
Two Decades of Change in Vegetation in Adirondack Spruce-Fir, Northern Hardwood and Pine-Dominated Forests

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Two decades of change in vegetation in Adirondack spruce-fir, northern hardwood and pine-dominated forests¹

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BEDISON, J. E., A. H. JOHNSON, S. A. WILLIG, S. L. RICHTER, AND A. MOYER (Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316). Two decades of change in vegetation in Adirondack spruce-fir, northern hardwood and pine-dominated forests. *J. Torrey Bot. Soc.* 134: 238–252. 2007.—In 2004 we remeasured trees in 42 permanent vegetation plots that had been established in Adirondack spruce-fir, northern hardwood, and pine-dominated stands in 1984. Over the 20-yr interval, live basal area (BA) in red spruce and/or balsam fir-dominated plots decreased by 15%. Blowdown was a major cause of balsam fir, but not red spruce mortality in two plots. Excluding the two blowdown plots, balsam fir live BA increased by 17%, while red spruce live BA decreased by 42% ($P < 0.05$). There was no significant change in the overall live BA of northern hardwood plots. However, excluding beech, the pooled northern hardwoods showed a significant decrease ($P \leq 0.05$) in live BA over the 20-yr interval. In contrast to the spruce-fir and northern hardwood plots, the live BA of pine-dominated plots increased by 19% over the 20-yr interval ($P \leq 0.01$). Changes in sapling densities in the spruce/fir plots were not significant, though fir in the 2–9.9 cm dbh class reached densities of > 3000 stems ha^{-1} in four plots where they filled large gaps. There was a trend toward increased red spruce sapling density ($P \leq 0.10$) in the upper northern hardwood zone (600–950 m). Sugar maple sapling density and BA decreased significantly ($P \leq 0.05$) in the northern hardwood plots during the twenty-year interval.

Key words: Adirondack forests, northern hardwood forests, permanent vegetation plots, red spruce decline.

In recent decades, questions concerning the productivity and health of northern hardwood and spruce-fir forests in the northeastern U.S. have been of interest to forest scientists from a variety of disciplines. Considerable research in the northern forests over the past two decades has focused on the decline and mortality of red spruce (*Picea rubens* Sarg.) in high elevation (> 900 m) conifer-dominated forests (Eagar and Adams 1992, Friedland et al. 1984, Johnson 1992, Shortle and Smith 1988, Scott et al. 1984). Similarly, observations of crown dieback and mortality of sugar maple (*Acer saccharum* Marsh.) prompted studies of forest health in northern hardwood forests (Allen et al. 1999, Drohan et al. 2002, Duchesne et al. 2002).

Perceptions of the seriousness of mortality, what it means to forest health in the north-

eastern U.S., and the avenues of investigation into important causes of spruce and maple mortality are varied. Weather events, native and introduced pests, natural aging, and competitive pressures in aggrading stands cause mortality. Castello et al. (1995) point out the integral role of pathogens in regulating the structure of forests, and Manion and Griffin (2001) contend that a baseline mortality rate of over 3% yr^{-1} averaged over all species is required to maintain the structure of “healthy” forests in the Adirondack region. For more than two decades, three species, red spruce, sugar maple, and beech, have been identified as under pressure in northeastern U.S. forests. For red spruce, sugar maple and beech, Manion and Griffin (2001) used growth rate, relative mortality and the distribution of stem sizes to determine that mortality rates of 2.6, 3.0 and 3.6% y^{-1} , respectively, would preserve the status quo of those species in the Adirondack forests. Those rates are high compared to the mortality rates of those species in healthy stands reported by other investigators (Peart et al. 1991, Forrester et al. 2003, Battles et al. 2003, McWilliams et al. 1997) and serve as a convenient reference for comparisons.

Since the 1980’s several researchers have proposed links between acid-rain induced

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changes in available Ca and Al in soils, and the vitality of both red spruce and sugar maple (Shortle and Smith 1988, Shortle and Bondietti 1992, Shortle et al. 1997, Bondietti et al. 1990, Lawrence et al. 1995, Lawrence et al. 1997). Widespread acceptance of the idea that changes in soil chemistry are important contributing stresses in those multiple stress diseases has been elusive, though the case is quite strong in sugar maple decline on old, highly weathered soils (e.g., Horsley et al. 2002).

In 1984 Andersen (1988) established permanently marked vegetation plots across the Adirondacks, measured all live and dead stems ≥ 2 cm dbh, and sampled organic and mineral horizons at the sites for future comparisons. The primary reason for establishing these plots was to quantify future changes in vegetation and soil chemistry to better understand if changing soil conditions are related to changes in the health and productivity of those stands.

In this paper we report the changes in major tree species between 1984 and 2004 in spruce-fir, northern hardwood, and pine-dominated plots within the Adirondack Forest Preserve. The goals of this study were to determine growth, mortality, and changes in basal area, stem density and species importance. Based on other recent studies of Adirondack forests, we expected that red spruce continued its well-documented high rate of mortality at high elevation (e.g., Battles et al. 2003), that large beech stems died from beech bark disease in northern hardwood forests (e.g., Manion and Griffin 2001), and that pines grew well with low mortality resulting from a lack of pathogens and environmental stresses from 1984–2004 (Manion and Griffin 2001, Widmann and McWilliams 2003).

ADIRONDACK FOREST TYPES. *High Elevation Spruce-Fir Forests.* Montane spruce-fir forests of the northeastern United States are characterized by red spruce (*Picea rubens* Sarg.), paper birch (*Betula papyrifera* var. *cordifolia* (Marsh.) Regel) and balsam fir (*Abies balsamea* (L.) Mill.) and are found at elevations ≥ 900 m (White and Cogbill 1991; nomenclature follows Harlow et al. 1996). Accelerated, region-wide red spruce mortality in the upper montane forests in the northern Appalachians was initiated in the 1960's and continued through the 1980's (Siccama et al. 1982, Johnson and Siccama 1983, Johnson and

McLaughlin 1986, Peart et al. 1991). This episode of mortality was first documented in the 1960's in reports on forest condition (reviewed in Johnson and McLaughlin 1986) and has been tracked at several locations in the Adirondack, Green and White Mountains since the late 1970's (Siccama et al. 1982, Foster and Reiners 1983, Johnson and Siccama 1983, Silver et al. 1991, Craig and Friedland 1991, Peart et al. 1991, Battles et al. 2003).

