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Laura Lusk
East Tennessee State University

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FOREST CHANGE AND BALSAM WOOLLY ADELGID INFESTATION IN HIGH ELEVATION FORESTS OF MT. MITCHELL, NORTH CAROLINA

Thesis submitted in partial fulfillment of Honors

By

Laura Lusk
The Honors College
Discovery Honors Program
East Tennessee State University

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Dr. Foster Levy, Faculty Mentor

Dr. Michael Cody, Faculty Reader

Dr. Tim McDowell, Faculty Reader

FOREST CHANGE IN HIGH ELEVATION FORESTS OF MT. MITCHELL, NORTH CAROLINA: RE-CENSUS AND ANALYSIS OF DATA COLLECTED OVER 40 YEARS

Laura Lusk[1], Matt Mutel[2], Elaine S. Walker[3], Foster Levy[1†]

ABSTRACT.-- The Black Mountain range of western North Carolina supports some of the most extensive, but threatened high elevation forests in the southern Appalachians. Of particular note, the insect pathogen, balsam woolly adelgid (*Adelges piceae* Ratzeburg) has been present on Mt. Mitchell for over fifty years. In anticipation of potential changes in forest composition, vegetation surveys were first conducted in 1966 on nine one-acre plots near the summit of Mt. Mitchell. These plots were re-surveyed in 1978, 1985 and 2002. The purpose of this study was to re-census those plots and use those data to analyze long-term trends in forest composition for fir, spruce-fir, and spruce-fir-hardwood forest types. Since the 1960s and 1970s, all three forest types have experienced a transition away from an understory with a preponderance of Fraser fir (*Abies fraseri* (Pursh) Poir.) seedlings and saplings, to forests with higher densities of canopy and sub-canopy fir. Canopy red spruce (*Picea rubens* Sarg.) has similarly increased in density in the fir and spruce-fir types but declined in the spruce-fir-hardwood forest type. In all types, there has been a sharp decline in hardwood seedlings/saplings since a hardwood seedling explosion in 1978. The current analyses indicate that fir and spruce-fir forests have regenerated since the most severe die-offs and that each forest type will experience future impacts from balsam woolly adelgid but these will occur in a non-synchronous pattern.

INTRODUCTION

The spruce-fir forest of the southern Appalachians is considered a critically endangered ecosystem because of past impacts such as land development, logging, and soil degradation as well as more recent threats that include air pollution, global warming, and the balsam woolly adelgid (*Adelges piceae* Ratzeburg) (bwa) (Hain and Arthur 1985, Noss and others,1995). The two characteristic conifer species of this ecosystem are red spruce (*Picea rubens* Sarg.), which in the southern Appalachians is disjunct from its main range in the northeastern United States, and Fraser fir (*Abies fraseri* (Pursh) Poir.), a regional endemic species with a limited range and patchy distribution (Burns and Honkala 1990).

The most extensive spruce-fir forests in the southern Appalachian region are found at Mt. Rogers and environs in southwest Virginia, Roan Mountain in east Tennessee and western North Carolina, the Black Mountains in western North Carolina, and in Great Smoky Mountains National Park. Of these, the Black Mountains have been subjected to the longest period of infestation by bwa. The first report of bwa in the southern mountains occurred in 1957 from a site in the Black Mountains on Mt. Mitchell (Speers 1958). Fir mortality on Mt. Mitchell reached 95 - 98 percent in spruce-fir and spruce-fir-hardwood stands but only 83 percent in fir stands (Witter and Ragenovich 1986). This severe and long-standing infestation exceeds the generation time of Fraser fir which may be as short as 15 years but longer under shaded and less optimal conditions (Burns and Honkala 1990). Because the Mt. Mitchell infestation has persisted through at least one and possibly three generations of fir, this site provides an opportunity to examine long-term effects of bwa (and other factors) on forest composition. Moreover, Mt. Mitchell has a long vegetation research history that includes data from permanent plots that have been surveyed periodically since 1966, that is, beginning just nine years after the first report of bwa on the mountain.

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[1] Department of Biological Sciences, East Tennessee State University, Johnson City, TN 37614
[2] Mount Mitchell State Park, 2388 State Highway 128, Burnsville, NC 28714
[3] James H. Quillen Veterans Affairs Medical Center, Mountain Home, TN 37684
[†] Corresponding author, 423-439-6926, email: levyf@etsu.edu

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The purpose of this study was to re-survey permanent plots that had been established on Mt. Mitchell and to examine trends in forest composition that have occurred over a 42 year period. We compared data from the current study with those from the initial survey in 1966 (Witter and Ragenovich 1986) and including subsequent surveys in 1978 and 1985 (Witter and Ragenovich 1986, Witter 1989), and 2002 (Sanders). For forests in which fir trees were dominant or co-dominant, we hypothesized the progressive decline in juvenile firs noted in earlier studies would continue as small trees mature and the canopy closes. Similarly, we expected to find a continuing increase in non-juvenile fir as the juveniles move into larger size classes. These hypotheses were contingent upon maintenance of non-epidemic infestations of bwa. However, if a new wave of widespread fir die-off was initiated during the past decade, we expected to observe a dramatic increase in the numbers of dead non-juvenile fir.

STUDY AREAS

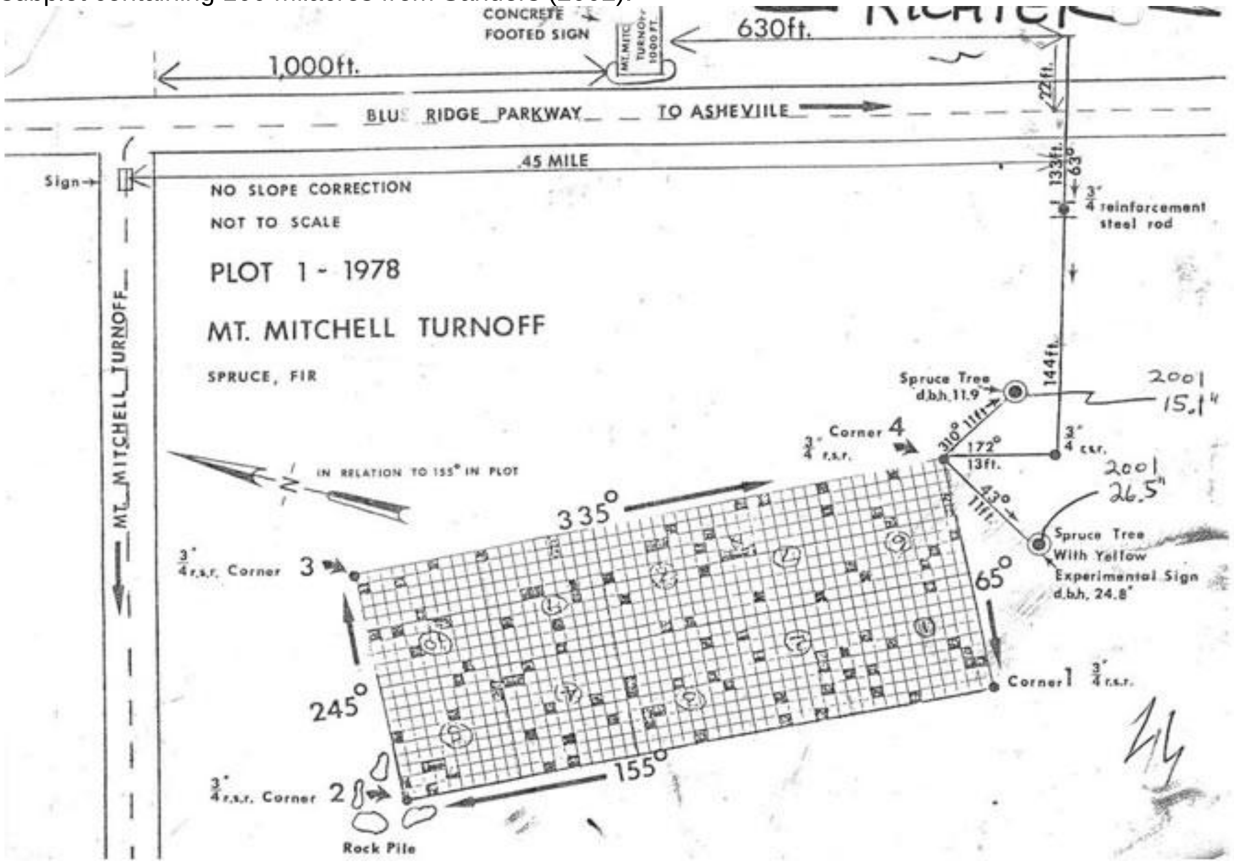
The study was conducted in the Black Mountains of North Carolina. Census plots were located within Mt. Mitchell State Park or on adjoining property of the Blue Ridge Parkway.

