CHANGES TO THE ADIRONDACK FOREST: IMPLICATIONS OF BEECH BARK DISEASE ON FOREST STRUCTURE AND SEED PRODUCTION

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Abstract

We assessed forest structure and tree seed production over 14 years in an unmanaged, 250-year-old northern hardwood stand in the central Adirondack Mountains. American beech (*Fagus grandifolia* Ehrh.) trees in the stand have been affected by Beech Bark Disease (BBD), caused by a combination of an invasive scale insect and a fungus that weakens and kills the tree. Following the initial spread of BBD in the 1960s, a cascade of changes was predicted to occur, including loss of large beech and lowered production of beechnuts, the primary hard mast species in the central Adirondacks and an important wildlife food. Large beech were indeed lost from the forest. However, contrary to predictions, more beechnuts were produced in the stand from 1994-2003 than 1988-1993. Since 1994, beechnut production was cyclical: an estimated 391,198-638,690 nuts/ha were produced every even year in the hardwood site. Other changes due to BBD have manifested in the stand. Although the very largest beech trees died when BBD originally invaded the stand, larger (>38cm diameter) trees continued to be lost. The number of medium-sized (15-38cm diameter) beech was stable over the 14-year period. While beech sapling abundance increased, these smaller trees showed advanced progression of BBD since 1989. Dominant sugar maples (*Acer saccharum* Marsh.) >38 cm diameter were lost from the stand and were among several northern hardwood species not regenerating. However, species richness and abundance in the shrub layer increased, perhaps as a result of gaps created by fallen canopy trees. Down woody material abundance increased but was of smaller size. BBD has continued to affect stand structure and production of hard mast in both predictable and unexpected ways.

Introduction

The American beech (*Fagus grandifolia* Ehrh.) is an integral component of the northern hardwood forest that covers parts of eastern Canada, the Adirondack Mountains of New York State, and New England. Beechnuts are the primary hard mast and the best source of energy in the region: beechnuts are used by at least 20 species (Martin et al. 1951) and perhaps as many as 40 species of wildlife (McCullough et al. 2000). Beech trees in northeastern North America have been affected by Beech Bark Disease (BBD), caused by a combination of an invasive scale insect, *Cryptococcus fagisuga*, and a native fungus, primarily *Nectria coccinea*, that weakens and kills the tree (Houston et al. 1979). Based on forest research in plots initially measured in 1954, the Advance Front of BBD arrived in the central Adirondack area in 1967, the Killing Front began in 1971 and the Aftermath Forest established in approximately 1974 (Mize and Lea 1978). After BBD initially moved through the region, a cascade of changes was predicted to occur. Costello (1992) estimated that BBD-affected trees >15 cm diameter would have lowered production of beechnuts. We assessed vegetative structure and composition and seed production over 14 years in an unmanaged, 250-year-old stand subjected to BBD to evaluate changes in the central Adirondack forest.

Methods

Fifty circular plots were established in 1988 on Huntington Wildlife Forest (HWF), a 6,000 ha research facility in Newcomb, NY in the central Adirondack Mountains operated by the State University of New York, College of Environmental Science and Forestry (74° 15' N, 44° 00' W). Twenty-five plots were established in an upland deciduous stand that contained primarily northern hardwoods such as sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis* Britton), SAF Type 25 (Society of American Foresters 1980). The other 25 plots were located downslope in a mixed deciduous/coniferous stand (hereafter, the mixed stand) that contained yellow birch, red maple (*A. rubrum* L.), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* [L.] Mill.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.), associated with sugar maple, beech, white pine (*Pinus strobus* L.) or Northern white cedar (*Thuja occidentalis* L.) (SAF Type 30). Soils in the study area were primarily glacial till (Somers 1986).