Northern Hardwood Forests. Northern hardwood forests of the Adirondack Mountains are dominated by American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britton) (Braun 1950, Likens and Bormann 1995). They dominate on medium and fine-textured soils at the lower elevations in this region (McGee 2001). Red spruce and eastern hemlock (*Tsuga canadensis* (L.) Carr) are the most important associated conifers (McGee 2001).

Pine Forests. Pine-dominated stands are generally found throughout the Adirondack Mountains at lower elevations where pines compete best on well-drained or excessively-drained coarse sands and gravels of lacustrine or deltaic origin (Cook et al. 1952). These forests are typically characterized by dominance of eastern white pine (*Pinus strobus* L.) or red pine (*Pinus resinosa* Ait.) and usually have a variety of associated hardwoods (Cook et al. 1952). Many of the pine-dominated stands on lower elevation glacial outwash are post-agricultural old-field stands (our observations). Little recent research has focused on pine forests of the Adirondack region.

Methods. **PLOT LOCATION.** Sites used in this study were located in the Adirondack State Park in the Adirondack Highlands ecological subregion of northeastern New York State (McNab and Avers 1994, Fig. 1). This mountainous area has peaks in excess of 1500 m and is characterized by cool, wet summers and cold, snowy winters. Elevations above 900 m are dominated by conifer forests that are subject to high wind speeds and immersion in cloudwater for a substantial fraction of the year (Mohnen et al. 1990, Reiners and Lang 1979, Siccama 1974). Soils vary from thin with frequent bedrock outcrops, to deep and sandy or deep and moderate-textured (April et al.

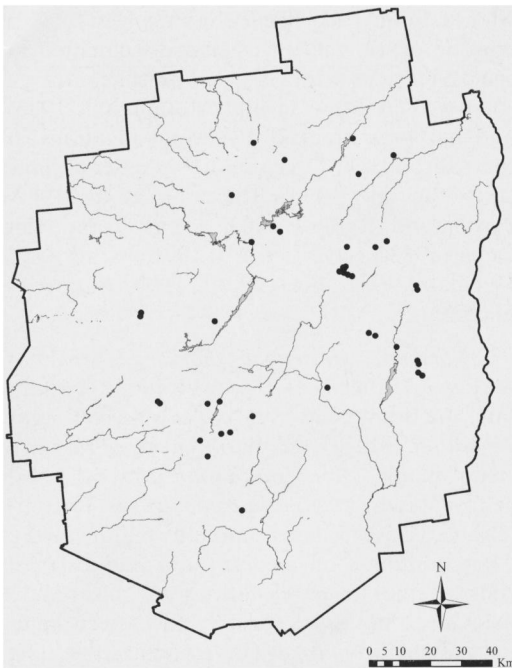


FIG. 1. Distribution of study plots throughout the Adirondack region relocated in 2004.

2004, Battles et al. 1992). Nearly all of the soils in this study were derived from acid glacial till or outwash (Johnson et al. 1994, Sullivan et al. 2006).

In 1930–1932, Carl C. Heimbürger (1933) inventoried the flora and soils of the Adirondack Mountains to classify forest types and their productivity. At each of > 100 points, he described and sampled soils and inventoried vegetation including herb, shrub and canopy species. In 1984, Andersen (1988) and Johnson et al. (1994) used Heimbürger's descriptions of landmarks, elevations, trails and floristic composition to relocate 48 of his sites scattered across the Adirondacks. The center of each plot was marked with either a fiberglass, plastic or metal stake in 1984. The main purpose of the 1984 study was to determine if soil pH and extractable Ca had changed measurably over the 5-decade interval (both had decreased, Andersen 1988, Johnson et al. 1994).

Heimbürger (1932) noted that he was looking for stands on well-drained soils that were relatively undisturbed, though his directions led us to several sites that appear to have been logged sometime in the 19th century. All of the spruce-fir plots located in 1984 were in

uneven aged stands that had never been logged and had naturally regenerated after disturbances that occurred well over a century prior to the study. The northern hardwood stands varied in their age structure, with some being uneven aged with dominant trees estimated to be > 200 yr old and some representing second growth after logging in the latter part of the 19th century. Most of the pine-dominated plots were in even-aged post agricultural stands with a variety of hardwoods present, though a few plots contained pines > 150 yr old. A full description of canopy, herb and shrub-layer vegetation was compiled for each site by Andersen (1988).

In 2004, we found 42 plots, all of which were located on public lands within the Adirondack Forest Preserve. Four sites had considerable blowdown, which most likely resulted from the downburst event of July 15, 1995 (Jenkins 1995). There was no detectable impact of the 1998 ice storm (Miller-Weeks et al. 1999) which damaged forests to the northeast of the area we sampled. We used maps and directions from fixed benchmarks to find the sites in 2004 and marked the plots' geographic coordinates using Global Positioning System (GPS) receivers. We measured all stems, live and dead ≥ 2 cm dbh and were able to account for essentially every tree ≥ 10 cm dbh that was present in 1984.

As the location of these plots was inherited from a study done in the early 1930's, they cannot be considered to be randomly located throughout the region; hence we confine our conclusions to the set of plots we studied. However, we are unaware of any bias that would cause this set of plots to be different from a stratified random sample of the three vegetation associations on Adirondack Park land.

To determine changes, we grouped the data by the dominant tree species: subalpine spruce/fir, northern hardwood and pine-dominated, and used a discriminant analysis to verify these groupings. Sites were largely stratified by elevation with pine sites occupying the lowest elevation and spruce/fir occupying the highest (Table 1).

Tree mortality rates (% y^{-1}) were calculated following Sheil et al. (1995, 1996):

$$m = [1 - (N_t/N_0)^{1/t}] * 100$$

where m is the mortality rate, N_t represents the

Table 1. Changes in basal area and importance of the major species in spruce-fir, northern hardwood and pine stands sampled in the Adirondack Mountains, 1984 and 2004.