METHODS

Field Methods

Less than 10 years after the balsam woolly adelgid was first noted on Mt. Mitchell, a study was initiated to examine long-term changes in the spruce-fir forests. In 1966, Witter established nine one-acre plots, each subdivided into 10 subplots of 66 ft sq. each. Each subplot encompassed a one-tenth acre block (Fig. 1).

Figure 1.--Schematic of Plot 1 with subplots labeled 1-10 (handwritten numbers in circles) with each subplot containing 100 milacres from Sanders (2002).



These nine plots were apportioned with three plots in each high elevation forest community that included a significant component of fir trees; from higher to lower elevations these were fir, spruce-fir, and spruce-fir-hardwood forest types. Plots were located in stands that had been impacted by bwa (Witter and Ragenovich 1986).

To re-survey these historic plots, we located the corner of each plot from permanent markers that had been placed by Sanders (2002). Sample plots within each subplot were randomly selected using a random number generator to calculate distances corresponding to "x" and "y" coordinates that were used to delineate sample plot center points. From these points, censuses of all woody plants were conducted in circular sample areas with 10.7 ft radius.

We collected data consistent with methods used by Witter and Ragenovich (1986) and subsequent studies (Witter 1989; Sanders 2002). For each sample plot within the ninety subplots, each woody plant was identified by species and the following measurements were recorded: height estimated to the nearest foot; diameter at breast height (d.b.h.); canopy position (canopy, sub-canopy, understory [>1 ft], or ground layer [≤1 ft]. Seedlings were defined as ≤6 inches in height. To make comparisons with previous studies, juveniles were defined as ≤8 ft and adults and non-juveniles were >8 ft. Height and d.b.h. of dead fir trees were also tallied.

Mountain ash (*Sorbus americana* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) comprised 80 - 100 percent of the hardwoods in the canopy and 77 - 93 percent of all hardwoods in each forest type. Numbers of hardwoods were combined across species to conform to data analysis in prior studies and because, other than mountain ash and yellow birch, no other hardwood species comprised more than 10 percent of either the canopy hardwoods or the total number of hardwoods.

Statistical Methods

Data Analysis

For comparisons among species and forest types with maximum resolution in trees sizes, data from the 2008 survey were organized by canopy position. For each canopy position, numbers of trees per species were compared across forest types using the heterogeneity chi square test of 3 x 3 contingency tables (3 species; 3 forest types). To facilitate comparisons of tree size distributions among forest types, trees were categorized into eight height classes, measured in feet (0.1-8; 8-19; 30-39; 40-49; 50-59; 60-69; 70-79). Correlation was used to examine the relationship between height and d.b.h., and between numbers of individuals of juvenile, non-juvenile, and dead trees within and among species.

Temporal Trends

To compare data from 2008 to earlier surveys, it was necessary to use the juvenile/non-juvenile data categorization of the earlier studies. To test for temporal trends over a 42-year period, data from the current study were combined with comparable data from the four prior studies. For the current study, the subplot sample area of 359.50 ft sq represented 1/121 acre. Data from the 10 subplots within each plot were summed and multiplied by 12.1 to convert to a per acre scale. Numbers of individuals per acre were regressed over time in a general linear model with separate regressions for juvenile and adult fir, spruce, hardwoods and dead fir trees.

Statistical analyses were conducted using SAS v9.1 (SAS Institute 2002). Stand Visualization Software was used to graphically display forest plot composition across census years (McGaughey 2002).

RESULTS

Current Demographic Patterns

The numbers of trees of each species varied dramatically among the three forest types as evidenced by highly significant differences in species composition among types for each forest canopy position (for all four canopy positions: $\chi^2 = 63.6 - 611.6$; df = 4; P <0.0001; n = 325 - 1643). Fir numerically dominated fir forest types in all forest strata of all fir forest plots (Fig. 2). In the canopy of the fir forest, the numbers of fir were significantly higher than spruce or hardwoods. In spruce-fir and spruce-fir-hardwood plots, the canopy and sub-canopy strata were a more even mix of fir, spruce and hardwoods (primarily mountain ash and yellow birch), but in these forests, hardwoods were less common in lower strata (Fig. 2) and the relative dominance of fir and spruce varied by plot. There were significant plot-to-plot differences in composition for each forest type. For example, in the spruce-fir forest type, spruce was more prevalent in one plot and fir in two plots, while in the spruce-fir-hardwood type, the distribution of fir, spruce and hardwoods was more even on average but also more variable by plot (Table 1). In the understory, juvenile fir again dominated in the fir forest type, but spruce and fir were both common in the spruce-fir and spruce-fir-hardwood types (Fig. 2). For all forest strata, hardwoods were at most, an equal or sub-equal component of the spruce-fir and spruce-fir-hardwood forests, but as in the fir forests, hardwoods were a minor component of lower strata (Fig. 2).

Table 1.--Number of non-juvenile (height >8 ft) fir, dead fir, spruce, and hardwood trees per acre by forest type and plot in 2008

Forest Type		Fir	Dead Fir	Spruce	Hardwood
Fir	Plot				
	5	532	109	230	61
	8	2432	0	12	121
	9	1210	0	157	339
Mean		1392	36	133	169
Spruce-Fir					
	1	508	1742	363	157
	4	387	254	278	266
	6	169	61	641	145
Mean		351	690	424	194
Spruce-Fir-Hardwood					
	2	569	97	157	339
	3	36	24	774	157
	7	508	97	24	375
Mean		375	73	315	290

In the spruce-fir type, non-juvenile dead fir were the most abundant component of one of the three plots and common in the other two plots (Table 1). In contrast, non-juvenile dead fir in the fir forest type were absent in two of three plots and a minor component of the third plot (Table 1) and in that plot, all dead fir trees were relatively small in size (≤19 ft) (Table 3). Juvenile dead fir followed a pattern of occurrence similar to non-juvenile dead fir in that plots with more non-juvenile dead fir tended to also have more juvenile dead fir (Table 2). In one plot of the spruce-fir type, the number of non-juvenile dead fir greatly exceeded the number of live trees of any species (Table 1). Thus, live fir were most prevalent in the fir

Table 2.--Number of juvenile (height ≤8 ft) fir, dead fir, spruce, and hardwood trees per acre by forest type and plot in 2008

