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

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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 more than 50 years. In anticipation of potential changes in forest composition, vegetation surveys were first conducted in 1966 on nine 1-acre plots near the summit of Mt. Mitchell. These plots were resurveyed in 1978, 1985, and 2002. The purpose of this study was to survey those plots again 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, hardwood seedlings/saplings have declined sharply 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 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, climate change, and the balsam woolly adelgid (*Adelges piceae* Ratzeburg) (BWA) (Hain and Arthur 1985, Noss et al.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 regionally 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, at Roan Mountain in east Tennessee and western North Carolina, in the Black Mountains in western North Carolina, and in Great Smoky Mountains National Park (Tennessee and North Carolina). 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, in 1957, was on Mt. Mitchell in the Black Mountains (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

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includes data from permanent plots that have been surveyed periodically since 1966–that is, beginning just 9 years after the first report of BWA on the mountain.

The purpose of this study was to resurvey permanent plots that had been established on Mt. Mitchell and to examine trends in forest composition that have occurred over 42 years. We compared data from the current study with those from the initial survey in 1966 (Witter and Ragenovich 1986) and subsequent surveys in 1978 and 1985 (Witter and Ragenovich 1986, Witter 1989) and 2002 (Sanders 2002). 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 nonjuvenile fir as the juveniles move into larger size classes. These hypotheses were contingent upon maintenance of non-epidemic infestations of BWA. If a new wave of widespread fir die-off was initiated during the past decade, however, we expected to observe a dramatic increase in the numbers of dead nonjuvenile 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, nine 1-acre plots were established; each was subdivided into 10 square subplots, 66 ft on a side, or one-tenth of an acre (Fig. 1). The 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 communities 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 resurvey these historic plots, we located the corner of each plot from permanent markers that had been placed by

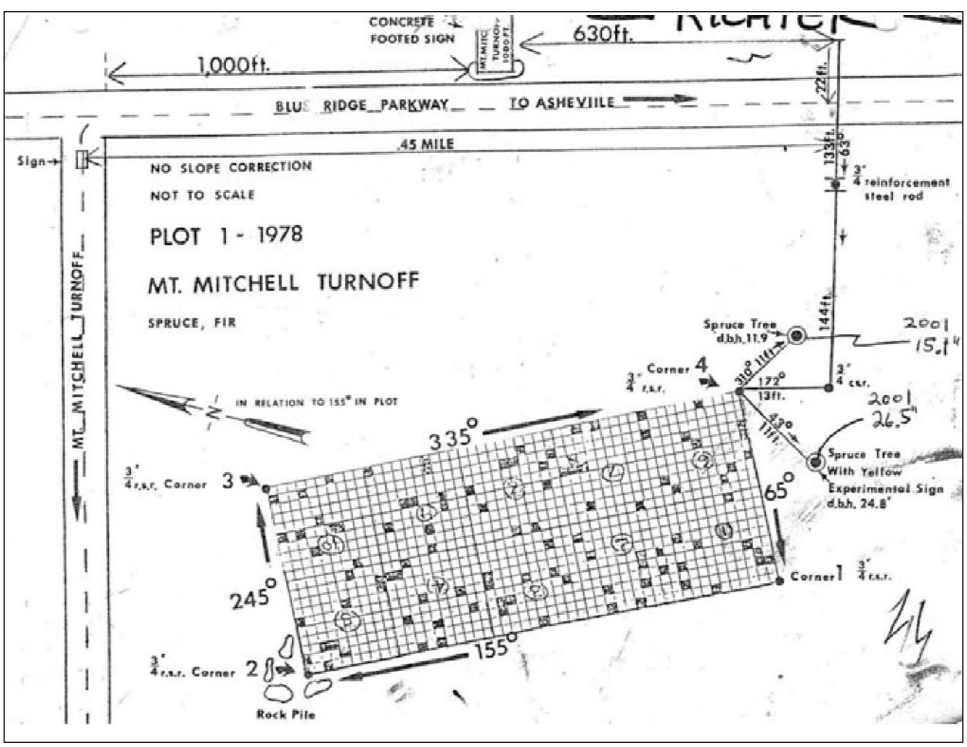

Figure 1.—Schematic of Plot 1 with subplots labeled 1-10 (handwritten numbers in circles). Each subplot contains 100 milacres. From Sanders (2002).

