seedlings declined in abundance from 1987 to 1989 (when sampling was completed). They suggested that low germination rates of the 1987 seed crop and/or summer drought in 1986 to 1988 may have been responsible.

Understory fir age class distributions in the four stand types are also unimodally distributed. Lower numbers of reproducing fir in PDF plots are probably responsible for the lower densities of 0 - 10 yr old seedlings observed in PDF plots relative to PLF plots. A smaller difference in overstory fir abundances in MLF and MDF stands (Figs. 3.4 and 3.6), therefore, results in a smaller seedling decline between the stand types. Since MDF canopies are mostly dominated by large spruce and some hardwoods (Figs. 3.4 and 3.6), PDF stands are most likely experiencing greater levels of desiccation and higher temperatures. These abiotic stresses are probably also contributing to declines in young seedling abundances, especially

during drought years such as 1986 - 1988 (Mohnen 1992). Competition from increasing abundances of shade-intolerant plants, such as *Rubus*, may also be a factor in young seedling declines (Pauley and Clebsch 1990; Chapter 4). While 0 - 5 yr old seedling densities in PDF stands are comparable to those in mixed fir stands, 6 - 10 yr old seedling densities are not as affected by canopy opening. The greater numbers of adult fir alive 6 - 10 years ago provided a cooler, moister environment as well as larger seed crops. Unless there are sufficient numbers of newly released and rapidly maturing fir to produce large seed crops, declining numbers of young fir seedlings will seriously threaten future fir populations.

In summary, future trends in understory fir distributions and abundances are uncertain. Decreases in the numbers of young seedlings, most likely caused in part by reproduction declines from adult fir death and increased heat and water stress, in stands primarily composed of dead fir present the possibility of reductions in future local fir populations. Production of cones at younger ages on earlier infested mountains suggests that age of first reproduction is fairly plastic. With more rapid growth of understory fir and earlier maturation of adult fir, the next phase of adelgid infestation and fir recovery will occur at a faster rate. If young fir can mature and produce viable seed before succumbing to the adelgid, a new generation capable of maintaining fir abundances near historical levels may be produced. Because of the large number of unknown factors, however, future trends in the production of viable fir seed cannot be predicted with these data, and the seedling densities required to maintain a viable population are unknown.

5.5.4 Cyclic patterns in Fraser fir populations

Eagar (1984) suggested that Fraser fir populations in the future may undergo a 35 - 60 yr cycle of infestation, mortality, recovery, and reinfestation. The sine wave model was fit to

overstory size class data and understory age class data in the hope of detecting an adelgid-induced periodicity from which inferences about future population patterns could be drawn. The difference in time since major mortality between the most separated mountains, about 20 yr (C. Eagar, personal communication), however, does not span one cycle. The wavelengths observed for the overstory size class distribution are on the order of 6 - 8 cm dbh. Wavelengths on this small order perhaps reflect the inhibitory effect that thick stands of "pole-sized" fir have on the regeneration of seedling fir (Cain 1935; Crandall 1958). Significant negative correlations of sapling sized fir with seedling fir also suggest strong intraspecific competition (unpublished data). It may be expected that in areas where the adelgid has altered the size class distributions of Fraser fir, the cyclic patterns would be obscured. Clingmans Dome, the mountain least impacted by the adelgid, has the smallest dbh wavelength; Mt. LeConte and Mt. Guyot have the largest. The sine wave model for Mt. Sterling also has a small wavelength value, but was the first peak in the Great Smoky Mountains to be infested by the adelgid. If smaller dbh wavelengths are an indication of intraspecific competition, then the wavelength value for Mt. Sterling may be a reflection of the reentrance of large numbers of small fir into the overstory.