	Basal Area \pm SE ($\text{m}^2 \text{ha}^{-1}$)			Species Importance (%)		
	1984	2004	<i>P</i> -value	1984	2004	<i>P</i> -value
Spruce/Fir Plots (1074m)*						
<i>Picea rubens</i>	9.8 \pm 1.6	5.7 \pm 1.6	0.03†	20	17	0.3
<i>Abies balsamea</i>	18.2 \pm 2.7	17.4 \pm 2.5	0.4	61	66	0.1
<i>Betula papyrifera</i>	6.4 \pm 1.0	5.8 \pm 1.4	0.3	16	15	0.3
All Live Stems	34.9 \pm 2.4	29.8 \pm 2.9	0.2			
Standing Dead Stems	20.1 \pm 2.9	16.0 \pm 3.2	0.2			
Standing Live + Dead	55.0 \pm 3.6	45.7 \pm 4.2	0.04			
<i>n</i> = 12						
Northern Hardwood Plots (581m)						
<i>Acer saccharum</i>	12.2 \pm 2.6	11.5 \pm 2.5	0.7	22	19	0.07
<i>Fagus grandifolia</i>	7.0 \pm 1.7	7.9 \pm 1.7	0.1	27	31	0.009
<i>Betula alleghaniensis</i>	8.6 \pm 1.6	7.1 \pm 1.7	0.3	10	9	0.2
All Live Stems	38.4 \pm 2.6	35.7 \pm 2.4	0.3			
Standing Dead Stems	7.6 \pm 1.5	10.4 \pm 2.8	0.3			
Standing Live + Dead	46.0 \pm 3.4	46.0 \pm 3.5	1.0			
Live stems excluding beech	31.6 \pm na	28.0 \pm na	0.05			
<i>n</i> = 20						
Pine Plots (433 m)						
<i>Pinus strobus</i>	30.6 \pm 6.4	39.4 \pm 6.9	0.008	42	43	0.8
<i>Pinus resinosa</i>	19.2 \pm 6.6	20.0 \pm 9.4	0.9	21	20	0.9
All Live Stems	50.2 \pm 4.6	59.6 \pm 5.6	0.005			
Standing Dead Stems	4.3 \pm 1.2	9.2 \pm 2.7	0.09			
Standing Live + Dead	54.6 \pm 5.7	68.8 \pm 6.6	0.002			
<i>n</i> = 10						

* Average elevation of all sites for a given forest type.

† 1-tailed test.

population count at the end of the time period t , and N_0 is the original population.

We used paired-sample student's *t*-tests ($\alpha = 0.05$) to evaluate the differences in live and dead basal area in 1984 compared to 2004. We used a one-tailed test when there was an expectation of either an increase or decrease based on the condition of the trees in the original survey. For instance, the crown condition of all red spruce in the plots in 1984 was determined (e.g., Johnson and McLaughlin, 1986), and it was clear that a large number of trees had severe crown dieback and we expected that they would be dead when we did the 2004 study. On the other hand, many plots had a great abundance of balsam fir < 1 m tall in 1984 growing in gaps, and we expected that many of these would have grown into the ≥ 2 cm dbh size class by 2004.

Species importance values were calculated as: (relative live density + relative live BA)/2 as described by Forrester et al. (2003). Importance values were arcsine transformed and evaluated using a paired-sample *t*-test. To evaluate changes in stem densities where distributions were non-normal as determined by a Shapiro-

Wilk Test, we used Wilcoxon Signed-Ranks Tests (Sokal and Rohlf 1995). Stem densities could not be adequately transformed to conform to the assumptions of normality.

Results. Discriminant analysis shows that the sites can be grouped into 3 distinct vegetation associations: spruce/fir, northern hardwood and pine (Fig. 2). The sites fall into three significantly different groups using 12 tree species and elevation (Roy's Max Root = 11.892, $P < 0.001$). The analysis reveals that 76% and 24% of the variation are explained by the first and second discriminant functions respectively. One northern hardwood site was misclassified as a pine site due to its low elevation and anomalously high proportion of balsam fir.

SPRUCE-FIR SITES. Comparisons for the 12 montane conifer sites dominated by red spruce and/or balsam fir showed that the average live BA of trees ≥ 2.0 cm dbh changed from 34.9 to 29.8 $\text{m}^2 \text{ha}^{-1}$ (n.s.) and the trees grew more slowly on average than in the other forests sampled (Table 1, 2). Most of the change in

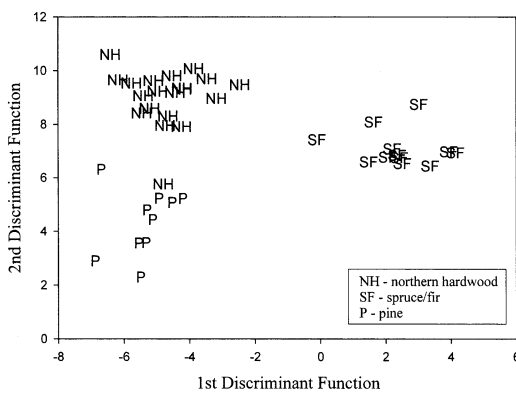


FIG. 2. Discriminant analysis of study sites in the Adirondack region and forest type classification into spruce-fir, northern hardwood, and pine-dominated sites.

live BA is attributable to red spruce, rather than balsam fir or white birch mortality. In the spruce/fir plots, red spruce live BA decreased significantly ($P \leq 0.05$) with a significant decrease in red spruce basal area of 15–19.9 cm dbh stems and large differences in basal area of stems ≥ 30 cm dbh (Table 1, 3). Red spruce density also decreased over the interval. The change was significant for stems in the 15–19.9 cm dbh (43 to 15 stems ha^{-1}) and ≥ 30 cm dbh (43 to 9 stems ha^{-1}) size classes (Table 4). From 1984 to 2004, red spruce experienced mortality rates of 1.6% y^{-1} across all size classes with a higher rate (6.7% y^{-1}) in the largest size classes (Table 5).

In spruce-fir plots, balsam fir BA and abundance did not change significantly, though there were trends toward decreasing fir basal area in the 15–19.9 cm dbh size class

and decreasing density in the 10–14.9 cm dbh size class ($P < 0.1$, Table 3, 4). The overall mortality rate for balsam fir was 2.6% y^{-1} for all size classes (Table 5) and there was a trend toward increased balsam fir importance ($P < 0.1$, Table 1) as red spruce BA and density decreased substantially.

For all species pooled, there was a significant decrease in live+dead basal area (55.0–45.7 $\text{m}^2 \text{ha}^{-1}$, $P < 0.05$) over the 20-year interval but no significant change in the standing dead BA (Table 1). This indicates that many of the standing dead trees present in 1984 were no longer standing in 2004 and that mortality of individuals alive in 1984 largely compensated for this loss.

Including the upper-elevation hardwood plots, the density of 2–9.9 cm dbh spruce showed a tendency to increase between 600 and 950 m elevation ($P = 0.1$, Fig. 3). The 2–9.9 cm dbh balsam fir stem density did not increase significantly, but at four sites at elevations ≥ 900 m they increased markedly reaching very high densities (> 3000 stems ha^{-1}) in large gaps (Fig. 3).

White birch in the spruce-fir stands did not change significantly in live BA, density or importance (Table 3, 4) and mortality was relatively low across all size classes (Table 4).