Vegetation structure and composition were measured in 1989 and remeasured in 2002. We measured live trees ≥11.4 cm (≥4.5 in) diameter at breast height (dbh, taken at 1.3m above the ground) on 0.04 ha circular plots (0.1 ac). We calculated Importance Value (IV) of tree species as:

$$((BA*n) / Total\ BA*N)*100,$$

Table 1.—Number of trees >11.4cm dbh, Basal Area/ha (m^2/ha), importance value, and percent of total Basal Area, Huntington Wildlife Forest, 1989 and 2002

	Number of Trees				Basal Area				Importance Value				Percent Total Basal Area			
	Hardwood		Mixed		Hardwood		Mixed		Hardwood		Mixed		Hardwood		Mixed	
Species	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002	1989	2002
American beech	313	269	50	72	11	9.9	1.1	1.8	21.08	26.83	0.45	1.08	30	35	3	5
Balsam fir	7	5	0	0	0.3	0.3	0.02	0.01	0	0	1	1				
Eastern hemlock	12	6	96	87	2	1.8	10.1	10.8	0.15	0.11	8.28	8.03	6	6	32	34
Paper birch	2	1	0	0	0.2	0.1	0	0	0	0	1	0				
Red maple	1	70	69	0.1	0	4.9	5.3	0	2.92	3.12	0	0	16	16		
Red spruce	13	6	65	62	0.8	0.6	4.4	4.8	0.07	0.04	2.46	2.56	2	2	14	15
Sugar maple	77	48	11	10	18.2	12.4	1.6	1.2	8.53	6.02	0.15	0.1	50	44	5	4
White ash	1	0	0	0	0	0	0	0	0	0						
Yellow birch	35	24	74	59	4.1	3.4	8.8	7.8	0.87	0.82	5.53	3.97	11	12	28	25
Total	452	353	375	365	36.3	28.1	31.4	32	100	100	100	100				

where n = number of individuals of one species and N = number of individuals of all species.

In 1989, only trees >24 cm dbh were measured, while in 2002 we recorded all variables for all live trees ≥11.4 cm dbh. We counted small trees <11.4 cm dbh and measured abundance (sparse, common, or abundant) of saplings and shrubs <1 cm dbh (hereafter called the shrub layer) on a 0.004 ha plot. In the 0.04 ha plot, we counted stumps, and counted snags and logs ≥11.4 cm dbh and ≥1.5 m long, and classified them after Maser *et al.* (1979) as having been dead <1 year (still had fine branches), 1-5 years (no fine branches, decay class 2), or >5 years (decay classes 3-5).

We recorded BBD progression (0 = no disease; 1 = light scale; 2 = moderate to heavy scale; 3 = light *Nectria* fungus, scale may be disappearing at this time; 4 = heavy fungus, bark cracked/pock-marked; 5 = heavy fungus, bark falling off, tree still alive), crown position, and crown condition (percent of dead crown). For the purposes of this study, only the 25 hardwood plots were used to evaluate BBD due to the low proportion of beech in the mixed site.

We established seed traps (13.9 L [5 gal] capacity buckets) in the center of each plot and collected seeds annually from July to November. If a bucket was tipped over due to disturbance by a bear or some other factor, we censored it from the survey for that year. We calculated mean beech and sugar maple seeds per trap and estimated seed production for the hardwood and mixed areas, but could include ranges and standard errors (SE) only for 1996-2003 due to a lack of per-trap data for earlier years.

Results

Basal Area/ha decreased in the hardwood site from 36 to 28 m^2/ha (158 to 122 ft^2/ac) from 1989 to 2002. BA/ha did not change in the mixed plots (31 to 32 m^2/ha or 137 to 139 ft^2/ac) from 1989 to 2002 (Table 1). The decrease in BA/ha in the hardwood site was due primarily to loss of sugar maples. Although there was also a decrease in beech and yellow birch BA/ha, the IV of beech increased over the study while the IV of sugar maple and yellow birch decreased. In the mixed site, beech IV increased and yellow birch IV decreased.

The total number of trees >10 cm dbh decreased markedly on hardwood plots from 452 in 1989 to 353 in 2002, but not on mixed plots (375 to 365 trees; Table 1). Number of beech trees declined in all size classes on hardwood plots except the 20-29.99 cm class which increased, but beech on mixed plots increased in the 10-19.99, 20-29.99, and 30-39.99 cm size classes (Table 2). The number of beech saplings (1-10 cm dbh) on hardwood plots increased from 71 to 115 over the study, yet the proportion of hardwood plots with beech in this size class was roughly the same in 1989 and 2002. Shrub layer richness increased from 3 to 9 species in the hardwood site. However, the proportion of plots with beech in the shrub layer increased from 68 to 80%.

