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Examination of forest recovery scenarios in a southern Appalachian *Picea*–*Abies* forest

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Summary

This study contrasts various forest recovery scenarios in a *Picea rubens* Sarg. *Abies fraseri* (Pursh.) Poir. forest 20 years after the onset of *Adelges picea* Ratz. and tests them against a 10-year data set from an intensive catchment study in the Great Smoky Mountains National Park. Standing live biomass, increment, ingrowth, mortality and net change in live biomass are analysed by species and elevation based on inventory data gathered in 1993, 1998 and 2003 at a network of 50 permanent plots stratified along nine elevation bands (1700–1900 m). Total standing live biomass at the study site remained stable between inventories (~260 Mg ha⁻¹). *Betula* showed little, if any, response to the recent set of catastrophic overstory disturbances. Biomass and increment of *Picea* increased somewhat; but overall, there is limited evidence that *Picea* is expanding. *Abies* showed significant increases in standing live biomass (from 3.3 to 12.7 Mg ha⁻¹), increment (380 to 850 kg ha⁻¹ year⁻¹) and ingrowth (320 to 610 kg ha⁻¹ year⁻¹) over time. While some scenarios have not fully played out yet, at this time, total elimination of *Abies* is not indicated and there is considerable evidence to support the stable *Picea* and *Abies* scenario.

Introduction

Red spruce (*Picea rubens* Sarg.) Fraser fir (*Abies fraseri* (Pursh) Poir.) forests of the central and southern Appalachian Mountains exist today as a series of high-elevation vegetation 'islands' located above 1500 m in elevation between 34 and 41 degrees north latitude (White and Cogbill, 1992), 74 per cent of which are within the boundaries of Great Smoky Mountain National Park (GSMNP, Dull *et al.*, 1988). They are remnants of the original post-glacial range, representing the lower elevation limits of their high-elevation ecological niche (Delcourt and Delcourt, 1988) and

are highly disturbed due to anthropogenic stressors as well as recent widespread infestations by the balsam woolly adelgid (BWA, *Adelges piceae* Ratz.). These recent disturbances have combined to form a sensitive ecosystem with an unknown future. Many researchers have suggested that forest dynamics may permanently change due to these recent disturbances (Witter and Ragenovich, 1986; Busing and Clebsch, 1987; McLaughlin *et al.*, 1987; Witter, 1989; Dale *et al.*, 1991; Nicholas *et al.*, 1992).

Many disturbance agents are acting on this forest. Windthrow has been responsible for significant mortality of overstory trees and the creation

of larger overstory gaps in southern Appalachian *Picea–Abies* forests during strong windstorms (White and Cogbill, 1992). Within the past 17 years, for example, three extremely large storms, hurricanes Hugo in 1989, Opal in 1995 (Smith, 1997) and Ivan in 2004, have swept through the area causing significant tree mortality via windthrow. Ice storms (Nicholas and Zedaker, 1989) have also been shown to cause significant mortality of overstory trees. As a consequence of these disturbances and in concert with steep slopes and abundant precipitation, the landscape is susceptible to landslides (White and Cogbill, 1992). While such disturbance is rare, it is nevertheless highly destructive. Logging has not been significant due to the historic inaccessibility (steep, high-elevation slopes) and current land management status (National Park, Pyle and Schafale, 1988). Fires are rare in these forests due to year-round moisture and wet climate and lush understory vegetation (White and Cogbill, 1992).

More recently, additional anthropogenic stressors are impacting these forests including infestations of exotic pests (Johnson *et al.*, 1991; Nicholas, 1992) and air pollution (Johnson and Lindberg, 1992). The invasion of the BWA has caused widespread mortality in even the most protected areas of the range of *Abies*. BWA feeds at the base of needles and at fissures in *Abies* bark, where its saliva alters growth patterns within stems, killing trees 3–9 years after infestation (Amman and Speers, 1965). This exotic pest was first discovered in the southern Appalachians in 1957 (Speers, 1958), GSMNP in 1963 (Ceisla *et al.*, 1963), and since then, BWA has invaded the entire range of *Abies* and has caused heavy mortality of this species (Johnson *et al.*, 1991), killing over 90 per cent of stems and virtually every individual fir tree <10 cm diameter at breast height (d.b.h.) (Smith and Nicholas, 2000). Though regeneration of *Abies* is occurring, it is not uniform and patchy across the landscape (Smith and Nicholas, 2000), and the responses of the other woody species in this forest overstory as well as the role of BWA on the future of this forest are still unknown.

The southern Appalachian *Picea–Abies* forest consists of three main overstory species as well as several minor hardwood species. Elevation is the major driver of ecosystem composition in this forest (Whittaker, 1956). Prior to the outbreak of the BWA infestation, *Picea* dominated

slopes from 1500 to 1800 m, transitioning to an *Abies*-dominated system at the higher ridges and peaks above 1800 m. Yellow birch (*Betula alleghaniensis* Britt.) is a smaller component of the overstory at lower elevations along with the shallow rooted (Burns and Honkala, 1990a) and windthrow-prone *Picea*. Other hardwoods, including mountain maple (*Acer spicatum* Lam.), striped maple (*Acer pensylvanicum* L.), serviceberry (*Amelanchier laevis* (Weigand) Ahles.), pin cherry (*Prunus pensylvanica* L. f.) and mountain ash (*Sorbus americana* Marshall) are minor components of the overstory and understory across elevations, with *Sorbus* extending into the highest elevations while the others are minor components at lower and mid elevations.