NORTHERN HARDWOOD SITES. In the northern hardwood plots, American beech was the only major species that had a greater average live BA in 2004 compared to 1984 (Table 1). The decrease in basal area of all live stems (from 38.4 to 35.7 $\text{m}^2 \text{ha}^{-1}$) was not significant. Beech increased in importance from 27

Table 2. Diameter growth rate (mm y^{-1}) from 1984–2004 of major species in spruce-fir, northern hardwood and pine-dominated stands sampled in this study.

	dbh growth \pm SE (mm y^{-1})	
	All	> 10 cm dbh
Spruce/Fir Plots		
<i>Picea rubens</i>	1.3 \pm 0.3	0.9 \pm 0.2
<i>Abies balsamea</i>	1.6 \pm 0.2	1.2 \pm 0.3
<i>Betula papyrifera</i>	0.9 \pm 0.2	0.9 \pm 0.3
Northern Hardwood Plots		
<i>Acer saccharum</i>	1.7 \pm 0.2	1.9 \pm 0.3
<i>Fagus grandifolia</i>	1.3 \pm 0.1	2.2 \pm 0.7
<i>Betula alleghaniensis</i>	2.1 \pm 0.6	2.2 \pm 0.3
<i>Picea rubens</i>	1.4 \pm 0.2	1.7 \pm 0.3
<i>Abies balsamea</i>	1.3 \pm 0.3	2.5 \pm 0.7
Pine Plots		
<i>Pinus strobus</i>	2.7 \pm 0.4	2.8 \pm 0.5
<i>Pinus resinosa</i>	1.7 \pm 0.3	1.6 \pm 0.4

Table 3. Distribution of basal area ($m^2 ha^{-1}$) by diameter size class (cm dbh) in plots sampled of major species within spruce-fir, northern hardwood and pine-dominated forests studied in 1984 and 2004 throughout the Adirondack region.

	Basal Area \pm SE ($m^2 ha^{-1}$)											
	2.0 - 9.9		10 - 14.9		15 - 19.9		20 - 24.9		25 - 29.9		≥ 30	
	1984	2004	1984	2004	1984	2004	1984	2004	1984	2004	1984	2004
Spruce-Fir												
<i>Picea rubens</i> ^a	0.5 \pm 0.1	0.5 \pm 0.3	0.6 \pm 0.3	0.4 \pm 0.2	1.0 \pm 0.4	0.4 \pm 0.02**	2.0 \pm 0.7	1.0 \pm 0.5	1.0 \pm 0.51	0 \pm 0.6	8.0 \pm 5.0	2.0 \pm 1.5
<i>Abies balsamea</i>	1.9 \pm 0.4	5.0 \pm 2.0 ^b	5.0 \pm 1	3.0 \pm 0.6	6.0 \pm 2.0	3.0 \pm 1.0 *	5.0 \pm 2.0	2.0 \pm 0.6	3.3 \pm 2.6	2.0 \pm 1.0	1.4 \pm 1.1	1.5 \pm 1.0
<i>Betula papyrifera</i>	0.6 \pm 0.3	0.2 \pm 0.1	1.0 \pm 0.5	1.0 \pm 0.7	0.8 \pm 0.6	2.0 \pm 0.8	1.0 \pm 0.4	0.8 \pm 0.4	2.0 \pm 0.7	0.5 \pm 0.4	2.0 \pm 1.0	2.0 \pm 0.8
All live stems	0.8 \pm 0.2	2.0 \pm 0.6	2.0 \pm 0.5	1.0 \pm 0.3*	2.0 \pm 0.5	1.0 \pm 0.3	2.0 \pm 0.5	1.4 \pm 0.3	2.0 \pm 0.7	1.0 \pm 0.4	3.0 \pm 1.0	1.4 \pm 0.5
Northern Hardwood												
<i>Acer saccharum</i>	0.3 \pm 0.08	0.2 \pm 0.07*	0.5 \pm 0.2	0.4 \pm 0.1	0.9 \pm 0.3	0.6 \pm 0.2	0.7 \pm 0.2	1.0 \pm 0.3	1.0 \pm 0.4	0.7 \pm 0.2	9.0 \pm 3.0	9.0 \pm 2.0
<i>Fagus grandifolia</i>	1.0 \pm 0.2	1.0 \pm 0.2	1.0 \pm 0.2	1.0 \pm 0.4	0.8 \pm 0.2	0.9 \pm 0.2	0.6 \pm 0.2	1.0 \pm 0.3**	1.0 \pm 0.4	1.0 \pm 0.3	2.4 \pm 1.5	2.4 \pm 1.6
<i>Betula alleghaniensis</i>	0.05 \pm 0.04	0.05 \pm 0.03	0.2 \pm 0.09	0.07 \pm 0.05	0.04 \pm 0.04	0.05 \pm 0.05	0.08 \pm 0.08	0.1 \pm 0.1	0.4 \pm 0.2	0.1 \pm 0.1	8.0 \pm 2.0	7.0 \pm 2.0
All live stems	0.4 \pm 0.07	0.4 \pm 0.08	0.5 \pm 0.08	0.4 \pm 0.08	0.5 \pm 0.1	0.4 \pm 0.08	0.4 \pm 0.1	0.5 \pm 0.1	0.6 \pm 0.1	0.5 \pm 0.1	4.0 \pm 0.7	4.0 \pm 0.6
Pine												
<i>Pinus strobus</i>	0.2 \pm 0.1	0.1 \pm 0.09	0.6 \pm 0.4	0.3 \pm 0.2	1.0 \pm 0.5	0.8 \pm 0.3	2.0 \pm 0.8	2.0 \pm 0.9	2.0 \pm 0.91	0 \pm 0.4	26.0 \pm 6.0	36.0 \pm 7.0***
<i>Pinus resinosa</i>	0.1 \pm 0.06	0.06 \pm 0.05	0.4 \pm 0.3	0.04 \pm 0.04	0.7 \pm 0.3	0.9 \pm 0.5	0.4 \pm 0.2	0.5 \pm 0.4	2.0 \pm 1.0	1.0 \pm 0.4	18.0 \pm 6.0	18.0 \pm 8.0
All Live Stems	0.3 \pm 0.06	0.4 \pm 0.1	0.2 \pm 0.07	0.2 \pm 0.06	0.4 \pm 0.1	0.3 \pm 0.1	0.5 \pm 0.2	0.6 \pm 0.2	0.6 \pm 0.2	0.6 \pm 0.2	6.0 \pm 1.0	7.0 \pm 2.0

* $P = 0.10$
 ** $P = 0.05$
 *** $P = 0.01$
^a *P. rubens* are 1-tailed tests
^b 1-tailed test

Table 4. Distribution of stem density (stems ha^{-1}) by diameter size class (cm dbh) for major species in spruce-fir, northern hardwood and pine-dominated sites studied in 1984 and 2004 throughout the Adirondack region.