Forest Type			Fir	Dead Fir	Spruce	Hardwood
Fir		Plot				
		5	1803	339	2239	0
		8	2795	0	0	24
		9	7608	0	182	0
	Mean		3969	109	811	12
Spruce-Fir						
		1	24	266	218	218
		4	944	85	593	24
		6	593	73	2977	12
	Mean		520	145	1258	85
Spruce-Fir-Hardwood						
		2	545	36	315	182
		3	145	0	2626	12
		7	714	157	835	73
	Mean		472	61	1258	85

Table 3.--Number of fir, spruce, and hardwood species per acre by height class and forest type in 2008

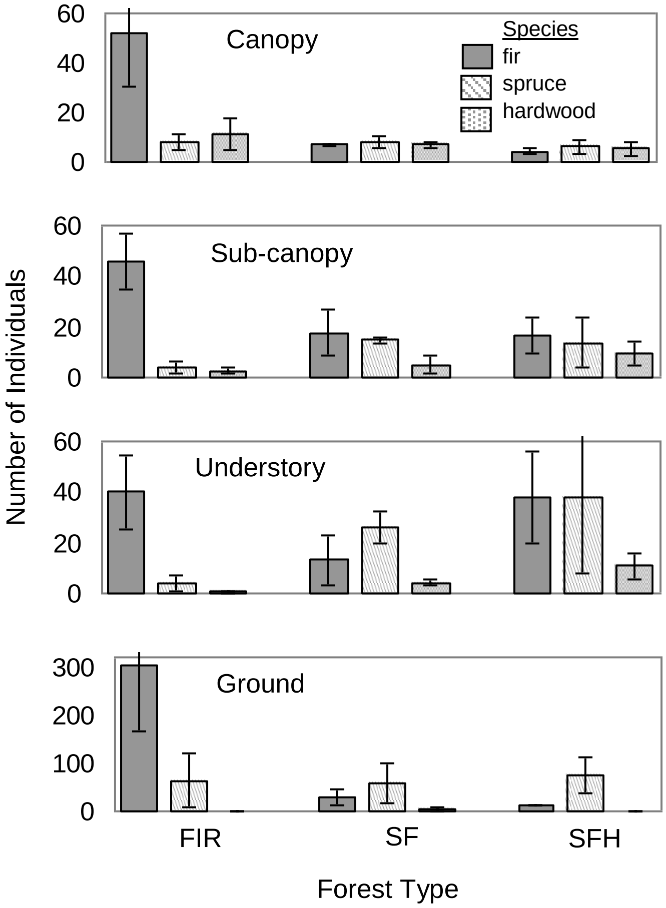
Forest Type	Species	Height Class (ft)							
		0.1-8	8-19	20-29	30-39	40-49	50-59	60-69	70-79
Fir									
	Fir	11906	1089	1186	1162	629	109	0	0
	Spruce	2420	97	85	73	73	61	12	0
	Hardwood	24	36	109	266	97	12	0	0
	Dead Fir	290	109	0	0	0	0	0	0
Spruce-Fir									
	Fir	1561	182	436	230	85	48	73	12
	Spruce	3787	532	363	121	157	73	36	0
	Hardwood	254	109	121	230	109	0	0	0
	Dead Fir	169	121	36	48	12	0	0	12
Spruce-Fir-Hardwood									
	Fir	1404	750	206	36	24	48	12	36
	Spruce	3775	472	194	145	48	73	12	0
	Hardwood	266	182	182	157	194	48	48	48
	Dead Fir	436	871	593	520	133	36	0	12

forest type, dead fir were most prevalent the spruce-fir forest type, and there was a more even distribution of each species in the spruce-fir-hardwood forest type.

There were significant negative correlations between the numbers of fir and spruce in the canopies of fir and spruce-fir forests (r = -0.39, P = 0.04; r = -0.30, P = 0.03; respectively) and in the understory of the spruce-fir-hardwood forest (r = -0.30, P = 0.05). Other associations were not significant for any other canopy stratum.

The size distribution of species also differed among species and forest types. Large (≥50 ft in height) fir trees were more common than large spruce in the spruce-fir forest but large trees of all species were most numerous in the spruce-fir-hardwood forest, in large part because this was the only type that supported large hardwoods and here they outnumbered large spruce and fir (Table 3). Large trees were relatively rare (an order of magnitude less common) in the fir forest. In the spruce-fir type, small (<20 ft) and large spruce were most common but at intermediate heights, there were more fir trees (Table 3). Fir seedlings were most numerous in the fir forest and relatively rare in the spruce-fir-hardwood forest compared to spruce seedlings that were common in all forest types. Hardwood seedlings were rare in all forest types.

Figure 2.--Number of trees in each forest stratum by species and forest type. From 2008 census. Error bars represent standard error of the mean of three plots within each forest type. Area of three plots represents 1/40 acre. Forest Types: FIR; SF=Spruce-Fir; SFH=spruce-fir-hardwood



Temporal Trends in Forest Composition

Forest composition changed dramatically and in a forest type-specific manner over more than 40 years. For all of the significant trends we report, regressions of number of trees on time explained a high proportion of the variation in numbers of individuals (adj. r^2 = 0.77 - 0.98). The numbers of juvenile fir declined significantly in spruce-fir and spruce-fir hardwood forests and showed a marginally significant decline in the fir type (Table 4; Fig. 3). In the fir type, the number of dead non-juvenile fir decreased exponentially as evidenced by a significant fit of a linear regression on the logarithm of number of trees but a non-significant fit to untransformed data (Table 4; Fig. 4).. Non-juvenile spruce experienced a significant increase in the spruce-fir type while in the spruce-fir-hardwood type, non-juvenile fir increased but hardwoods decreased in numbers. Non-juvenile fir peaked and then declined in fir and spruce-fir types (Table 4; Fig. 5).

Table 4.--Stem densities per acre of juvenile (height ≤8 ft) and non-juvenile (height >8 ft) fir, dead fir, spruce, and hardwood species by forest type from 1966-2008. For significant temporal trends detected by regression analysis, P values associated with regressions are shown below columns, where * P <0.05; **P <0.01; ***P <0.001; (*) P = 0.05-0.10

		Fir		Dead Fir		Spruce		Hardwood	
Forest Type	Year	≤8ft	>8ft	≤8ft	>8ft	≤8ft	>8ft	≤8ft	>8ft
Fir	1966	13407	323	237	1523	230	83	43	247
	1978	7409	320	650	450	294	203	1666	294
	1985	2990	1690	720	230	130	220	610	160
	2002	433	2347			77	120	13	317
	2008	3969	1392	109	36	811	133	12	169
		(*)			**				
Spruce-Fir	1966	15540	6	420	273	1754	247	40	73
	1978	7973	423	1403	118	6723	207	2033	193
	1985	5000	2030	950	60	6970	320	1510	410
	2002	330	887			1070	433	150	217
	2008	550	351	145	690	1258	424	85	194
		**					*		
Spruce-Fir-Hardwood	1966	3047	17	67	347	333	233	744	717
	1978	2007	20	3	97	867	213	1730	793
	1985	1680	120	10	20	2280	190	2410	530
	2002	600	340			1463	363	287	297
	2008	472	375	61	73	1258	315	85	290
		***	**						*

Figure 3.--Graphical views of juvenile trees for each census period from 1966 to 2008 in each forest type. To facilitate resolution of trees and tree species, trees are shown at 10 percent of actual density.