Prior to the BWA, southern Appalachian *Picea–Abies* forests held considerable biomass in the form of live standing trees (200–310 Mg ha⁻¹, Whittaker, 1966). For years after the onset of the BWA, the mortality of insect-killed *Abies* trees, as well as the subsequent windfall of many large *Picea* trees due to exposure in a newly opened canopy (Busing, 2004), overwhelmed the ability of the existing trees (increment) and new trees (ingrowth) to compensate, causing the overstory biomass pool to shrink. The ability of this forest to once again hold large amounts of biomass in the overstory is a critical step in the post-BWA recovery of this system.

The future of this ecosystem is uncertain and many scenarios have been suggested ranging from a full forest recovery of *Abies* to the extinction of the species. Witter (1989) predicted that *Abies* would persist to some degree in the overstory based solely on the fact that trees currently survive to cone-bearing age, but said little regarding the stand structure of the *Abies* component of future *Picea–Abies* forests. McLaughlin *et al.* (1987) and McLaughlin and Tjoelker (1992) predicted that the effects of acidic precipitation on soil processes and nutrient availability would lead to slower growth rates of overstory tree species. Subsequent increased susceptibility of *Picea* and *Abies* to pathogens and mortality is possibly the cause of regional *Picea* decline observed in the 1980s (McLaughlin *et al.*, 1987). It has also been suggested that *Abies* may evolve resistance to the effects of the BWA (Witter and Ragenovich, 1986) and that the forest may return to pre-BWA conditions.

Dale *et al.* (1991) used Leslie matrices to forecast four possible scenarios of *Abies* response to the BWA including the complete extinction of *Abies* under repeated attacks of the BWA, complete recovery of *Abies* after the BWA dies off, stable coexistence of BWA and *Abies* and finally persistent oscillations in space and time between the populations of BWA and *Abies*. The predictions of Dale *et al.* (1991) did not incorporate information regarding the indirect response of other important forest species, *Picea*, *Betula* and other hardwoods, to the BWA-induced *Abies* mortality. Nicholas *et al.* (1992) stressed that not enough is known to adequately predict the future of *Abies* in the overstory and that much will be learned by the second, imminent wave of BWA-induced mortality.

Busing and Clebsch (1987) used a FORET gap model to predict several possible outcomes based on the combined impacts of BWA and acid deposition. If BWA negatively affected *Abies* while acid deposition negatively affected *Picea* (McLaughlin *et al.*, 1987), a decline in both species as well as the potential for the release of *Betula* may occur. This scenario may also be supported by the release of other minor understory hardwood species into the overstory. However, if BWA causes significant damage to *Abies* populations without the negative effect of acid deposition on *Picea*, then *Picea* may increase its dominance at higher elevations. Details about the BWA epidemiology and assumptions underlying the projections of future southern Appalachian *Picea-Abies* forests can be found in the above-cited references.

Based on the above literature, future *Picea-Abies* forests may comply with one of several forest change scenarios:

- 1 Expansion of *Betula*,
- 2 Introduction of other hardwoods as overstory species,
- 3 Increased dominance of *Picea* at higher elevations,
- 4 Elimination of *Abies* and
- 5 Stabilizing populations of *Picea* and *Abies* over time.

To date, reliable data on forest dynamics of southern Appalachian *Picea-Abies* forests has been largely lacking (Peart *et al.*, 1992) for a variety of reasons, i.e. unrepresentative sampling design, small sample sizes, lack of permanently

marked plots and trees, too brief a monitoring period and the use of subjective measurements. Reliable data are difficult to collect because vegetation characteristics and composition can vary greatly from peak to peak and even between stands on the same peak.

While many scenarios have been advanced in recent years regarding the future of this forest (Witter and Ragenovich, 1986; Busing and Clebsch, 1987; McLaughlin *et al.*, 1987; Witter, 1989; Dale *et al.*, 1991; Nicholas *et al.*, 1992), an analysis of the viability of these scenarios has not been performed. The objective of this study is to analyse these individual forest change scenarios (expansion of birch and other hardwoods, increased dominance of *Picea*, elimination of *Abies* and the stabilization of *Picea* and *Abies*) proposed by others and determine whether current forest dynamics in a forested watershed within the GSMNP support any of these projections.

This research examined current biomass pools of a southern Appalachian *Picea-Abies* forest, as well as changes over a 10-year period in order to determine the present status of these forests. We then examined the nature of recent biomass changes in terms of increment, ingrowth, mortality and overall mass balance and assess if there is evidence to support any of the scenarios relative to the major overstory species. Biomass dynamics (pool size, changes in increment, ingrowth, mortality and overall balance) over a 10-year period were used to examine significant shifts in each species over that time period. We used changes in standing live biomass pools and as well as changes in increment, ingrowth, mortality and overall mass balance as indicators of overstory change because this method is able to differentiate between the individual components of forest growth. We used dynamics in one watershed to understand some of the processes that may be occurring at larger scales.

Material and methods

Because 74 per cent of existing *Picea-Abies* forest land area in the southern US exists within GSMNP, conducting this research within the park is appropriate. This study was performed at the Noland Divide Watershed (NDW, 35° 34' N, 83° 29' W), a 17.4-ha, high-elevation catchment

within GSMNP, because of the broad elevation gradient (1700–1910 m) and resulting variability in overstory species composition, thought to represent much of the range of forest conditions occurring within the park. Pre-existing plot infrastructure, as well as access to previously collected data, and similar parent material allowed analysis of forest dynamics over a 10-year period while controlling for some confounding factors (parent material, aspect and climate). The study area has not been impacted by logging or fire (Pyle and Schafale, 1988), but has been severely impacted by the BWA (Pauley and Clebsch, 1990; Barker *et al.*, 2002). The soils are mainly Inceptisols, occasionally with spodic characteristics (McCracken *et al.*, 1962; Van Miegroet *et al.*, 1993), and are underlain by Thunderhead Sandstone (King *et al.*, 1968). They are generally shallow (<50 cm depth to bedrock) and have a silt loam to sandy loam texture (Van Miegroet *et al.*, 2007). Precipitation is >200 cm annually and is distributed evenly throughout the year (Johnson and Lindberg, 1992). Ten per cent of annual precipitation falls as snow and covers the ground for an average of 50 days per year (Johnson *et al.*, 1991). Mean air temperatures range from -2°C in February to 17°C in August with a frost-free period from May through September (Shanks, 1954; Johnson *et al.*, 1991).