The wavelength values for the understory age class distributions are remarkably similar. The consistency of the understory age class wavelengths across mountains suggests that the cause is unconnected to the adelgid. Two types of cyclic or episodic phenomena have been reported for fir species. One is the wave pattern of reproduction reported for fir in the northern Appalachians and Japan (Sprugel 1976; Kohyama and Fujita 1981), but this has not been reported for Fraser fir in the southern Appalachians (White 1984). The other potentially cycle-inducing phenomenon is the 2 - 4 yr interval between production of large Fraser fir seed crops (USDA Forest Service 1974). These large seed crops are observed over the entire range

of Fraser fir, regardless of adelgid damage. Since no other aspect of fir regeneration is independent of the population structure and environmental changes wrought by the adelgid, it is possible that the sine wave model wavelengths of understory fir age are generated by episodic fir seed production. The 6.35 yr - 6.41 yr wavelengths for understory fir represent one half of the smallest mean return interval between large seed crops that can be detected using 5 yr age classes.

5.6 Conclusions

This study has found that Fraser fir are younger on average for a given size on earlier infested mountains. Understory fir are beginning to enter the overstory on the mountains impacted earlier by the adelgid. Cone production also occurs at younger ages on average on earlier infested mountains; however, Fraser fir only produce large seed crops every 2 - 4 years (USDA Forest Service 1974) and only three of the five mountains were sampled during one of these large seed crop years. The size distributions of overstory fir on mountains impacted by the adelgid earlier are characterized by fewer individuals in the larger size classes of fir and relatively higher densities of smaller fir most likely caused by the selective mortality of larger fir. The understory age class distributions, however, remain remarkably unchanged over the mountain chronosequence. The understory age distributions have the unimodal shape characteristic of other episodically regenerating tree species (Leak 1975; Smallidge and Leopold 1994). Perhaps most importantly, this study has found that in stands dominated by dead fir, densities of 0 - 10 yr old seedlings are much lower than those in intact fir stands. Since the study sites do not span an entire cycle of infestation and recovery, the attempt to detect adelgid induced cycles in fir abundances was a failure.

Chapter VI

Summary

With catastrophic levels of fir mortality at the summit of Clingmans Dome, the last peak to become infested (Eagar 1978, 1984), the initial phase of balsam woolly adelgid (*Adelges piceae* Ratz.) infestation and mortality of Fraser fir (*Abies fraseri* (Pursh) Poir.) in the Great Smoky Mountains is virtually complete. Over the five mountains of the study site, nearly 70% of standing overstory (≥ 5 cm dbh) fir basal area was dead. Abundances of overstory fir and other species were not uniformly distributed. Elevation remained the most important variable in influencing large scale patterns of canopy dominance. Just as in pre-adelgid fir and spruce-fir forests, Fraser fir dominated the higher elevation peaks with red spruce (*Picea rubens* Sarg.) and hardwoods, especially *Betula lutea* Michx. f., becoming more important at lower elevations. Time since major adelgid infestation and subsequent mortality also played a role in determining densities of overstory fir. Selective mortality of larger fir stems and recruitment from the understory was most likely responsible for changing the size and age distributions of overstory fir. Over time, size and age distributions on all the mountains will probably change as increasing numbers of young fir enter the overstory and the last of the large survivors die off.

The proportion of standing fir that is dead has been used as an estimate or comparative measure of the damage caused by the adelgid (Dull et al. 1988; Nicholas et al. 1992a), but is subject to temporal variation in the factors that control it: mortality, the fall of dead stems, and recruitment. The interaction of these three factors resulted in a right-skewed bell-shaped response curve when the proportion of dead stems was modeled over time using logistic regression. The initial wave of adelgid-caused mortality causes a sharp increase in the

percentage of standing fir stems that are dead, while recruitment from the understory and treefall are slower processes that produce a more gradual decline over time.

The widespread death of overstory Fraser fir has resulted in a more open canopy that allows greater insolation than in the cooler, darker, and moister pre-adelgid forest (Boner 1979; DeSelm and Boner 1984; Busing et al. 1988). These environmental changes have in turn produced changes in the understory vegetation (DeSelm and Boner 1984; Busing et al. 1988). Densities of small fir seedlings ($\leq$ 0.25 m tall) were significantly lower in pure dead fir stands (PDF) than in pure live fir (PLF) stands. For these size classes, basal area in overstory fir was the most important environmental/overstory variable in a multivariate regression. Age class data showing much lower 0 - 10 yr old seedling densities in PDF plots compared with PLF plots imply that lower densities of small seedlings in highly disturbed plots were only partially due to recruitment to larger size classes. The above observations suggest that as the last remaining pre-adelgid overstory fir die, reductions in viable-seed producing adults will continue the process of dwindling the pool of young seedlings, at least for the short term.