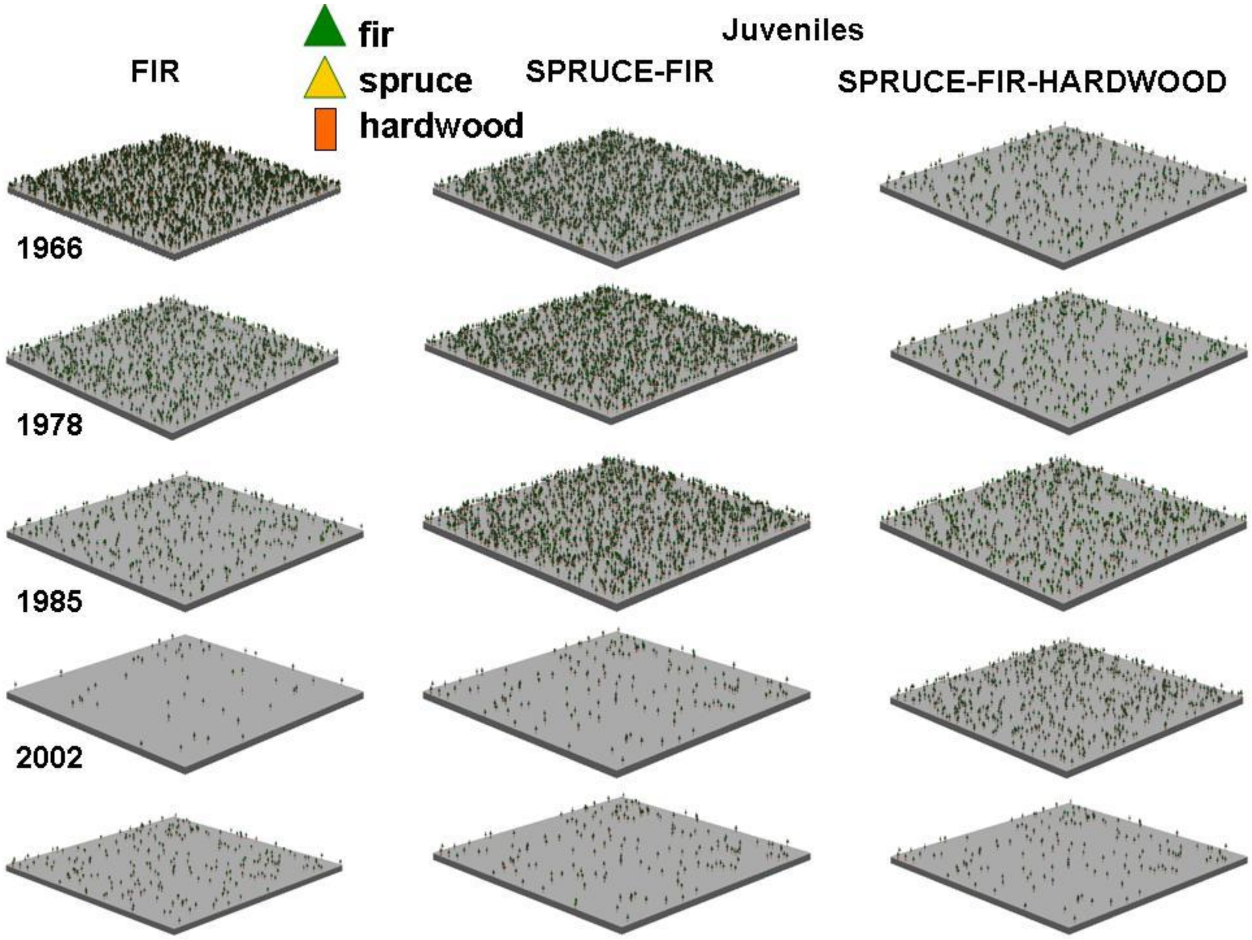


Figure 4.--Graphical views of dead Fraser fir for each census period from 1966 to 2008 in each forest type. To facilitate resolution of trees and tree species, trees are shown at 10 percent of actual density.