In this study, we used a repeated overstory inventory of fifty 20×20 m permanent plots in and around this high-elevation catchment placed systematically along nine elevation bands (1700, 1725, 1755, 1785, 1800, 1835, 1865, 1890, 1910 m, Figure 1). Overstory tree inventories were conducted at the NDW in 1993, 1998 and 2003, using protocols described by Zedaker and Nicholas (1990). In 1993, all trees ≥ 5 cm d.b.h. (1.37 m) were measured and tagged with a permanent and unique ID tag. Species and d.b.h. of each live and dead overstory tree were recorded. In 1998 and 2003, ingrowth was tagged as they entered the stand. Live trees that had fallen over since the last inventory were considered windthrow.

Biomass of foliage, live branches, dead branches, bole bark and bole wood of each tree were calculated from d.b.h. using allometric equations developed for *Picea*, *Abies* and *Betula* by Nicholas (1992). Biomass of other overstory species and shrubs were estimated with the predictive equations of Weaver (1972).

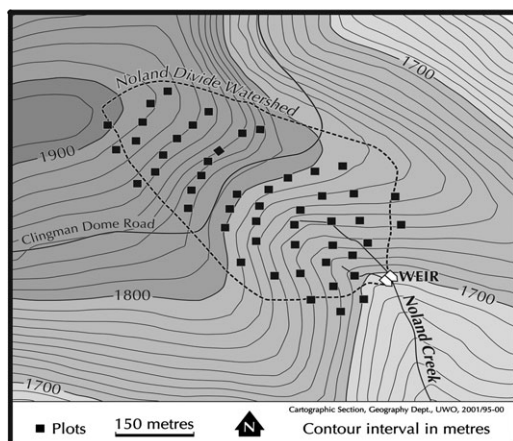


Figure 1. Map of the NDW of GSMNP and the systematic network of 50 permanent plots.

Standing live biomass at each time period was estimated by summing individual tree biomass values across individual plots. In order to investigate dynamics between time periods, we divided annualized change in live overstory biomass into three components; live increment, ingrowth and mortality. Increment was defined as the positive difference in individual tree biomass between inventory periods, ingrowth was defined as the mass of a tree that grew to >5cm d.b.h. since the previous inventory and mortality was defined as the whole-tree biomass of a tree that died since the previous inventory. Summing plot-level increment, ingrowth and mortality provided a mass balance for each plot and a picture of the biomass dynamics across the entire watershed. A positive mass balance for a particular site corresponded with a biomass gain for the period, while a negative mass balance indicated that the site had lost biomass during the period.

Significant differences in standing live biomass between 1993 and 2003 were determined for each of the three main species, *Abies*, *Betula* and *Picea* as well as the group of other hardwoods, using a series of repeated measures analyses of variance (ANOVAs) (SAS Institute Inc., 2002). Analyses were performed across the watershed as well as by elevation band to determine changes at each elevation. Due to the fact that there was only one plot in the highest elevation band (1910 m), making analysis of this band impossible, data from

that band were pooled with the data from the next highest band (1890 m), for a total of eight elevation bands. We were interested in how biomass dynamics for the entire overstory and individual overstory species changed over time, rather than how species composition changed across the elevation gradient. Temporal trends were tested with simple one-way repeated ANOVAs, using 1993 and 2003 biomass values, with no test for interactions because they were not germane to our study question and the effect of elevation on species composition and standing biomass has already been documented (Whittaker, 1956). With eight elevation bands, and four species groups, the analysis of standing live biomass required over 30 separate analyses. Statistical analysis and model construction were adapted from Cody and Smith (1997). Change in increment, ingrowth, mortality and overall mass balance was determined by species during the 1993–1998 and 1998–2003 time periods using a repeated measures ANOVA (SAS Institute Inc., 2002), similar to the method used for standing live biomass. Significant change in ingrowth, increment, mortality and overall balance from the first time period to the second time period was determined for each species group at each elevation band. Differences between the means were tested for significance by Duncan's mean comparison test. Significant changes over time will be used to determine whether evidence exists to support the postulated scenarios about declines and/or increases in the major overstory species.

Results

Overall, average standing live biomass for the NDW did not significantly change over the 10-year period from 267 Mg ha⁻¹ in 1993 to 260 Mg ha⁻¹ in 2003 (Table 1). When analysed individually, however, all three main species changed significantly over this time period; *Abies* ($P < 0.0001$) from 3.3 to 12.7 Mg ha⁻¹, *Betula* ($P < 0.0013$) from 56 to 61 Mg ha⁻¹ and *Picea* ($P < 0.0344$) from 206 to 184 Mg ha⁻¹.

Standing live biomass across a 10-year period increased for *Abies* across four of the eight elevation bands (Table 1), not only at the high elevations but at middle and low elevations as well. Significant increases ranged from 156 to 631 per

cent. No significant changes in *Picea* and *Betula* standing live biomass occurred at any elevation over a 10-year period. Standing live biomass of 'other hardwood species' did not increase from 1993 to 2003 at any elevation band. Density and basal area information are presented in Table 1.