Over the long term, maintenance of the Fraser fir population and range at something similar to historical levels depends on the ability of understory, sapling, and suppressed fir that have escaped stem infestation to reach maturity and produce sufficient amounts of viable seed (Busing et al. 1988; Pauley and Clebsch 1990; Nicholas et al. 1992b). Sapling-sized fir had a slight tendency to increase in abundance with time since canopy death. Also, mean fir age for a given size class was significantly lower in several size classes on the earlier infested peaks. These observations, and possible increases in smaller size class overstory fir in earlier infested sites, indicate that recruitment to the overstory is proceeding rapidly on these peaks. This is in agreement with observations of vigorous recruitment from the earlier impacted Black Mountains by Witter and Ragenovich (1986) and Witter (1988). Overstory fir basal areas in

the permanent plots, established using a stratified sampling regime, tended to increase towards the earlier infested peaks, but not in the more comprehensive temporary plots. This shows that recovery is by no means a uniform phenomenon. Cone production is probably more closely related to size than age of fir since it occurred at younger mean ages on earlier infested peaks. Several considerations, however, preclude a prediction of full recovery, including: 1) the densities of seed-producing fir required to maintain a sizable seedling pool are unknown; 2) the amount of viable seed produced by fir varies by age, size, environmental conditions, and vigor of the tree; 3) adelgid infestation decreases seed production and increases the incidence of seed predation (Fedde 1973 a and b) and may not permit sufficient reproduction before the tree dies; and 4) changing environmental conditions may jeopardize seedling survival (Pauley and Clebsch 1990).

Not only have the growth rates of young Fraser fir increased following the death of canopy fir, but the abundances of bryophytes, herbaceous and subshrub species, shrubs, and understory spruce and hardwoods have also changed. Bryophytes are probably particularly sensitive to the warmer and drier conditions caused by increased insolation in severely impacted, formerly fir-dominated stands. The same was observed by Crandall (1958) in fir blowdowns and by Boner (1979) in adelgid killed fir stands. Herbaceous vegetation coverage, including *Rubus canadensis* L., on the other hand, may respond positively to canopy opening. Although abundance of potentially competitive vegetation, such as *Rubus* (Pauley 1989; Pauley and Clebsch 1990), was combined in this study with small herbs, such as *Oxalis acetosella* L., there was a slight negative correlation between herb/sub-shrub cover and unbranched and branched but $\leq$ 0.25 m tall fir seedlings. Regressions of fir seedlings on shrubs, spruce, and hardwoods < 1.37 m tall did not result in negative regression coefficients, although larger individuals ($\geq$ 1.37 m tall and < 5 cm) were negatively correlated with small fir seedlings.

Densities of large shrubs and spruce and hardwood saplings were not yet increasing, but there were higher densities of spruce seedlings and small shrubs in mixed canopy stands where the fir component was dead. While interactions with other species do not appear to be a serious threat to understory fir at present, a more favorable environment for potential competitors may allow some species to increase to levels where fir establishment opportunities are diminished.

The processes of adelgid infestation and fir death, and therefore understory change in response to fir death, are spatially and temporally patchy (Eagar 1978). In addition, fir seed dispersal may be limited (Sullivan and Peterson 1994) and densities of young, small seedlings were positively associated with a reproductive overstory. Future fir distribution will likely be more clumped. The permanent plots in this study were established using a stratified sampling regime to investigate forest dynamics under four different canopy compositions that are likely to occur together in space and time in future spruce-fir forests. At lower elevations, where mixed canopies are more common, fir may slowly become excluded in places by decreases in adult fir abundances, changing environmental conditions, and increases in woody plant densities. At higher elevations, where fir previously dominated the canopy, the main threats to fir regeneration are probably harsher environmental conditions and invasion by competitive herbaceous/sub-shrub species. Rather than a second wave of balsam woolly adelgid mortality sweeping across the landscape, future cycles of infestation will most likely be driven by varying rates of fir recovery in patches experiencing different biotic and abiotic stressors.

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