Beech snags tended to be older in 2002: 71% died within the last 5 years in 1989, whereas only 41% died within the past 5 years in 2002 (Table 2). The number of beech snags and stumps did not change, but the number of logs increased six-fold. However, the mean size of logs (± SD) declined from 43 ± 10cm to 26 ± 10cm.

No trees were found without some trace of scale. In the hardwood site in 1989, 56% of beech trees had light scale infestation, 21% were heavily infested with scale, 22% had both scale and *Nectria* fungus, and 2% had severe *Nectria* infestation and damage (n = 63). By 2002, 12% of trees had light scale infestation, 66% had heavy scale and 22% had heavy *Nectria* infestation (n = 269).

Beechnut masting occurred on a 2-year cycle (high in even years, low or none in odd years). Mean annual total number of beechnuts in the hardwood site was 26 ± 7 (range 0-76), and in the mixed site was 6 ± 2 (range 0-28). Mean number of beechnuts per trap ranged from 0 in several years to 4 in the hardwood site and 0-1.4 in the mixed site (Figure 1a). Estimated beechnut production ranged from complete failure to 638,690 nuts/ha in the hardwood site and was 0-223,542 nuts/ha in the mixed site. If we assume that odd years contribute little to the trend over time, in even years beechnut production tended to increase over time in the hardwood (R^2 = 0.55) and mixed (R^2 = 0.73) areas.

Over that same period, mean annual total number of sugar maple seeds in the hardwood site was 199 ± 60 (range 0-772) and was 39 ± 11 in the mixed site (range 0-131). Sugar maple seed production was highest in 1988 with a mean 31 seeds per trap (Figure 1b) and an estimated 4,930,689 seeds/ha in the hardwood site. Sugar maple also tended to mast in even years, though sugar maple produced some seed in most years and was not as strongly cyclical as beech. In even years, sugar maple seed production declined weakly over time in the hardwood site (R^2 = 0.20), but did not trend in the mixed site (R^2 = 0.02).

Table 2.—Comparison of characteristics of 25 hardwood plots, Huntington Wildlife Forest, 1989 and 2002

Characteristic	1989	2002
Number of Beech Trees >10 cm dbh by Size Class (cm)		
10-19.99	199	143
20-29.99	80	103
30-39.99	24	17
40-49.99	7	3
>50	3	3
Total stems >10cm	313	269
Small Beech Trees 1-10 cm dbh		
Number stems	71	115
Percent stems (%)	97	94
Shrub Layer < 1 cm dbh		
Number species	3	9
Percent plots with beech (%)	68	80
Beech Coarse Woody Debris		
Number snags/stumps	62	63
Percent snags dead in last 5 yrs (%)	71	41
Number logs	13	85
Average size logs ± SD (cm)	43 ± 10	26 ± 10

Discussion

Although by the 1980s the largest beech in this 250-year-old hardwood site were dead, from 1989-2002, the site continued to lose larger (>38cm dbh) trees to BBD. Basal area declined in the hardwood site, and beech increased in importance while other hardwoods decreased. Despite four decades of BBD presence on HWF, smaller trees appear to be increasingly affected by BBD. By 2002, even trees as small as 11.4 cm dbh all had signs of the disease. The number of large beech stabilized between 1989 and 2002, while the number of <25 cm trees declined in our study area. Didier (2003), using US Forest Service Forest Inventory and Analysis data, showed that after 1968, larger beech declined tremendously and smaller beech increased in number throughout the Adirondack region. If the trend continues, BBD is likely to weaken or kill increasingly smaller trees in the future.

Other characteristics of the area in our study also changed. While there were many more logs on the ground in 2002 than in 1989, mean log diameter was roughly half as large. This difference in coarse woody debris may affect small mammal and salamander populations that rely on dead woody material for feeding sites and cover (Bowman et al. 2000, Dupuis et al. 1995). Alternatively, the increase in species richness and abundance of shrub layer species may indicate that gaps left by dead canopy trees are enabling some shrubs and