	Stem Density \pm SE (stems ha^{-1})													
	All Sizes		2.0 - 9.9		10 - 14.9		15 - 19.9		20 - 24.9		25 - 29.9		≥ 30	
	1984	2004	1984	2004	1984	2004	1984	2004	1984	2004	1984	2004	2004	
Spruce-Fir														
<i>Picea rubens</i> ^a	447 \pm 97	481 \pm 173	254 \pm 78	374 \pm 173	49 \pm 26	29 \pm 13	43 \pm 17	15 \pm 7**	39 \pm 1931	\pm 14	19 \pm 7	22 \pm 10	43 \pm 22	9 \pm 6**
<i>Abies balsamea</i>	1594 \pm 354	2844 \pm 869	773 \pm 174	2360 \pm 879 ^b	411 \pm 94	234 \pm 49*	237 \pm 39	116 \pm 39	106 \pm 4177	\pm 21	52 \pm 4141	\pm 23	15 \pm 11	15 \pm 12
<i>Betula papyrifera</i>	340 \pm 99	270 \pm 80	143 \pm 71	70 \pm 28	92 \pm 41	84 \pm 49	29 \pm 34	70 \pm 34	24 \pm 1019	\pm 9	25 \pm 11	9 \pm 6	25 \pm 12	19 \pm 9
All live stems	653 \pm 134	984 \pm 292	317 \pm 69	758 \pm 280	151 \pm 37	99 \pm 22*	87 \pm 22	56 \pm 15	48 \pm 1338	\pm 8	27 \pm 1220	\pm 7	24 \pm 7	13 \pm 4
Northern Hardwood														
<i>Acer saccharum</i>	264 \pm 49	207 \pm 39**	114 \pm 32	68 \pm 24**	41 \pm 12	30 \pm 10	36 \pm 13	25 \pm 9	16 \pm 5	25 \pm 9	17 \pm 6	10 \pm 4	39 \pm 9	49 \pm 12
<i>Fagus grandifolia</i>	710 \pm 126	723 \pm 88	539 \pm 119	515 \pm 82	90 \pm 22	104 \pm 31	32 \pm 7	39 \pm 11	16 \pm 5	33 \pm 8**	15 \pm 6	17 \pm 5	18 \pm 9	16 \pm 8
<i>Betula alleghaniensis</i>	76 \pm 19	47 \pm 8*	23 \pm 14	9 \pm 7	12 \pm 7	5 \pm 3	2 \pm 2	2 \pm 2	2 \pm 2	2 \pm 2	3 \pm 2	2 \pm 2	33 \pm 8	26 \pm 7
All live stems	301 \pm 43	311 \pm 43**	200 \pm 36	219 \pm 38	38 \pm 7	32 \pm 6*	20 \pm 4	18 \pm 3	11 \pm 2	14 \pm 3	9 \pm 2	8 \pm 2	23 \pm 4	21 \pm 4
Pine														
<i>Pinus strobus</i>	413 \pm 99	330 \pm 75*	88 \pm 60	32 \pm 29	52 \pm 28	19 \pm 13	46 \pm 20	33 \pm 14	40 \pm 2142	\pm 22	37 \pm 1626	\pm 17	149 \pm 33	178 \pm 39*
<i>Pinus resinosa</i>	267 \pm 108	228 \pm 115	26 \pm 10	15 \pm 10	28 \pm 23	3 \pm 3	28 \pm 15	37 \pm 25	9 \pm 6	14 \pm 10	26 \pm 1918	\pm 6	151 \pm 58	143 \pm 78
All Live Stems	276 \pm 50	246 \pm 49**	179 \pm 48	150 \pm 44**	20 \pm 5	20 \pm 5	17 \pm 4	13 \pm 4	13 \pm 4	15 \pm 4	10 \pm 3	7 \pm 3	39 \pm 10	41 \pm 12

* $P = 0.10$

** $P = 0.05$

*** $P = 0.01$

^a *P. rubens* are 1-tailed tests

^b 1-tailed test

Table 5. Mortality rates (% y^{-1}) by diameter size class (cm dbh) in plots sampled of major species within spruce-fir, northern hardwood and pine-dominated forests studied in 1984 and 2004.

	Mortality Rate (% y^{-1})						
	All sizes	2.0 – 9.9	10 – 14.9	15 – 19.9	20 – 24.9	25 – 29.9	≥ 30
Spruce/Fir Plots							
<i>Picea rubens</i>	1.6	—*	1.7	5.0	0.5	—	6.7
<i>Abies balsamea</i>	2.6	—	1.9	2.4	1.2	—	2.0
<i>Betula papyrifera</i>	0.7	3.4	0.5	—	1.7	2.5	0.0
All Species	2.2	—	1.6	1.5	0.3	—	2.6
Northern Hardwood Plots							
<i>Acer saccharum</i>	1.9	2.4	2.0	1.3	—	2.0	—
<i>Fagus grandifolia</i>	1.0	—	—	—	—	—	1.5
<i>Betula alleghaniensis</i>	3.5	6.1	3.4	0.0	0.0	3.4	1.8
All Species	1.8	—	1.0	0.5	—	0.5	0.7
Pine Plots							
<i>Pinus strobus</i>	1.2	4.4	4.0	1.2	—	1.8	—
<i>Pinus resinosa</i>	0.1	2.0	8.6	—	—	2.0	—
All Species	1.0	1.5	1.9	1.4	0.6	2.9	0.2

* In-growth exceeded death

to 31% ($P = 0.009$, Table 1). Pooling all species except beech, there was a significant decrease ($P = 0.05$) in live BA of 11% (Table 1). Table 5 shows moderate mortality rates for most species, though yellow birch mortality rates are comparatively high for most size classes.

The density of live 2–9.9 cm dbh sugar maple decreased significantly ($P \leq 0.05$) over the 20-year period and contributed to a significant overall decrease in live stem density in northern hardwood plots ($P \leq 0.05$, Table 4). In the 12 northern hardwood plots that contained sugar maples in the 2–9.9 cm dbh size class in 1984, 11 showed a decrease in live sugar maple sapling density. There was a trend toward decreasing importance of sugar maple in the northern hardwood plots ($P = 0.07$) during the interval.