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 a 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 90 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 nonjuveniles 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.) constituted 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 hardwood species made up 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 tree 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 (three species, three 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; 20-29; 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, nonjuvenile, and dead trees within and among species.

Temporal Trends

To compare data from 2008 to earlier surveys, it was necessary to use the juvenile/nonjuvenile 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 sq. ft. 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 version 9.1 (SAS Institute, Cary, NC). 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 shown by highly significant differences in species composition among types for each forest canopy position (for all four canopy positions: χ^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 number of fir was significantly higher than that of 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). In these forests, however, hardwoods were less common in lower strata (Fig. 2), and the relative dominance of fir and spruce varied by plot. Significant plot-to-plot differences in composition occurred 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

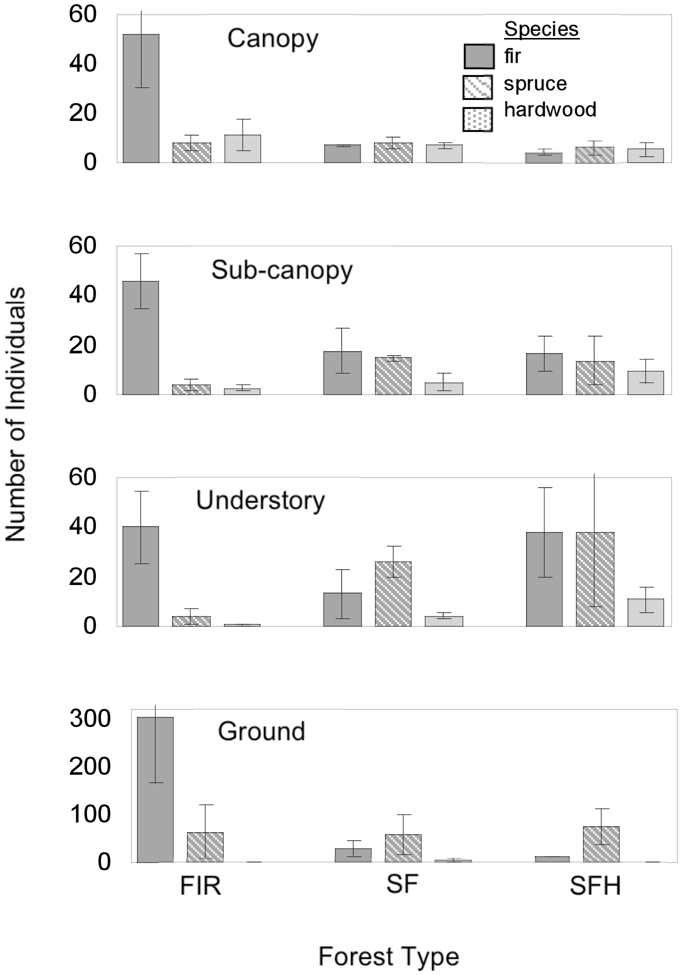

Figure 2.—Number of trees in each forest stratum by species and forest type. From 2008 census. Error bars represent standard error of the mean of three plots within each forest type. Area of three plots represents 1/40 acre. Forest Types: FIR; SF=Spruce-Fir; SFH=spruce-fir-hardwood.

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 both spruce and fir were 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).

In the spruce-fir type, nonjuvenile dead fir were the most abundant component of one of the three plots and common in the other two plots (Table 1). In contrast, nonjuvenile dead fir in the fir forest type were absent in two of three plots and a minor component of the third plot (Table 1); 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 nonjuvenile dead fir in that plots with more nonjuvenile dead fir tended also to have more juvenile dead fir (Table 2). In one plot of the spruce-fir type, the number of nonjuvenile dead fir greatly exceeded the number of live trees of any species (Table 1). Thus, live fir were most prevalent in the fir forest type, dead fir were most prevalent in the spruce-fir forest type, and there was a more even distribution of each species in the spruce-fir-hardwood forest type.

Significant negative correlations occurred 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. Large trees of all species, however, were most numerous in the spruce-fir-hardwood forest, in large part because this was the only type that supported large hardwoods. There they outnumbered large spruce and fir (Table 3). Large trees were 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, which were common in all forest types. Hardwood seedlings were rare in all forest types.