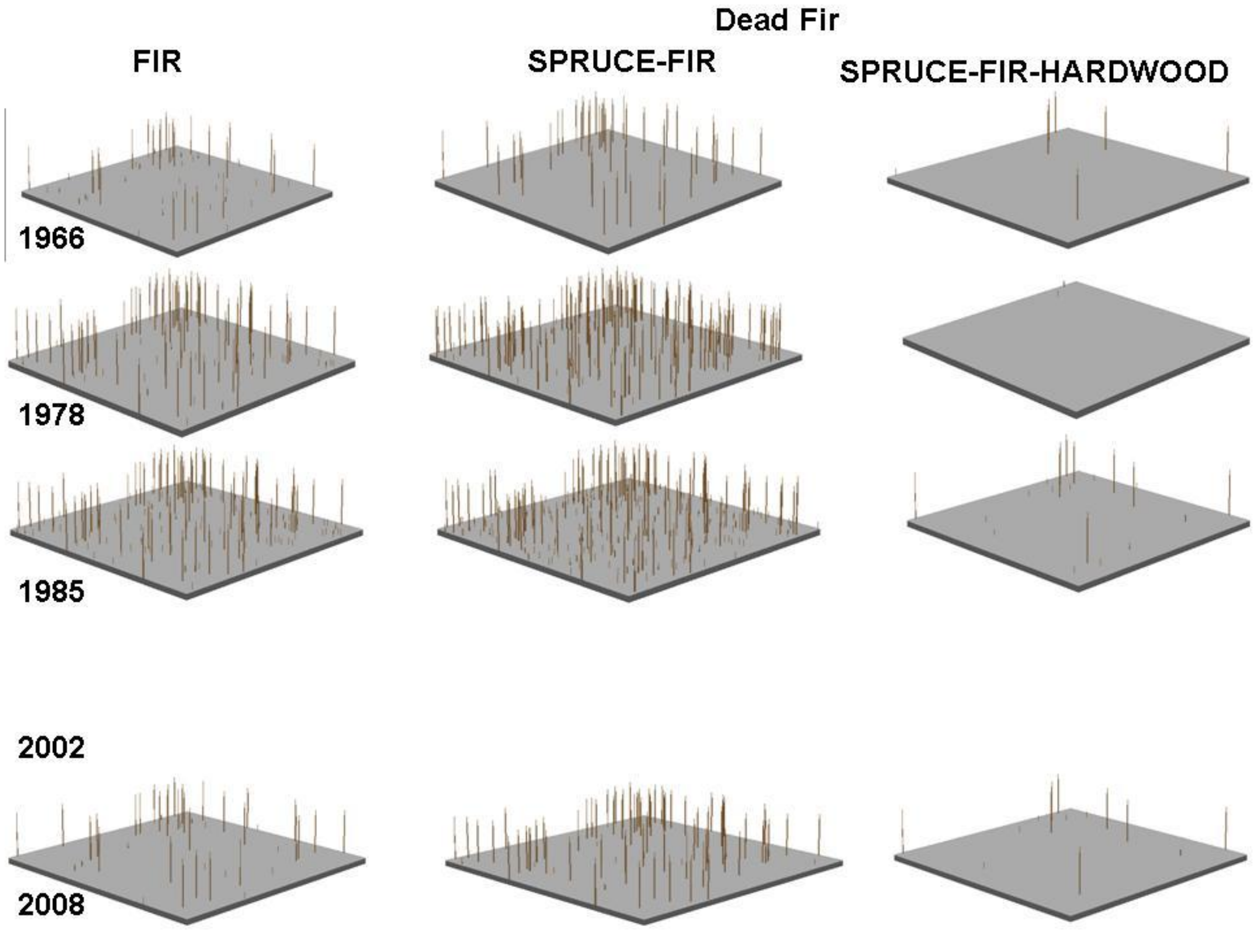
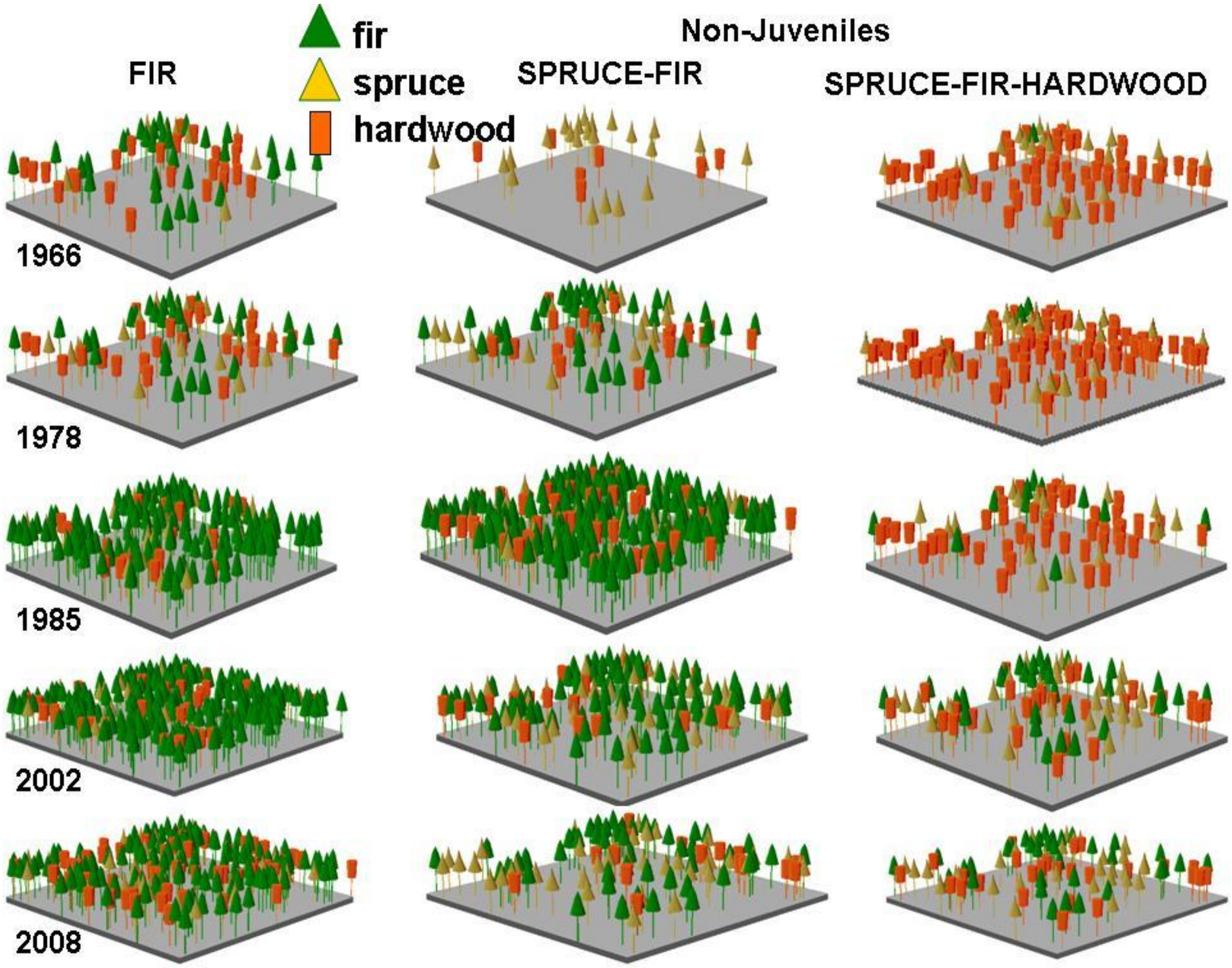


Figure 5.--Graphical views of non-juvenile trees for each census period from 1966 to 2008 in each forest type. To facilitate resolution of trees and tree species, trees are shown at 10 percent of actual density.



DISCUSSION

Current Forest Composition

After the massive fir die-off at Mt. Mitchell in the 1960s and 1970s, fir has returned to dominance in the canopy of the fir forest type and to co-dominance in the spruce-fir and spruce-fir-hardwood types (Fig. 3). In each type there also are abundant numbers of juveniles and seedlings, but their densities decline with canopy closure. The fir forest type is most densely populated with fir trees in all forest strata but with fewer large trees compared to other forest types. Fir does not typically attain its maximum size in the highest elevation pure fir stands such as those near the summits of the Black Mountains (Burns and Honkala 1990). In the fir and spruce-fir forest types, the numbers of canopy fir and spruce were negatively correlated as they were in the understory of the spruce-fir-hardwood type. The negative correlations between fir and spruce may reflect differences in niches or competitive interactions. Bwa maintains a presence in each forest type as noted by direct observation as well as by numerous mature dead fir in each forest type.

Fir populations were recently surveyed on five mountains in Great Smoky Mountain National Park, the only more southern expanse of Fraser fir relative to the Black Mountains (Moore and others 2008).

Comparisons between the Great Smokys and the Black Mountains may be instructive because both have long histories of bwa infestation. In both locations, Mt. Mitchell and the Smoky Mountains, there were plot-to-plot differences in composition. The mountains surveyed in the Smoky Mountains were chosen to encompass a time series, from 1970 - 1990, of major bwa infestation dates that corresponded to elevation and directional infestation trends (Smith and Nicholas 2000, Allen and Kupfer 2001). The fir forest type of Mt. Mitchell was most similar to Mt. LeConte in showing high densities (>400 stems per acre) of saplings (2 - 6 inch d.b.h.) but otherwise the Mt. Mitchell fir forest supported higher numbers of fir saplings than any of the mountains in the Smoky Mountains. In larger size classes, the number of fir trees in the Mt. Mitchell fir forests was more similar to mountains in the Smoky Mountains but in the spruce-fir and spruce-fir-hardwood types of Mt. Mitchell larger fir trees tended to be less common than in the mountains of the Smoky Mountains.

Temporal Trends

Although data collection in the Mt. Mitchell permanent plots began in 1966, by 1985 it was acknowledged that insufficient time had passed for an accurate assessment of long-term consequences of bwa impacts because regenerating fir trees had not reached reproductive maturity (Witter and Ragenovich 1986). However, such an assessment is now feasible because in the thirty to forty years that have elapsed, fir seedlings that established under open canopies have attained mature sizes and realized their reproductive potential.

It was not possible to thoroughly examine patterns of temporal change within forest strata at Mt. Mitchell because prior surveys failed to report canopy positions for individual trees. However, the prior studies delineated size as greater or less than 8 ft which permitted temporal analyses based on differences between juvenile and non-juvenile trees. Declines in juvenile fir, from thousands of individuals per acre to less than 500 by the 2002 survey, were noted in all forest types. Although fir seedlings were abundant in most Mt. Mitchell plots in 1966, by 1978 a pattern of decreasing seedling numbers, particularly in spruce-fir and spruce-fir-hardwood forests was first noted (Witter and Ragnovich1986). With the current data, it is now evident that in each forest type, these declines were accompanied by increases in non-juvenile fir, although in the spruce-fir type, non-juvenile numbers peaked in 1985 and declined since then. The relationship between numbers of juvenile and non-juvenile fir was highlighted by very strong negative correlations between numbers of juvenile and non-juvenile fir in the fir ($r = -0.90$; $P = 0.04$) and spruce-fir-hardwood ($r = -0.93$; $P = 0.02$) forest types. The numbers of juvenile and dead non-juvenile fir showed a positive correlation in the fir forest ($r = 0.96$; $P = 0.04$). In the spruce-fir-hardwood type, juvenile fir tended to thrive under hardwoods as evidenced by a strong positive correlation between the numbers of juvenile fir and non-juvenile hardwood ($r = 0.89$; $P = 0.04$).