Across the northern hardwood plots, there was a trend toward decreasing live yellow birch density (from 76 to 47 stems ha^{-1} , $P \leq 0.1$, Table 4), but live BA was not significantly less in 2004 (Table 1). From 1984 to 2004 yellow birch importance was not significantly different (Table 1), as yellow birch diameter growth was the highest (2.1 $mm y^{-1}$) of the major species in the northern hardwood plots.

PINE SITES. Stand-level changes for the pine plots include a highly significant increase ($P \leq 0.01$) in total live and total live+dead basal area. There was a significant decrease in density of all live stems which was driven by significant decreases of 2–9.9 cm dbh stems,

and total live basal area increased from 50.2 to 59.6 $m^2 ha^{-1}$ ($P = 0.005$) (Table 1, 4). White pine live BA increased significantly from 30.6 to 39.4 $m^2 ha^{-1}$ on average (Table 1) and was driven by a highly significant increase in basal area and density of stems ≥ 30 cm dbh (Table 3, 4). White pine diameter growth was the fastest (2.7 $mm y^{-1}$) of all species in this study (Table 2).

The trends are similar for the total live+dead stem basal area (Table 1). However, the red pine live BA change (+4%) was not significant and there were no significant changes in live red pine density in any size class (Table 3). Overall, there was more variability in basal area in all categories within the pine stands

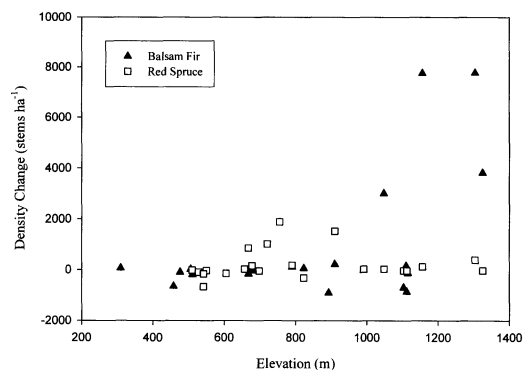


FIG. 3. Changes in density of red spruce and balsam fir in the 2–9.9 cm dbh class, 1984 to 2004 in all plots sampled in 2004 throughout the Adirondack region.

compared to the spruce-fir and northern hardwood stands (Table 1).

Discussion. SPRUCE-FIR PLOTS. Balsam fir fared better than red spruce in the high elevation plots with live BA decreasing by an average of 4% vs. 42% respectively, with much of the spruce decrease observed in the ≥ 30 cm size class (Table 5). This follows the pattern established by several studies conducted in the 1980's which tracked the mortality of these species (Siccama et al. 1982, Scott et al. 1984, Silver et al. 1991, Battles et al. 1992). Spruce mortality rates in these plots (1.6–6.7% y^{-1}) are slightly greater than those reported by Battles et al. (2003) at two sites on the Whiteface Mt. massif (1.2–3.6% y^{-1}).

Manion and Griffin (2001) note that wind damage from the July 1995 downburst storms was an important cause of red spruce mortality in their study of Adirondack Park forests. They indicate that 42% of the dead spruce they recorded in their survey had been downed by wind. As their study was conducted on public lands, < 800 m from roadways, it does not include much of the high elevation spruce-fir forest, virtually all of which is > 800 m from roads. In our spruce-fir plots, the reduction in live fir BA is accounted for by blowdown of nearly everything in two plots. This did not influence the red spruce BA change very much however, because in 1984 there were no spruce in one of the plots, and only a few in the other. Removing the two high elevation blowdown plots (S. Marcy Brook and Pillsbury Mt.) showed that balsam fir BA *increased* by 17% in the other 10 plots while red spruce BA *decreased* by 42%.

Regionally, red spruce importance decreases at elevations ≥ 900 m (Foster and Reiners 1983, White and Cogbill 1991) as it appears to reach its physiological limits, especially the ability of its foliage to withstand freezing events (winter injury) (DeHayes et al. 1999, DeHayes 1991). Acids in ambient cloudwater reduce its ability to withstand winter injury, reducing freezing resistance by about 6°C (see reviews by Johnson 1992, DeHayes et al. 1990, 1999) and has also been shown to reduce the frost hardiness in red spruce seedlings at high elevations (Fowler et al. 1989). Frequent winter injury was a component of spruce decline through the 1980's at higher elevations (Johnson 1992). Because some of the mortality was recent, and some not, it was not realistic

to determine the causes of red spruce mortality, though we observed crown dieback on many live red spruce that suggests the multiple stress decline disease that caused widespread mortality in the 1980's (Johnson 1992) was still in progress in 2004.

At lower elevations during the 1980's other causal agents of red spruce mortality were present across the Adirondacks and northern Appalachians. Spruce beetle (*Dendroctonus rufipennis* Kirby) was found to be active in the Adirondacks with about 30% of the dead red spruce trees showing evidence of infestation up to 1100 m and higher rates of infestation below 760 m (Souto and McCreery 1988, see review by Peart et al. 1991). Eastern dwarf mistletoe was also present at that time and associated with areas of abundant dead trees (e.g., > 30% standing dead) but was not considered a primary cause of spruce mortality.

The conifer swift moth (*Korscheltellus gracilis* Grote) was also observed in spruce/fir forests of the Adirondacks. In their review, Peart et al. (1991) report that the preferred food of the larvae is spruce and fir roots, and that red spruce and balsam fir regeneration is susceptible to damage from this agent. It has not been linked to the high mortality that has occurred in the overstory spruce over the past several decades however.

In plots above 900 m, the abundance of red spruce saplings did not change significantly, while balsam fir thickets now occupy the large gaps left by the mortality of large canopy trees. In the plots where spruce and/or fir mortality was advanced in 1984, the fir regeneration was in the 2–9.9 cm dbh class in 2004. In plots where the mortality appears to be more recent (including the blowdown plots) balsam fir seedlings (< 1 m tall) are abundant, but not measured in this study. Over the next several decades the high elevation plots will likely be converted to predominantly fir stands with increases in BA and density in all size classes as spruce is being systematically replaced.

White birch did not change significantly in basal area, density, or importance and the mortality rate was relatively low. There are no other signs to indicate that white birch in upper elevation spruce-fir forests is experiencing any instability and we expect that it will maintain its current status in the future forest.