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

Table 1.—Number of nonjuvenile (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	2,432	0	12	121
		9	1,210	0	157	339
	Mean		1,392	36	133	169
Spruce-fir						
		1	508	1,742	363	157
		4	387	254	278	266
		6	169	61	641	145
	Mean		351	690	424	194
Spruce-fir-hardwood						
		569	97	157	339	569
		36	24	774	157	36
		508	97	24	375	508
	Mean	375	73	315	290	375

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	1,803	339	2,239	0
		8	2,795	0	0	24
		9	7,608	0	182	0
	Mean		3,969	109	811	12
Spruce-fir						
		1	24	266	218	218
		4	944	85	593	24
		6	593	73	2,977	12
	Mean		520	145	1,258	85
Spruce-fir-hardwood						
		2	545	36	315	182
		3	145	0	2,626	12
		7	714	157	835	73
	Mean		472	61	1,258	85

nonjuvenile fir decreased exponentially as demonstrated by a significant fit of a linear regression on the logarithm of number of trees but a non-significant fit to untransformed data. Nonjuvenile spruce experienced a significant increase in the spruce-fir type while in the spruce-fir-hardwood type, nonjuvenile fir increased but hardwoods decreased in numbers. Nonjuvenile fir peaked and then declined in fir and spruce-fir types (Table 4; Fig. 3).

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, juveniles and seedlings are present in abundance but their densities

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	11,906	1,089	1,186	1,162	629	109	0	0
	Spruce	2,420	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	1,561	182	436	230	85	48	73	12
	Spruce	3,787	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	1,404	750	206	36	24	48	12	36
	Spruce	3,775	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

Table 4.—Stem densities per acre of juvenile (height ≤8 ft) and nonjuvenile (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	13,407	323	237	1,523	230	83	43	247
	1978	7,409	320	650	450	294	203	1,666	294
	1985	2,990	1,690	720	230	130	220	610	160
	2002	433	2,347			77	120	13	317
	2008	3,969	1,392	109	36	811	133	12	169
		(*)			**				
Spruce-Fir	1966	15,540	6	420	273	1,754	247	40	73
	1978	7,973	423	1,403	118	6,723	207	2,033	193
	1985	5,000	2,030	950	60	6,970	320	1,510	410
	2002	330	887			1,070	433	150	217
	2008	550	351	145	690	1,258	424	85	194
		**					*		
Spruce-Fir-Hardwood	1966	3,047	17	67	347	333	233	744	717
	1978	2,007	20	3	97	867	213	1,730	793
	1985	1,680	120	10	20	2,280	190	2,410	530
	2002	600	340			1,463	363	287	297
	2008	472	375	61	73	1,258	315	85	290
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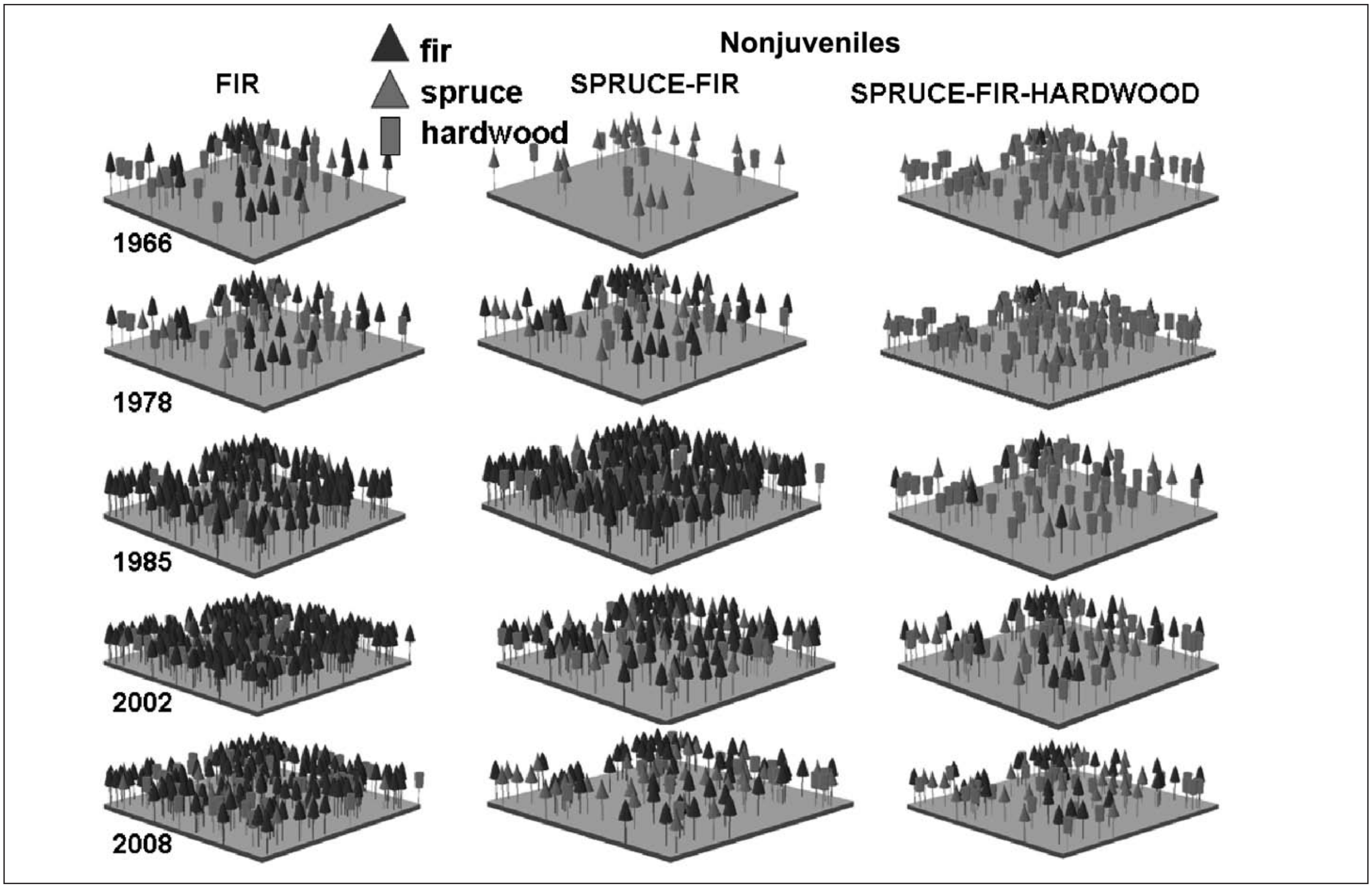