Across the watershed and across species, increment, the growth of existing trees, increased significantly ($P < 0.0001$) from 4100 to 5500 kg ha⁻¹ year⁻¹ from the 1993 to 1998 to the 1998 to 2003 time periods (Table 2). Across all elevations, *Abies* ($P < 0.0001$, 380 to 850 kg ha⁻¹ year⁻¹) and *Picea* ($P < 0.0022$, 2800 to 3700 kg ha⁻¹ year⁻¹) increased significantly, while *Betula* remained unchanged. The combined increment of the three main species increased significantly at one low and two high-elevation bands. When analysed by elevation band, different overstory species responded differently, but no specific elevation consistently stood out. Increment of *Abies* increased by 75 to 190 per cent over the 10-year period at three elevation bands in the middle and upper watershed. *Picea* significantly increased at one lower elevation band by 36 per cent. *Betula* showed no significant change in increment from the first to the second inventory period at any elevation band.

Ingrowth, the growth of new trees, also increased significantly ($P > 0.0001$) across the watershed and across species, from 450 to 840 kg ha⁻¹ year⁻¹ between the two inventory periods (Table 2). Across elevations, ingrowth of *Abies* increased significantly ($P < 0.0001$) from 320 to 610 kg ha⁻¹ year⁻¹. Ingrowth of *Picea* also increased significantly ($P < 0.0005$) from 100 to 180 kg ha⁻¹ year⁻¹, while ingrowth rates of *Betula* (28 to 44 kg ha⁻¹ year⁻¹) remained unchanged. The combined ingrowth of the three main species increased significantly at two middle and two high-elevation bands. When analysed by elevation band, the rate of *Abies* ingrowth increased significantly between the two time periods at four elevation bands in the lower, middle and upper watershed. Significant increases ranged from 92 to 347 per cent. *Betula* ingrowth rates significantly increased at one middle elevation band by 743 per cent. *Picea* ingrowth increased significantly at two elevation bands in the middle and upper watershed by 80 and 144 per cent, respectively.

Overall, mortality was similar for the 1993–1998 time period (5900 kg ha⁻¹ year⁻¹)

Table 1: Standing live biomass (Mg ha⁻¹), number of trees per hectare, and basal area (m² ha⁻¹) for four species groups at eight elevation bands at two time periods within the Noland Divide Watershed of Great Smoky Mountain National Park (#standard deviation)

Elevation (m)	1993					2003					
	<i>Abies</i>	<i>Betula</i>	<i>Picea</i>	Other	Combined	<i>Abies</i>	<i>Betula</i>	<i>Picea</i>	Other	Combined	
Standing live biomass (Mg ha ⁻¹)	1700	0.4 ± 0.3	109 ± 131	229 ± 131	3.4 ± 5.8	341 ± 152	2.9 ± 1.8	121 ± 143	194 ± 109	2.0 ± 1.4	319 ± 153
	1725	1.1 ± 1.8	113 ± 116	183 ± 125	1.8 ± 2.1	299 ± 81	6.5 ± 10	130 ± 134	163 ± 81	2.0 ± 2.1	302 ± 97
	1755	0.5 ± 0.6**	76 ± 79	215 ± 108	1.3 ± 1.6	292 ± 109	3.9 ± 2.7**	76 ± 74	214 ± 95	1.7 ± 2.7	296 ± 94
	1785	0.9 ± 1.9**	43 ± 59	197 ± 111	3.0 ± 4.2	244 ± 73	5.7 ± 5.2**	47 ± 56	150 ± 88	3.1 ± 3.9	206 ± 64
	1800	0.9 ± 1.8	64 ± 27	244 ± 66	0.4 ± 0.6	309 ± 77	5.3 ± 6.4	67 ± 25	275 ± 68	0.8 ± 0.9	349 ± 70
	1835	1.6 ± 1.6**	39 ± 66	221 ± 75	0.5 ± 0.9	262 ± 64	12 ± 6.1**	45 ± 72	210 ± 136	0.5 ± 0.8	267 ± 119
	1865	4.1 ± 7.1	10 ± 18	218 ± 106	1.9 ± 2.8	234 ± 107	21 ± 19	12 ± 21	182 ± 106	2.5 ± 3.8	216 ± 99
	1890	18 ± 10*	1.4 ± 2.1	165 ± 56	1.3 ± 1.9	185 ± 60	46 ± 27*	2.6 ± 3.1	122 ± 70	1.9 ± 2.4	172 ± 71
Trees per hectare	Overall	3.3 ± 6.8**	56 ± 78**	206 ± 97*	1.7 ± 2.8	267 ± 95	12.7 ± 18.2**	61 ± 85**	184 ± 99*	1.9 ± 2.6	260 ± 105
	1700	38 ± 25	131 ± 90	550 ± 134	100 ± 91	819 ± 247	250 ± 157	144 ± 99	706 ± 134	144 ± 107	1244 ± 178
	1725	82 ± 140	82 ± 55	314 ± 171	121 ± 134	600 ± 171	396 ± 620	89 ± 52	350 ± 164	100 ± 95	936 ± 521
	1755	50 ± 60	281 ± 176	463 ± 144	75 ± 76	869 ± 222	294 ± 184	263 ± 156	556 ± 174	63 ± 81	1175 ± 305
	1785	75 ± 132	200 ± 210	397 ± 189	81 ± 72	753 ± 381	353 ± 278	209 ± 145	566 ± 377	125 ± 149	1253 ± 463
	1800	81 ± 146	163 ± 139	406 ± 83	44 ± 52	694 ± 243	319 ± 267	188 ± 153	650 ± 219	56 ± 66	1213 ± 512
	1835	125 ± 118	89 ± 64	307 ± 120	18 ± 37	539 ± 243	636 ± 379	129 ± 85	496 ± 136	39 ± 43	1300 ± 455
	1865	242 ± 336	46 ± 89	271 ± 81	33 ± 49	592 ± 287	1175 ± 1117	54 ± 75	388 ± 151	25 ± 27	1642 ± 1012
Basal area (m ² ha ⁻¹)	1890	925 ± 503	42 ± 79	233 ± 83	42 ± 49	1242 ± 466	1613 ± 853	58 ± 85	308 ± 177	54 ± 53	2033 ± 839
	Overall	199 ± 350	135 ± 147	362 ± 158	65 ± 79	760 ± 348	628 ± 708	146 ± 128	490 ± 236	75 ± 91	1339 ± 631
	1700	0.1 ± 0.1	14 ± 15	34 ± 18	1.7 ± 2.0	49 ± 18	0.9 ± 0.6	15 ± 16	30 ± 16	0.9 ± 0.8	47 ± 17
	1725	0.3 ± 0.6	13 ± 13	28 ± 18	0.8 ± 0.9	42 ± 11	2.0 ± 3.2	15 ± 14	25 ± 12	0.7 ± 0.8	43 ± 9.1
	1755	0.2 ± 0.2	11 ± 10	31 ± 13	0.9 ± 1.0	43 ± 13	1.2 ± 0.8	11 ± 8.6	31 ± 10	0.7 ± 0.9	44 ± 11
	1785	0.3 ± 0.6	6.5 ± 8.5	30 ± 15	0.8 ± 0.9	37 ± 10	1.8 ± 1.6	7.0 ± 8.0	23 ± 11	1.1 ± 1.5	33 ± 8.0
	1800	0.3 ± 0.6	8.9 ± 2.2	35 ± 8.3	0.2 ± 0.3	44 ± 9.0	1.6 ± 1.9	9.4 ± 2.6	39 ± 8.5	0.3 ± 0.4	50 ± 9.0
	1835	0.5 ± 0.5	5.1 ± 7.9	32 ± 12	0.1 ± 0.2	38 ± 10	3.6 ± 1.9	5.8 ± 8.5	31 ± 19	0.2 ± 0.2	41 ± 18
Overall	1865	1.2 ± 2.1	1.7 ± 3.1	33 ± 14	0.5 ± 0.8	36 ± 14	6.3 ± 6.0	2.0 ± 3.5	27 ± 14	0.6 ± 0.9	36 ± 12
	1890	5.2 ± 2.7	0.3 ± 0.4	25 ± 7.0	0.5 ± 0.7	31 ± 8.6	13 ± 7.6	0.5 ± 0.6	18 ± 10	0.5 ± 0.7	32 ± 11
		1.0 ± 2.0	7.4 ± 9.4	31 ± 13	0.7 ± 1.0	40 ± 12	3.8 ± 5.2	8.0 ± 9.8	28 ± 13	0.7 ± 0.9	40 ± 12