The correlations between juvenile, non-juvenile and dead fir trees suggest that juvenile fir are most successful after the loss of fir in the canopy. Further, the declines in juvenile and increases in non-juvenile fir following in the aftermath of widespread die-offs of mature fir is most likely a reflection of natural succession to forests in which fir will again comprise a major component of the sub-canopy and canopy. Reductions in juvenile fir, including seedlings, may reflect natural thinning in densely stocked stands caused by competitive interactions and a transition to less favorable conditions characterized by poor sunlight penetration and a deepening litter layer.

In 1986, Witter and Ragenovich acknowledged that a full determination of the impact of bwa was premature but based on the magnitude of fir regeneration and growth between 1966 and 1986, they suspected that the initial wave of fir regeneration was sufficient to maintain fir as a major constituent of the Mt. Mitchell high elevation forests. While bwa continues to infest these forests, our observations show regenerated fir are producing cones and seedlings in numbers that vary in a plot- and forest type-specific manner. Whereas Witter and Ragenovich reported no trees with d.b.h. greater than four inches, our 2008 survey found fir trees larger than that size in all nine plots. All but one plot harbored fir trees between six and nine inches d.b.h. Moreover, over 16 percent of all fir trees were between 40 and 70 feet in height and trees this size were found in all plots. These data indicate that regenerated fir continues to mature on Mt. Mitchell.

A deterministic model of bwa-fir dynamics showed that after loss of mature fir trees, a likely outcome is cyclic oscillations in bwa and fir populations with plot-specific dynamics that are dependent upon dispersal of each species and the effects of temperature on bwa survival (Dale, et al. 1991). Cycles, rather than extinction, are predicted because bwa tends not to feed on young fir. Significant increases in fir were also noted over a 10-year span from 1993-2003 in the spruce-fir forests of the Noland Divide Watershed of Great Smoky Mountain National Park (Moore and others 2008). Fir biomass increased nearly four-fold across an elevation gradient while spruce and birch biomass showed either no differences or more modest increases but fir also experienced an increase in mortality. On Mt. Mitchell, current forest composition and long-term trends pointed to the re-emergence of forest stands with fir as a canopy dominant. Our observations are consistent with predictions of forest composition following bwa infestation based on models and derived from empirical observations: all indicate that the re-emergence of fir in the forest canopy is not unexpected.

CONCLUSIONS

1. Fir dominated all strata of high elevation pure fir stands and is a co-dominant with spruce and hardwoods (mountain ash; yellow birch) in spruce-fir and spruce-fir-hardwood forests.

2. Numbers of canopy spruce and fir showed an inverse relationship.

3. Significant temporal decreases in juvenile fir were accompanied by increases of non-juvenile fir in all three forest types.

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BALSAM WOOLLY ADELGID INFESTATION ON FRASER FIR IN THREE FOREST TYPES IN THE BLACK MOUNTAINS, NORTH CAROLINA

INTRODUCTION

Infestation of the European balsam woolly adelgid (*Adelges piceae* Ratzeburg) (bwa) on Fraser fir (*Abies fraseri* (Pursh) Poir.) was first detected on Mt. Mitchell in North Carolina in 1957, but bwa was established most likely nearly two decades earlier (Eagar 1984). Mount Mitchell, the tallest peak east of the Mississippi River, provided an ideal location and climate for bwa to reproduce and disseminate to nearby Fraser fir stands (Eagar 1984). Dramatic fir mortality rates that followed shortly after the initial bwa infestation caused great concern for the future survival of Fraser fir, an economically important species whose range is limited to the higher elevations of North Carolina, Tennessee, and Virginia (Witter and Ragenovich 1986).

In North America, there are three main stages of the bwa life cycle: the egg, three nymphal instars (of which the first is termed the “crawler”), and the adult wingless, parthenogenic female (Hollingsworth and Hain 1991). The sexual stage does not appear to occur in North America, presumably because of the absence of an acceptable secondary spruce host (Eagar 1984). The “crawler,” distinguished by its mobility compared to the remainder of the adelgid’s stationary life, emerges from its egg to locate an appropriate feeding sight where it will remain until its death (Eagar 1984). The host tree’s bark experiences dramatic chemical and structural changes from bwa attack. Fraser fir initially reacts by increasing the number and size of bark parenchyma cells surrounding the adelgid’s insertion of its stylet (Hollingsworth and Hain 1991). Cork cells then encompass the feeding zone, parenchyma cells disintegrate, and resin penetrates the zone (Hollingsworth and Hain 1991). Interference with the translocation of water in the effected xylem tissue results from bwa feeding on the host’s bark (Hollingsworth and Hain 1991).

Dispersal of bwa relies on wind, a passive mechanism that consequently influences the pattern of infestation whereby taller trees in the canopy tend to support higher infestations of bwa. Infestations then spread more easily to other hosts (Eagar 1984). In addition to wind as the primary agent of bwa dispersal, fir seedling and sapling infestation results mainly from gravity, but humans, Christmas tree commerce, and animals also aid in bwa dissemination (Eagar 1984).

Currently, no cost or time efficient methods of bwa control are known since the bwa lacks destructive parasites or diseases. Moreover, the introduction of foreign and native insect predators has shown little impact on bwa mortality (Eagar 1984). The one biotic factor that does hinder bwa population growth is the host trees’ carrying capacity. When the fir population carrying capacity is exceeded, the adelgid population decreases drastically, and the host soon dies. Insecticides show some signs of killing bwa, but the logistic and economic difficulties of physically applying the chemicals to individual trees is cumbersome and time-consuming, with a need for multiple applications annually. Moreover pesticide loads are controlled by regulatory agencies such as the Environmental Protection Agency (Eagar 1984).

Aside from the adelgid’s impact on Fraser fir in the Southern Appalachians, additional environmental factors and human disturbance are hypothesized to account for fir die-off, but the extent to which each factor affects the spruce-fir forests is not clear. Fraser fir is considered especially fragile and susceptible to atmospheric deposition of pollutants which stress trees and predispose the fir ecosystem to adelgid attack (Hain and Arthur 1985). More directly, atmospheric deposition weakens firs’ natural resistance, and when bwa attacks, they are less capable of warding off the pests. Thus, atmospheric deposition—of which gaseous pollutants such as ozone, sulfur dioxide, nitrogen oxides, and airborne metallic particles are the most notable—and bwa attack are interconnected factors that in combination may increase fir mortality (Hain and Arthur 1985). Mount Mitchell’s close proximity and downwind location relative to larger, more industrialized cities, including Asheville and Knoxville, may exacerbate the deposition problem.

Historically, the Appalachian spruce-fir forests experienced their first anthropic attack centuries ago when man-made disturbances threatened their future existence. Agricultural clearings and minor logging reduced the spruce-fir population from a half-million ha in the early 1600s to approximately 300,000 ha by 1845. Logging, grazing, and wildfires further reduced these forests to under 24,000 ha by the early 1940s (Witter 1989). As a result of these disturbances, the vital soil and soil-building components of the rich soil of the spruce-fir forests—moist soil, organic matter, and nutrients—had been diminished (Witter 1989).