Figure 3.—Graphical views of nonjuvenile trees for each census period from 1966 to 2008 in each forest type. To facilitate resolution of trees and tree species, trees are shown at 10 percent of actual density.

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 Mountains National Park, the only more southern expanse of Fraser fir relative to the Black Mountains (Moore et al. 2008). Comparisons between the Great Smokys and the Black Mountains may be instructive because they both have long histories of BWA infestation. Both the Smoky Mountains and Mt. Mitchell showed plot-to-plot differences in composition. The mountains surveyed in the Smokies 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- to 6-inch d.b.h.), but otherwise the Mt. Mitchell fir forest supported more 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. In the spruce-fir and spruce-fir-hardwood types of Mt. Mitchell, however, larger fir trees tended to be less common than in the mountains of the Smokies.

Temporal Trends

Although data collection in the Mt. Mitchell permanent plots began in 1966, even 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). Such an assessment is now feasible, however; in the ensuing 30-40 years, 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 did not report canopy positions for individual trees. Nonetheless, the prior studies delineated size as greater or less than 8 ft, which permitted temporal analyses based on differences between juvenile and nonjuvenile 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 nonjuvenile fir, although in the spruce-fir type, nonjuvenile numbers peaked in 1985 and then declined. The relationship between numbers of juvenile and nonjuvenile fir was highlighted by very strong negative correlations between numbers of juvenile and nonjuvenile 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 nonjuvenile 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 shown by a strong positive correlation between the numbers of juvenile fir and nonjuvenile hardwood ($r = 0.89$; $P = 0.04$).

The correlations between juvenile and nonjuvenile or 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 nonjuvenile fir in the aftermath of widespread die-offs of mature fir probably reflect natural succession to forests in which fir will again be 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 4 in., our 2008 survey found fir trees larger than that size in all nine plots. All but one plot harbored fir trees between 6 and 9 in. d.b.h. Moreover, greater than 16 percent of all fir trees were between 40 and 70 ft 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 between 1993 and 2003 in the spruce-fir forests of the Noland Divide Watershed of Great Smoky Mountains National Park (Moore et al. 2008). Fir biomass increased nearly fourfold across an elevation gradient while spruce and birch biomass showed either no differences or more modest increases. Fir, however, 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 nonjuvenile fir in all three forest types.

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