Bold indicates significant differences in standing live biomass for a given elevation range and species combination between 1993 and 2003 at the *0.5 and **0.01.

Table 2: Rates (kg ha⁻¹ year⁻¹) of biomass ingrowth increment mortality and overall balance for three species at eight elevation bands at two time periods within the Noland Divide Watershed of Great Smoky Mountain National Park (\pm standard deviation)

Elevation (m)	1993–1998				1998–2003			
	<i>Abies</i>	<i>Betula</i>	<i>Picea</i>	Combined	<i>Abies</i>	<i>Betula</i>	<i>Picea</i>	Combined
Ingrowth	1700	125 \pm 155	10 \pm 20	101 \pm 99	236 \pm 244	27 \pm 32	243 \pm 117	549 \pm 176
	1725	181 \pm 374	6.1 \pm 16	38 \pm 37	225 \pm 370	36 \pm 37	83 \pm 92	560 \pm 654
	1755	83 \pm 80*	34 \pm 67	128 \pm 134	246 \pm 184	19 \pm 26	96 \pm 66	488 \pm 307
	1785	175 \pm 161	15 \pm 30**	128 \pm 197*	319 \pm 344*	130 \pm 93**	231 \pm 259*	819 \pm 574*
	1800	100 \pm 90**	20 \pm 23	164 \pm 141	284 \pm 227*	57 \pm 89	196 \pm 143	560 \pm 311*
Increment	1835	356 \pm 283*	77 \pm 76	81 \pm 96	514 \pm 369*	22 \pm 41	301 \pm 345	1007 \pm 531*
	1865	684 \pm 911*	8.6 \pm 21	80 \pm 68*	773 \pm 923*	19 \pm 30	196 \pm 142*	1586 \pm 1217*
	1890	888 \pm 642	39 \pm 69	99 \pm 113	1026 \pm 659	26 \pm 42	148 \pm 155	1079 \pm 596
	Overall	323 \pm 488**	28 \pm 51	100 \pm 119**	451 \pm 520**	44 \pm 64	182 \pm 195**	837 \pm 683**
	1700	22 \pm 17	876 \pm 910	3827 \pm 2864	4724 \pm 2819	1996 \pm 1987	3721 \pm 2013	5858 \pm 1826
Mortality	1725	152 \pm 257	1564 \pm 1788	2971 \pm 1282	4687 \pm 1424*	2468 \pm 2464	3281 \pm 1400	6107 \pm 1340*
	1755	67 \pm 74	1385 \pm 1010	3193 \pm 1117*	4645 \pm 808	1137 \pm 1064	4350 \pm 1631*	5680 \pm 1668
	1785	119 \pm 197*	1006 \pm 1275	3247 \pm 1913	4372 \pm 1689	775 \pm 850	3200 \pm 1376	4290 \pm 1209
	1800	135 \pm 249	605 \pm 404	3152 \pm 1798	3891 \pm 1977	841 \pm 1180	5572 \pm 1879	6766 \pm 2328
	1835	274 \pm 212*	659 \pm 776	2500 \pm 1572	3433 \pm 1549	396 \pm 357	4073 \pm 3613	5264 \pm 3712
Overall	1865	423 \pm 610	228 \pm 520	2509 \pm 1477	3160 \pm 1620*	302 \pm 553	3331 \pm 1579	5081 \pm 972*
	1890	1887 \pm 1167*	109 \pm 145	1552 \pm 759	3548 \pm 1266**	134 \pm 165	2318 \pm 1675	5745 \pm 2037**
	Overall	379 \pm 728**	853 \pm 1087	2842 \pm 1599**	4074 \pm 1598**	986 \pm 1411	3659 \pm 2045**	5496 \pm 2011**
	1700	-32 \pm 64	0 \pm 0	-13242 \pm 25650	-13274 \pm 25628	-37 \pm 74	-698 \pm 1288	-769 \pm 1241
	1725	-8.1 \pm 22	-26 \pm 68	-2338 \pm 6186	-2372 \pm 6171	-348 \pm 920	-7787 \pm 12292	-8180 \pm 12174
Balance	1755	-5.6 \pm 16	-364 \pm 754	-1362 \pm 3496	-1732 \pm 4250	-1750 \pm 3296	-6440 \pm 10957	-8232 \pm 10251
	1785	-9.3 \pm 26	-743 \pm 2026	-4278 \pm 6605	-5031 \pm 6375	-83 \pm 224	-11311 \pm 13100	-11691 \pm 13001
	1800	0 \pm 0	-384 \pm 767	-1045 \pm 2089	-1428 \pm 1971	-10 \pm 20	-1265 \pm 2487	-1301 \pm 2463
	1835	0 \pm 0	-22 \pm 58	-7673 \pm 12741	-7696 \pm 12725	0 \pm 0	-1412 \pm 3476	-1497 \pm 3443
	1865	-59 \pm 99	-169 \pm 415	-9696 \pm 9628	-9925 \pm 9645	0 \pm 0	-2421 \pm 5894	-2952 \pm 6790