Climate and other natural physical stresses are also hypothesized to contribute to fir mortality. Temperature may indirectly affect fir survivorship since bwa vigor is dependent on temperature changes. The rate of bwa development is retarded by lower temperatures, and bwa mortality is high in extreme cold (Dale et al. 1991). In the western United States higher temperatures increase the number of adelgids that will survive the first instar overwintering stage, consequently improving their winter survival (Mitchell and Buffam 2001). The spruce-fir forests endemic to higher elevations of Central and Southern Appalachians are already threatened by bwa, and may be especially at risk of mortality due to climate changes (Potter et al. 2009). It is likely that new climatic conditions will cause forest tree species to either adapt to the changes or move to more suitable environments.

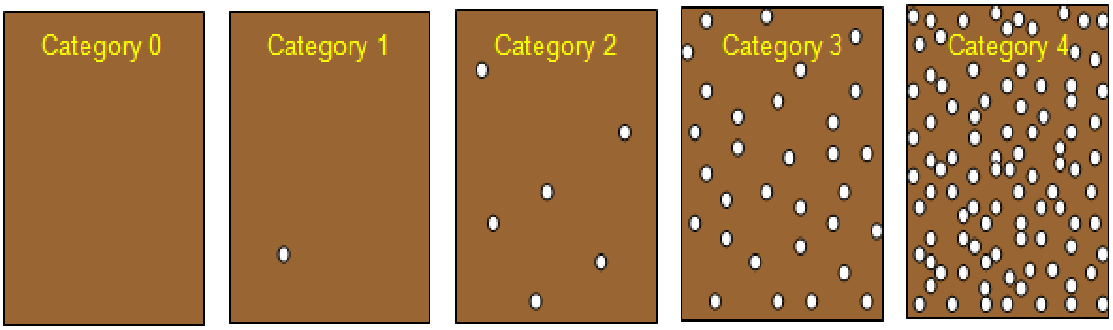
The purpose of this study was to re-survey permanent plots that had been established in 1966 (Witter and Ragenovich 1986) on Mt. Mitchell and to examine individual trees in addition to landscape patterns over time (refer to Lusk et al. 2009). In this study, we expected to observe clusters of high areas of bwa infestation on Fraser fir since the adelgid is essentially immobile. Also, since bwa attacks only Fraser fir, we hypothesized that the pure fir stands would have a higher level of infestation compared to the other two forest types (spruce-fir and spruce-fir-hardwood). With fir predominating in pure fir stands, it was likely that bwa would be most prevalent in these stands, and the close proximity of suitable hosts would suggest that the adelgid would be more likely to infest neighboring firs.

METHODS

Field Methods

For each of the nine one-acre plots established by Witter in 1966 (refer to Lusk et al. 2009 for location and details), the density of bwa was assessed using categorical measures of infestation for all live Fraser firs > 4 feet tallied within the sample areas. Prevalence of bwa on the trunks of Fraser firs was assayed as five different frequency classes where; 0=none, 1=few/rare (< 5% coverage of trunk), 2=occasional (5%-20% coverage), 3=dense (21%-50% coverage), and 4=nearly complete trunk coverage (> 50%) (Fig. 1). The assay area was a region of the trunk from approximately 3.3 m - 4.0 ft above ground).

Figure 1. —Schematic of bwa infestation density categories. The five rectangles represent fir tree trunks, and the circles within the rectangles denote woolly coverage of bwa.



Four field researchers were involved in assessing infestation density. Before infestation data were collected, the four researchers conducted a training session in the field to ensure scoring was consistent across all researchers. Thus, random firs were chosen as sample trees, and each researcher individually categorized the tree by visually estimating the infestation density using the 0-4 scale. Our categorical designations were invariably the same, or differed occasionally by +/- one class. Subsequently one person recorded the data while the others scored bwa infestation.

Statistical Methods

Data Analysis

Three forest types—fir, spruce-fir, and spruce-fir-hardwood—were used for the data analysis performed using SAS 9.1.To compare the bwa density on Fraser fir to height, a chi square test for heterogeneity of 3 x 5 contingency table (3 forest types; 5 different frequency classes for bwa infestation) was performed. Additionally, for each forest type, the percent of Fraser fir either not infested (0) or infested (1) was compared using the heterogeneity chi square test of 3 x 2 contingency table (3 forest types; 2 infestation categories). These tests determined whether significant differences in bwa density were present among forest types.

To compare the relationship between bwa density and height, regression analysis was performed for each forest type and for the trees from of all forest types to generate a regression equation that could be used to predict bwa density depending on the fir height.

Similarly, regression of bwa density was performed, this time on a different parameter—d.b.h. To better establish the relationship between the two variables (height and d.b.h.) the correlation procedure was performed to indicate the strength and the direction of the relationship.

RESULTS

Density of bwa for Each Forest Type

The intensity of bwa infestation differed significantly among forest types. These differences were highlighted in an analysis of frequencies on a contingency table (Table 1) consisting of 3 forest types (fir, spruce-fir, and spruce-fir-hardwood) by 5 infestation densities ($\chi^2 = 38.2$, df = 8, $P < 0.0001$). Surprisingly, bwa was least prevalent in the denser infestation categories (2-4) in the fir type but had the highest representation of the denser categories in the spruce-fir-hardwood type. For example, in the fir forest type 40.2 percent of the Fraser fir were uninfested while only 22.7 and 37.2 percent were uninfested in the spruce-fir and spruce-fir-hardwood types, respectively. Similarly, there were evident differences among forest types when comparing lower and higher infestation densities (categories 0-1 vs. 2 - 4) where the fir type had the lowest prevalence of high density infestations (fir = 12.2 percent; spruce-fir = 25.0 percent; spruce-fir-hardwood = 32.1 percent). Furthermore, a simple comparison of uninfested to infested trees (categories 0 vs. 1-4) fir trees also indicated significantly lower infestation density in the fir forest type where there were 59.8 percent infested in the fir type compared to 77.3 percent the spruce-fir type (Table 2) ($\chi^2 = 9.33$, df = 2, $P < 0.01$). Therefore, regardless of how the categorical data are grouped, the results are consistent in showing that the fir forest type was less densely infested by bwa.

Table 1.--Number and (percent) of Fraser fir for each bwa infestation class by forest type

Forest Type	Classes of bwa density				
	0	1	2	3	4
Fir	148 (40.2)	175 (47.5)	35 (9.51)	10 (2.72)	0 (0.00)
Spruce-Fir	20 (22.7)	46 (52.3)	16 (18.2)	4 (4.55)	2 (2.27)
Spruce-Fir-Hardwood	29 (37.2)	24 (30.8)	20 (25.6)	5 (6.41)	0 (0.00)
Total	197 (36.9)	245 (35.9)	71 (13.3)	19 (3.56)	2 (0.37)

Table 2.--Number (percent) of either uninfested (0) to infested (1) Fraser fir by forest type.

Forest Type	Classes of bwa density	
	0	1
Fir	148 (40.2)	220 (59.8)
Spruce-Fir	20 (22.7)	68 (77.3)
Spruce-Fir-Hardwood	29 (37.2)	49 (62.8)
Total	196 (36.9)	337 (63.1)

For the regression data of bwa density on height (Table 3), the analysis (F = 13.03, df = 533, R^2 = 0.024, P = 0.0003) for all three forest types as a whole verified that the results are significant; therefore, height is an accurate predictor of bwa infestation. High variability of the bwa infestation for each tree height indicates why only 2.4 percent of the variation is explained by the regression. When performing regressions for each of the three forest types individually, only fir forests showed significant results (F= 27.12, df = 367, R^2 = 0.069, P <0.0001). Thus, in the fir forests, height is an explanatory factor for the occurrence of bwa, but in the spruce-fir and spruce-fir-hardwood forest types, the bwa density cannot adequately be predicted by the height of the fir tree.