NORTHERN HARDWOOD PLOTS. Beech bark disease (BBD) has influenced the Adirondack northern hardwood forests since the 1960's (Houston 1984) and its effects were observed on a majority of large American beech in our plots. This disease is caused by a combination of beech scale (*Cryptococcus fagisuga* Lindinger) and fungi (*Nectria* spp.) and < 1% of American beech trees show natural resistance (Houston 1975, 1994). Larger trees are more susceptible (Houston 1975), and this is reflected in the higher mortality rate for beech ≥ 30 cm dbh in the plots ($1.5\% \text{ y}^{-1}$ vs. $1\% \text{ y}^{-1}$ for all stems dbh, Table 5).

Thickets of beech sprouts grew well and replaced the BA lost from the mortality of the larger trees resulting in an increase in average basal area and low overall mortality in the 20-year interval in this set of plots. These results are similar to those of Forrester et al. (2003) who reported the 1985–2000 change in biomass in the Huntington Forest, though they recorded a slight overall decrease in beech biomass. Houston (1975) showed that mature and overmature individuals were removed from stands affected by BBD in Maine and replaced by thickets of young stems. This trend has also been seen elsewhere in Adirondack forests where beech have reached higher densities in smaller size classes in old-growth stands than in second-growth stands (Latty 2005).

Forrester et al. (2003) note that the onset of the “killing front” phase of beech bark disease in the Adirondacks occurred in the 1980's and that Adirondack forests are now in the “aftermath” phase of the disease (Houston 1994, sensu Shigo 1972). To this point, the beech in our plots have outgrown the mortality caused by beech bark disease. Similar trends have been observed in other northern hardwood stands (Houston 1975, Le Guerrier et al. 2003, Runkle 1990).

Sugar maple live BA was only slightly lower (< 6%) but not significantly different in 2004. We do not know the causes of the maple mortality in these plots, nor are we able to generalize about the time of the mortality. Accurate determination of an initiating event, such as the drought Fahey (1998) linked to decreased sugar maple, is difficult when the sampling interval is 20 years. We observed what appeared to be recent death of a few very large (≥ 60 cm) trees that may have been near the end of their normal lifespan, but ingrowth

compensated for those losses in the ≥ 30 cm dbh size class (Table 4).

The decrease in the density of live stems 2–9.9 cm dbh in 11 of 12 plots in which sugar maple saplings were present in 1984 ($P \leq 0.05$, Table 4) merits some attention. We do not know if this represents natural thinning and/or the influence of other factors. In the Hubbard Brook Experimental Forest, Hane (2003) suggests that sugar maple seedling survival is suppressed by dense thickets of beech saplings. On average, the stands in this study were not aggrading, so it is difficult to confidently attribute sugar maple sapling death to normal stand development.

The results for sugar maple are consistent with the 1985–2000 changes at the Huntington Forest reported by Forrester et al. (2003) and with the 1985–1993 changes at the Arnot Forest reported by Fahey (1998). Forrester et al. (2003) observed a significant 10% decrease in sugar maple biomass ($P < 0.04$), and calculated that the highest mortality rate for sugar maple ($4.1\% \text{ y}^{-1}$) was in the 10–15 cm dbh class. Fahey (1998) observed significant decreases in both sugar maple density and basal area in all size classes with the highest mortality rate ($5.2\% \text{ y}^{-1}$) in the < 6 cm dbh size class. Forrester et al. (2003) predict an increase in beech importance relative to sugar maple and this scenario appears appropriate for the beech and maple in our plots as well.

While not widely observed in the Adirondacks, an ongoing decline disease of sugar maple has attracted attention in southern Canada, Vermont, and northern Pennsylvania (Bernier and Brazeau 1988a, b, Horsley et al. 2002, McLaughlin 1998, Ouimet and Camiré 1995). These authors suggested that weather conditions, insect defoliation, and poor soil nutrition acted together as causal agents. Increased environmental stress related to elevation may be a factor promoting maple mortality in our plots. Sugar maple > 10 cm dbh within North American Maple Project plots showed increased mortality at elevations > 300 m from 1988–1997 (Allen et al. 1999) and the average elevation of northern hardwood sites in this study is 581 m.

Yellow birch accounted for about 22% of the live BA of the plots in 1984 but tended to decrease in overall density ($P \leq 0.1$) through 2004. Average yellow birch live BA decreased by 17%, attributable to relatively high mortality rates across all size classes which is

consistent with trends reported by Fahey (1998) in the Arnot Forest. Manion and Griffin (2001) noted that yellow birch mortality was higher than their estimated baseline values and suggested that it will decrease in importance. They also noted that there were no consistent symptoms that would explain the mortality they observed. Further investigation is needed to determine reasons for the mortality observed in this species.

It is interesting to note the trend toward increasing red spruce density in the 2–9.9 cm dbh in the hardwood forest zone immediately below the montane conifer forests (Fig. 3). Red spruce was a more important species in the northern hardwood forests prior to settlement by Europeans. It then became an important timber species with the largest sizes found in the upper northern hardwood forest zone (White and Cogbill 1991). Logging in the 19th and early 20th centuries and the resulting fires reduced its abundance in the Adirondacks, apparently dramatically (White and Cogbill 1991).

Red spruce in the lower elevation northern hardwood plots exhibited little crown dieback or other widespread signs of poor health in 2004. Neither live BA nor density across all size classes changed significantly for red spruce in these plots over the interval (data not shown). The mortality rate of red spruce ≥ 10 cm dbh in these plots ($1.8\% \text{ y}^{-1}$) was lower than that recorded in the high elevation plots, and also substantially lower than that listed by Manion and Griffin ($2.6\% \text{ y}^{-1}$, 2001). Perhaps the increase in red spruce abundance in the upper northern hardwood forest and lower montane conifer forest signals that a century of minimal human intervention in the Adirondack Park is now resulting in a return to pre-settlement vegetation patterns in the upper hardwood forest zone.

PINE PLOTS. There were few data to use in estimating pine mortality rates as the ten stands in this data base had mostly large canopy trees in 1984, most of which were still living in 2004. White pine live BA increased while red pine showed no significant change in live BA or density. The increase in live white pine BA contributed to the significant overall increase in live and live+dead basal area in the pine sites (Table 1). The average red pine live BA change is largely influenced by mortality in one plot where most of the large red pines

were dead in 2004. Aside from that plot, red pine live BA increased by 26% (data not shown).

The pine-dominated sites in this study contrast with the northern hardwood and spruce-fir sites. They had the largest average live BA in 1984, and especially white pine did very well through 2004. The trees in those plots grew faster than trees in the other plots and mortality was the least of the three forest types studied (Table 5). These results are consistent with region-wide observations where white pine seems to be doing well and there is currently no evidence of widespread pathogen invasion in the Adirondacks (North-eastern Forest Experiment Station 2002; Widmann and McWilliams 2003; Manion and Griffin 2001). Manion and Griffin (2001) showed that white pine across the Adirondacks had about twice the annual diameter growth as the other major Adirondack species.