Overall	1890	-379 \pm 536	-37 \pm 91	-8068 \pm 8264	-8484 \pm 8214	-34 \pm 84	-4560 \pm 9308	-5523 \pm 9428
	Overall	-59 \pm 213*	-239 \pm 890	-5579 \pm 10204	-5877 \pm 10187	-219 \pm 547*	5123 \pm 9369	-5725 \pm 9370
	1700	115 \pm 175*	886 \pm 909	9314 \pm 27180	8313 \pm 27448	1986 \pm 2030	3267 \pm 2682	5639 \pm 2664
	1725	326 \pm 615	1544 \pm 1815	670 \pm 6014	2540 \pm 6831	2157 \pm 2223	-4422 \pm 11803	-1513 \pm 12109
	1755	145 \pm 133**	1056 \pm 1529	1959 \pm 3384	3159 \pm 4405	-594 \pm 2285	-1994 \pm 10804	-2065 \pm 10634
Overall	1785	284 \pm 292*	279 \pm 1283	-903 \pm 7245	-340 \pm 7198	608 \pm 1117	-7880 \pm 12824	-6582 \pm 12665
	1800	235 \pm 332	241 \pm 732	2271 \pm 3396	2747 \pm 3786	888 \pm 1145	4504 \pm 3006	6025 \pm 3907
	1835	630 \pm 393*	714 \pm 798	-5092 \pm 13923	-3748 \pm 13944	418 \pm 360	2963 \pm 5648	4774 \pm 5800
	1865	1048 \pm 1239	68 \pm 106	-7107 \pm 10470	-5992 \pm 9735	321 \pm 548	1106 \pm 5214	3716 \pm 6637
	1890	2396 \pm 2060	111 \pm 119	-6416 \pm 8721	-3910 \pm 8252	126 \pm 111	-2094 \pm 9246	1300 \pm 8861
Overall	Overall	644 \pm 1090**	641 \pm 1181	-2636 \pm 10879	-1352 \pm 10888	646 \pm 1640	-1281 \pm 9487	608 \pm 9667

Bold indicates significant differences in growth characteristics (ingrowth, increment, mortality and overall balance) for a given elevation range and species combination between the 1993 and 1998 time period and the 1998 and 2003 time period at the *0.05 and **0.01 levels.

and the 1998–2003 time period ($5700 \text{ kg ha}^{-1} \text{ year}^{-1}$). Across elevations, mortality of *Abies* increased significantly ($P < 0.0285$) from 60 to $220 \text{ kg ha}^{-1} \text{ year}^{-1}$ while *Betula* and *Picea* mortality remained constant. Inventory data and field observations of downed wood indicated that windthrow was responsible for the virtually all *Picea* mortality.

The overall stand biomass balance for the overstory, consisting of increment, ingrowth and mortality for each species, reversed from a negative value in the 1993–1998 time period ($-1350 \text{ kg ha}^{-1} \text{ year}^{-1}$) to a positive value in the 1998–2003 time period ($610 \text{ kg ha}^{-1} \text{ year}^{-1}$) across the range of elevations and species, though this change was not statistically significant. *Abies* showed a significant increase in mass balance ($P < 0.0001$) from 640 to $1240 \text{ kg ha}^{-1} \text{ year}^{-1}$ across all elevations, as well as a significant positive change in mass balance in four middle and lower elevation bands (121 to 262 per cent). *Betula* had small rates of ingrowth, moderate rates of increment and low rates of mortality of existing trees, and these rates showed no significant increase between the two time periods. In *Picea*, higher elevation bands showed a decline in biomass during the first time period while the lower elevation bands showed a net increase. The opposite was true during the second time period where high elevations corresponded with positive mass balances and low elevations corresponded with negative mass balances.