Table 3.--Regression analysis of bwa density on height by forest type.

Type	d.f.	F	Pr>F	R-Square	Equation
All	533	13.09	0.0003	0.024	y=0.0097x + 0.60
Fir	367	27.12	<0.0001	0.069	y=0.016x + 0.31
Spruce-Fir	87	1.05	0.3093	0.012	y=0.0070x + 0.91
Spruce-Fir-Hardwood	77	0.19	0.6635	0.0025	y=-0.0029x + 1.07

To test for a relationship between d.b.h. and bwa, bwa was regressed on d.b.h. using the General Linear Model in linear regression. That regression showed that for combined data for all three forest types the relationship was positive and significant (F= 18.4, df = 535, R^2 = 0.0333, P <0.0001) indicating that trees with larger d.b.h. tended to have higher levels of bwa infestation. The size/bwa relationship was significant for fir forests as well (F= 33.98, df = 367, R^2 = 0.085, P <0.0001) but was not significant for other forest types (Table 4). Therefore, for all three forest types as a whole along with fir forest types exclusively, the d.b.h. is an important predictor of bwa density. The similarity of the relationships between density and height or d.b.h. is not surprising because height and d.b.h. are correlated for all three forest types together (R = 0.77; P < 0.0001). This strong correlation between height and d.b.h.—when height is > 8 ft and d.b.h. > 0—also holds true for each individual forest type, and it is strongest for the spruce-fir-hardwood forests (Table 5).

Table 4.--Regression analysis of bwa density on d.b.h. by forest type.

Type	d.f.	F	Pr>F	R-Square	Equation
All	535	18.4	<0.0001	0.0333	y=0.047x + 0.60
Fir	367	34	<0.0001	0.085	y=0.016x + 0.31
Spruce-Fir	87	0.01	0.9305	0.0001	y=0.0070x + 0.91
Spruce-Fir-Hardwood	79	1.76	0.1879	0.00221	y=-0.0029x + 1.07

Table 5.--Correlation between height and d.b.h. by forest type.

Type	R	P
All	0.77	<0.0001
Fir	0.72	<0.0001
Spruce-Fir	0.77	<0.0001
Spruce-Fir-Hardwood	0.8	<0.0001

DISCUSSION

The density of bwa infestation differed among the forest types. Fir trees in the fir forest type had lower infestation scores compared to fir trees in spruce-fir and spruce-fir-hardwoods forest types. This result appeared counterintuitive because the fir forest type had the highest density of the bwa host, and with high density of host trees, bwa dissemination is expected to be maximized. However, one explanation for this unexpected result lies in the significant variation of bwa density per plot. This plot specificity slightly skewed the statistical findings for bwa density depending on forest type. For instance, while fir in the fir forest type were largely uninfested in Plot 8 and Plot 9 (78.1 percent and 86.9 percent, respectively), this high percentage of uninfested trees contrasted with Plot 5 where only 36.2 percent were uninfested. While the mean infestation density may have been lowest in fir forests, the variation among plots was also high.

Another potential explanation for lower infestation density in the fir forest type may be related to the observation that there were fewer large fir trees in fir forests compared to the other types. Fir rarely reaches its maximum height in these high elevation plots (Lusk et al. 2009) which may be caused by sub-optimal growing conditions or it may be that this forest is still regenerating after prior disturbances such as logging in the first half of the twentieth century and fir-die off in the second half of the twentieth century. Since our results verified that height and d.b.h. are accurate predictors of bwa it is likely that we can reason that the younger, smaller trees in the fir forest type are not as susceptible to bwa attack. Fraser fir trees in pure fir stands do not have resistance against bwa infestation, but more likely, bwa is less prevalent in these forest types because of bwa feeding preferences for trees larger than seedlings and saplings. Thus, we observed bwa presence in all plots surveyed, but the infestation levels among these plots varied significantly.

Large fir trees can sustain dense populations of bwa for several years before dying, and bwa often preferentially attacks larger trees because their crowns are exposed to air currents which carry the adelgid (Eagar 1984). Suppressed trees, however, experience a higher mortality rate despite their lower infestation levels. One probable reason that larger trees experience higher levels of bwa is the morphological changes in bark with age. Thus, young stems are more resistant to bwa because their tight, smooth, grey bark behaves as a protective barrier against bwa attack (Eagar 1984). However, suppressed trees may be more susceptible to non-bwa mortality that leads to stand thinning.

A study assessing the effects of bwa infestation in stands of Pacific silver fir (*A. amabilis* (Dougl.) Lindl.), grand fir (*A. grandis* (Dougl.) Lindl.) and subalpine fir (*A. lasiocarpa* (Hook.) Nutt) was performed in the Cascade Range of Oregon and Washington (Mitchell and Buffam 2001). The methods of the Cascade study were similar to ours. From the late 1950s to early 1960s, seven plots were established and surveyed annually until 1980 after which they were re-surveyed approximately every 5 to 10 years.

Mitchell and Buffam assessed the condition of fir trees during the same seasonal period as in our study (September and October), a time when the woolly wax was evident. They scored their trees numerically using a similar categorical scale: zero; light, <1/ft^2; medium, <1-10ft^2; and heavy, >10/ft^2 (Mitchell and Buffam 2001). Their findings were similar to ours in showing that host trees at the lowest elevations (those in the spruce-fir and spruce-fir-hardwood forest types) were more densely infested by bwa. However, Mitchell and Buffam found that pole-sized grand fir had the densest infestations, and bwa's damaging effects were most noticeable on the small trees (Mitchell and Buffam 2001). In our study, we observed the opposite trend, with larger Fraser fir being more susceptible to denser bwa infestation.

Since our study on the summit of Mt. Mitchell was the first to look specifically at the infestation levels of the bwa on individual trees, we cannot accurately predict the trajectory of bwa infestations and impacts. However, from the long-term trends of forest composition that suggest a cyclic pattern of fir mortality and regeneration, we can predict that bwa will remain a problem in the future (Lusk et al. 2009). While there is evidence that bwa establishes permanent residency after initially colonizing fir stands, it is highly unlikely that bwa will completely eliminate Fraser fir (Mitchell and Buffam 2001). In fact, a recent study conducted on plots located within the spruce-fir forests of the Black Mountains of North Carolina demonstrates rapid regeneration of dense, healthy fir at elevation of 1980 m, especially in areas where fir mortality had been observed (Bowers and Bruck 2009). However, this recovery is not likely to withstand future bwa attacks since fir stems will eventually reach the size at which they become susceptible to infestation (Bowers and Bruck 2009). Thus, cyclic patterns of fir death and renewal will likely continue to occur as infested, dying larger trees are replaced by healthy saplings until they reach the adelgid-susceptible age and size classes. An additional study that analyzed aerial photographs from more than three decades demonstrates how the amount of coverage in different forest types has changed over time (McManamay et al. 2009). McManamay reports a decrease in bwa infestation in fir-dominated forests by 80 percent but an increase in spruce-fir co-dominated forests by 209 percent (McManamay et al. 2009). In conclusion, we observed more severe bwa infestation in non-fir forest types, and larger fir trees were more susceptible to bwa attack.

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