COMPARISONS OF ANNUAL MORTALITY RATES. Manion and Griffin (2001) conducted a survey of live and dead stems at 67 unidentified locations in the Adirondack Park using randomly located prism plots on public lands within 800 m of roadways. They established “baseline” mortality rates for each of the major species that are required to maintain the status quo of forest composition and structure based on diameter growth rates (Table 6). For estimates of the diameter growth rates of the trees in their sample, they used diameter growth data from the Eastwide Data Base (McWilliams et al. 1997). Those data were obtained from plots in the Adirondacks established on private forestland, at least some of which is managed. Most of the “baseline” mortality values in Table 6 are high relative to those observed across the northern forests, and they are balanced by the relatively high diameter growth rates they report.

Except for yellow birch, the mortality rates for major species in our hardwood and spruce/fir plots are lower than the “baseline” mortality values of Manion and Griffin (2001), and the status quo of species importance and stand structure was not maintained in the montane spruce-fir and northern hardwood plots we studied (Table 5, 6). The loss of live BA during the 20-year interval resulted from the fact that diameter growth rates of the live trees in our plots did not compensate for the mortality. The average

Table 6. Comparison of mortality rates and diameter growth rates for selected species. The baseline mortality rate is that of Manion and Griffin (2001) and represents their calculation of mortality required to keep the status quo of forest composition and structure given the diameter growth rates in the Eastwide data set (McWilliams et al. 1997).

Species	Manion & Griffin (2001) ¹		This Study ¹		Huntington Forest ^a	
	Baseline mortality (% y ⁻¹)	dbh growth (mm y ⁻¹)	Mortality rate (% y ⁻¹)	dbh growth (mm y ⁻¹)	Mortality rate (% y ⁻¹)	dbh growth [‡] (mm y ⁻¹)
<i>Acer saccharum</i>	3.0	3.0	0.5	2.3	1.9	1.5
<i>Fagus grandifolia</i>	3.6	3.2	-	2.2	3.5	1.9
<i>Betula alleghaniensis</i>	1.5	2.7	2.7	2.1	1.9	1.8
<i>Picea rubens</i>	2.6	2.6	1.6	1.3		
<i>Abies balsamea</i>	5.3	3.6	1.2	1.6		
<i>Pinus strobus</i>	3.3	5.0	0.3	3.5		

¹ Mortality and growth rate calculated on stems ≥ 10 cm dbh.

^a Forrester *et al.* (2003).

[‡] calculated on stems in all size classes.

diameter growth rate of all trees for all size classes in this study (1.6 mm y⁻¹) was about 45% lower than the 3.4 mm y⁻¹ average of the trees used by Manion and Griffin (2001). In this regard, substantially lower mortality rates than those calculated by Manion and Griffin (2001, 3.0% y⁻¹ average for all species) would have been necessary to maintain forest structure as it was in 1984.

There are some obvious possibilities regarding reasons for the difference. The forests in the Adirondack region, especially those located near roads, are most-likely still changing and cannot be considered stable after major disturbances in the late 19th and early 20th centuries, whereas virtually all of our stands were > 800 m from roads. Nearly all of the high elevation spruce-fir forest in the Adirondacks is inaccessible by road and it is unlikely that the sample used by Manion and Griffin (2001) is representative of these sub-alpine forests. Because of the elevational differences and the many edaphic factors that change, trends in growth and mortality of spruce and fir in our plots would not be expected to be similar to those in the Manion and Griffin (2001) study. For instance, inspection of Table 6 shows that the red spruce and balsam fir diameter growth rates used by Manion and Griffin are at least twice those measured in our montane spruce-fir plots. Further, we question whether the growth rates used by Manion and Griffin from private land are suitable values for all of the major northern hardwood species whose relative mortality they determined on Adirondack Park lands. The diameter growth rates of sugar maple, beech and yellow birch growing

in unmanaged stands measured in this study and in the study of Forrester *et al.* (2003) are substantially lower than those used by Manion and Griffin. Growth rates derived from species in managed stands may not be representative of those measured in unmanaged stands as stand management tends to promote the growth of selected species and individuals.

The white pine mortality rate reported here (0.3% y⁻¹) is considerably less than the baseline calculated for the Adirondack Mountains (Manion and Griffin 2001; 3.3% y⁻¹) and similar to those at the Caroline A. Fox Research Forest (Widmann and McWilliams 2003; 0.3% y⁻¹). According to Manion and Griffin (2001), a lower than baseline mortality rate would suggest a changing forest structure or instability leading to higher future mortality rates. It appears at the present time however, that the pines are growing well on the sites they occupy. Our plots show no evidence of any instability in structure or composition over the past 20 years.

Conclusions. Changes in high-elevation Adirondack spruce-fir forests documented in the 1980's continued through the last two decades in the plots we measured. Recruitment and diameter growth of red spruce did not compensate for the loss of larger individuals. Red spruce in the 2–9.9 cm dbh class did not change in the stands above 950 m indicating that the developing overstory will likely be dominated by balsam fir which colonized the gaps. Over the next few decades, the abundance of fir saplings (2–9.9 cm dbh) and fir seedlings now < 1 m tall in these gaps in the upper-elevation plots suggests that this species

will increase dramatically in importance relative to red spruce. However, red spruce abundance in the 2–9.9 cm dbh size range tended to increase in plots in the upper hardwood forest zone. This long-lived, shade tolerant species may have the potential to reestablish its historic importance there if current trends continue.

The live basal area of northern hardwood plots did not increase over the 20-year interval, and considering all species except beech, there was a significant decrease in average live BA. Overall, beech importance is increasing relative to other associated species though large beech may be less important in the future. Predictions of trends in sugar maple and yellow birch importance cannot be confidently predicted.

Pine-dominated plots showed a significant increase in live BA. This was driven by an increase in white pine, though red pine did well in 9 of 10 plots. There were no observable effects of blowdown and mortality rates were low. In the absence of major disturbance, pine-dominated forests in the Adirondacks will likely continue to aggrade toward their maximum biomass potential in the near future.

Direct or proximal causes of mortality in several species should be investigated further as part of any effort to understand why red spruce continued to die at relatively high rates and why the northern hardwood plots was not aggrading. In future work we will compare these changes in vegetation with changes in the chemistry of organic and mineral horizons to determine if there are any parallel changes in forest health and soil chemistry.

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