Variability was very large in these analyses, and coefficients of variation were often over 100 per cent. Thus, while trends can be observed, it is obvious that results are not uniform across this watershed. Nevertheless, significant differences between time periods for biomass pools and fluxes existed, despite the large degree of variability. These differences can be interpreted as general temporal trends within this watershed.

Discussion

The methods and data presented here provide a framework for testing specific scenarios against a current 10-year data set. In general, there is no evidence that this forest is in the midst of a decline. In fact, many components of this forest are aggrading in terms of standing live biomass and

growth, especially *Abies* and at low-, middle- and high-elevation bands. Overstory standing biomass estimates were similar to other post-adelgid research in the southern Appalachians (260 Mg ha^{-1} in this study compared with 258 Mg ha^{-1} measured in the mid-1980s at the nearby Spruce 'Becking' site and 265 and 308 Mg ha^{-1} at the two nearby Smokies 'Tower' sites, Johnson and Lindberg, 1992).

Betula expansion

There is no evidence that *Betula* will become more dominant or expand into higher elevations. There is considerable standing live biomass, especially at the lower elevations, however, higher elevations continue to carry little standing live biomass of *Betula*. Also, there has been no increase of standing live *Betula* at any particular high-elevation band. While standing live biomass increased significantly across the entire watershed, this accounted for only a 10 per cent increase. While there is considerable increment of existing trees, this does not result in an increase in net biomass balance over the measurement period. Ingrowth of *Betula* was generally quite low, and did not significantly increase over time. The magnitude of *Betula* ingrowth does not seem sufficient to dramatically alter future stand composition, because *Betula* ingrowth is dwarfed by the magnitude of *Abies* ingrowth across elevations. The capture of new spaces in the overstory would be a critical step in the expansion of this species, but that is not occurring in this watershed.

Though more shade tolerant than other *Betula* species in North America, *Betula allegheniensis* is reported to be a fast growing tree species and capable of capturing moderately sized gaps in the overstory (Burns and Honkala, 1990b). Relative to the shallow-rooted *Picea* and slightly deeper-rooted *Abies*, *Betula* has a more extensive and deeper root system (White and Cogbill, 1992). This would decrease the likelihood of this species succumbing to windthrow unlike the other major overstory species. We are suggesting that while *Betula* may acquire limited additional spaces in the overstory at mid elevations (as exemplified by the 1785-m elevation band, Table 2), we find no evidence for the expansion of *Betula*, especially at the higher elevations.

Other hardwoods

A set of other hardwood species including *A. spicatum*, *A. pensylvanicum*, *A. laevis*, *P. pensylvanica* and *S. americana* may, under some conditions, be able to compete for overstory positions (Eyre, 1980; Burns and Honkala, 1990b). Growth characteristics of these species suggest that they may become more important in terms of overstory live biomass. Over our 10-year study period, these hardwood species did not significantly change standing biomass at any elevation band. None of these species were able to capture canopy openings created by BWA. In addition, though these species may be more competitive under other edaphic conditions, in the *Picea*–*Abies* system they likely do not have the growth form necessary to successfully compete with *Picea* and *Abies* trees that have faster growth rates and taller maximum heights. A shift in canopy species composition might have resulted if both *Picea* and *Abies* were undergoing significant and repeated disturbance (Busing and Clebsch, 1987). However, there is little evidence to suggest that the disturbances acting on *Picea* and *Abies* will be repeated and significant enough to cause long-term forest change. Due to the complete lack of change in standing live biomass of ‘other’ tree species, robust presence of *Abies* in the understory, apparent resiliency of and strong increment of the major overstory species, there is no evidence to support the *Other hardwoods* scenario from above.

Picea dominance

The *Picea* dominance scenario suggested the possibility of *Picea* responding to an open canopy by taking a more dominant overstory role, especially at high elevations where *Abies* was more prevalent pre-BWA. In our analysis, this scenario would manifest itself by large amounts and increasing standing live biomass, a positive change in increment and ingrowth from the first to the second inventory period, as well as an overall positive mass balance for the overstory. *Picea* did not meet all of these criteria, but met some. *Picea* accounted for the majority of standing live biomass; however, this standing stock did not significantly increase over the 10-year period from 1993 to 2003, unlike *Abies*. The majority

of increment was also dominated by *Picea*, but increment significantly increased at only one low-elevation band between the two time periods. Ingrowth of *Picea* increased at two elevation bands but was considerably less than that of *Abies*, even at lower elevations.

Large amounts of *Picea* died during our survey period. *Picea* was responsible for 95 and 89 per cent of all mortality in the two time periods; however, due to the large between-plot variability in plot mortality, likely driven by the heterogeneity in forest structure, no statistically significant differences in mortality between time periods emerged for any of the species at any elevation. It appears that heavy mortality of *Picea* followed that of BWA-induced *Abies* mortality by 15–20 years. Though some degree of windthrow mortality was anticipated and observed in several studies (Hollingsworth and Hain, 1991; Peart *et al.*, 1992; Busing and Pauley, 1994; Busing 2004), the magnitude of this mortality in our study area was unexpected. Scenarios of increased *Picea* dominance were based partially on the expectation that the *Picea* overstory would sustain little mortality via windthrow after the initial catastrophic *Abies* mortality. This did not occur, however, and the biomass and growth dynamics of both *Picea* and *Abies* have been considerably set back.

Windthrow-induced *Picea* mortality appears to have moved from higher elevations to lower elevations. This mortality started first in the higher elevations with lower *Picea* dominance (fewer, more spread out *Picea* trees) during the 1993–1998 time period and was observed later at the lower elevations with high *Picea* dominance (stands of more dense *Picea* trees) during the 1998–2003 time period. In contrast, the wave of BWA-induced *Abies* mortality began at the lower elevations of the *Abies* population and moved up to the mountaintops (White and Cogbill, 1992). Because the *Picea* windthrow mortality did not follow the same spatiotemporal pattern as the adelgid mortality, we are suggesting that the large amount of *Picea* mortality is a function of canopy openness and exposure to winds and elements, rather than a function of time since BWA disturbance.

Mortality and the overall mass balance at the lowest elevation band seemed to emulate processes occurring at the highest elevations with higher levels of mortality from 1993 to 1998

and lower levels of mortality from 1998 to 2003. However, the four plots in this band showed some of the highest data variability. One particular low-elevation plot (C1700) lost over 70 per cent of its standing live biomass between the 1993 and 1998 surveys due to a very large multi-tree windthrow event. The timing of this event coincided with the large amount of individual *Picea* stem windthrow occurring in higher elevations. It is hypothesized that C1700's location along a ridge position made it more vulnerable to a large windthrow event and may explain its temporal resemblance to the higher elevation bands. Others have found that *Picea* on exposed ridges are more susceptible to mortality (Busing and Pauley, 1994). The lowest band displayed the type of heterogeneity in forest structure that is very typical of this forest overstory.

Despite considerable windthrow, *Picea* is still holding considerable biomass in the overstory and is contributing the majority of increment. *Picea* shows some significant increases in increment and ingrowth. However, it is not apparent that *Picea* is taking over many overstory positions previously held by *Abies*. *Picea* will remain a considerable component of this forest overstory, but there is only limited evidence to support the *Picea* dominance scenario from above.

Abies elimination

There is no evidence to support the elimination of *Abies* as suggested by Smith (1997). While some aspects of the future of *Abies* are unknown, such as future interactions of *Abies* and the BWA, all evidence suggests that, in general, *Abies* is currently making a rapid recovery. *Abies* is again becoming a substantial part of the forest overstory in terms of standing live biomass. This species is making significant gains in biomass acquisition over time and *Abies* seedlings are dominating ingrowth at all elevations, even surpassing those by *Picea* at the lower elevations. Relatively large (several over 25 cm d.b.h.) *Abies* trees have matured and are currently producing cones, though viability rates of those seeds may be significantly lower than normal (Nicholas *et al.*, 1992). With the adequate regeneration we have observed, we have no direct evidence to support the *Abies* elimination scenario from above.

Stable Picea–Abies

Two important factors influencing the future of *Abies* are the nature and timing of the next, imminent wave of BWA-induced mortality. The more time passes before the BWA returns, the more time this recovering forest has to return to pre-BWA conditions. The nature of the next wave of BWA-induced mortality (i.e. number and size of trees killed) will tell us much about the long-term prognosis of this host-pathogen relationship. Frequent and severe *Abies* mortality events, similar to American chestnut, will signal a dramatic departure of this forest type from pre-BWA conditions, while infrequent and mild-mortality events (similar to gypsy moth) may yield a forest that is quite similar to pre-BWA forests with stable populations of *Picea* and *Abies*.

Across the watershed, standing live biomass of overstory trees is no longer in decline. Between 1993 and 2003, the forest has evolved from losing biomass each year in the 1993–1998 time period to a forest that is positively accruing biomass in the 1998–2003 time period. Standing live biomass values are similar to measurements taken pre-BWA (200–310 mg ha⁻¹, Whittaker, 1966), though there is likely a difference in the diameters of the trees where this biomass is stored. The recovery of *Abies* is mainly responsible for this turnaround. Many large *Picea* on the edges of overstory gaps, the most susceptible to windthrow, have fallen and the overall mass balance is expected to become increasingly positive in coming years due to the lack of additional *Picea* mortality. Both *Picea* and *Abies* have asserted themselves in the mid-story by producing abundant ingrowth that is appearing in the smaller size classes, also indicated by higher tree density in the 1998–2003 time period. Our biomass and growth trends support a recovery of *Abies* while *Picea* remains a solid component of the overstory. These data indicate a stabilizing relationship between the two overstory species and support the stable *Picea–Abies* scenario from above.

Examination of 10-year inventory data from 50 plots in and around a catchment of the GSMNP does not support many of the scenarios that have been suggested in the literature about the future of this forest. Though this high-elevation forest in this area has possibly not seen the last of the exotic BWA; there is little, if any, direct evidence

that the initial wave of adelgid-induced mortality has had a catastrophic impact on this forest type. Under current conditions, neither *Betula* nor any of the other hardwood species seem poised to take a more dominant role in the overstory of this forested watershed. *Picea* will remain the dominant species at lower elevations, but will maintain a relatively low density in the higher elevations due to the prolific ingrowth of the next generation of *Abies* trees. A wave of windthrow mortality has swept through the standing *Picea* trees here, but is unlikely to cause further large-scale damage in the near future due to the fact that the largest and most wind-prone stems have already fallen. There is no evidence to support the possible extinction of *Abies*, only reason to suspect a slightly modified role in the forest overstory. *Abies* is now doing quite well across all elevations and can be expected to make a consistent recovery until the next wave of BWA-induced mortality. In spite of its limited inference space, valuable insights can be gleaned from the study of this Southern Appalachian forest.

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Conflict of Interest Statement

None declared.

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