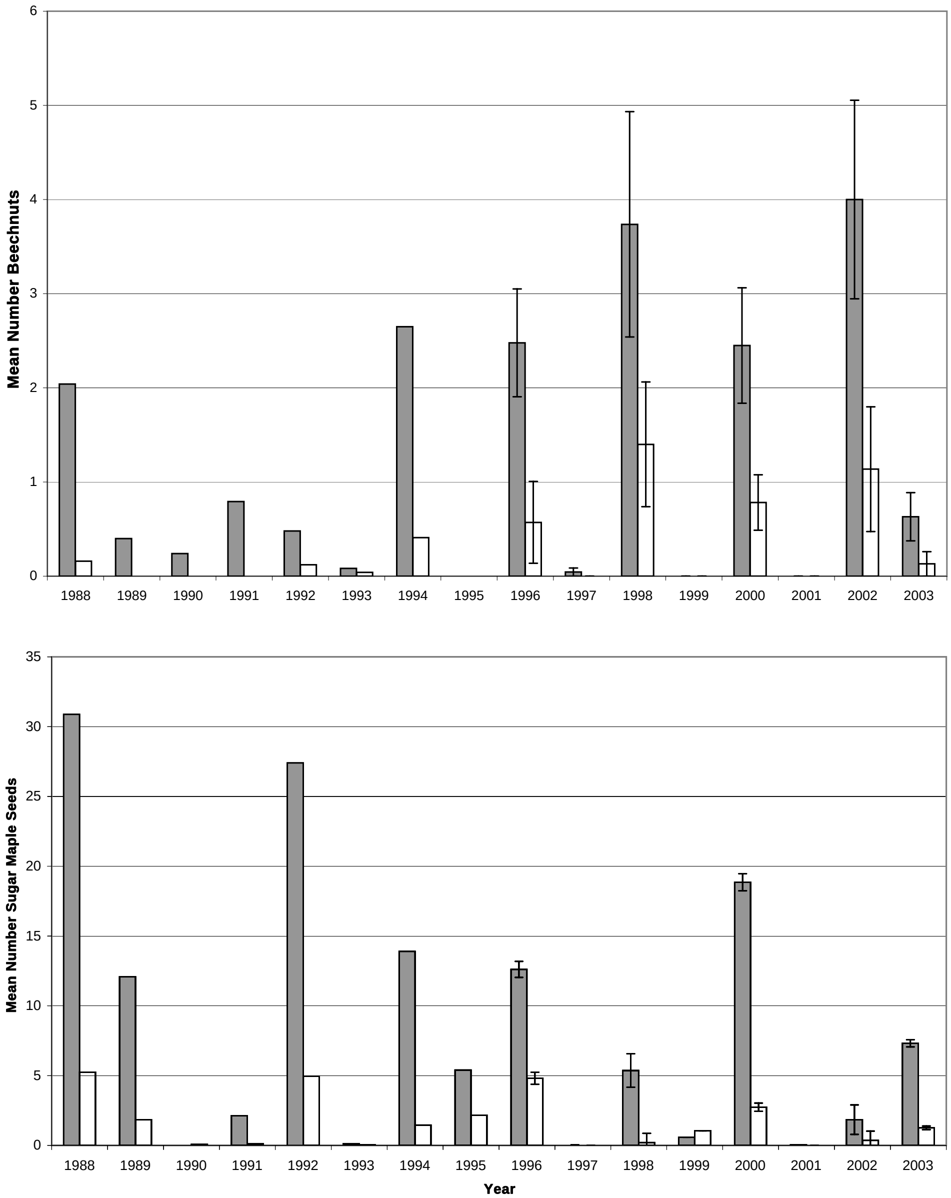

Figure 1.–Mean number of a) American beech and b) sugar maple seeds, in hardwood (gray bars) and mixed hardwood/conifer (white bars) stands, Huntington Wildlife Forest, NY, 1988-2003, with 1 SE in 1996-2003.

saplings to establish. However, sugar maple, yellow birch and white ash are not regenerating, and beech and witch hobble (*Viburnum alnifolium*) are increasing in abundance in the shrub layer. White-tailed deer (*Odocoileus virginianus*) undoubtedly had some impact on regeneration through browsing vegetation at this height (Kelty and Nyland 1981), but deer densities during the 1990s on HWF were approximately 2-4/km^2 (Adirondack Ecological Center, unpublished data) and deer at such low densities should have affected regeneration far less than the higher densities found elsewhere in the northeastern US (Horsley et al. 2003).

Beechnuts in the hardwood site were produced on a two-year cycle beginning in 1994, with an estimated >391,198 seeds/ha in even years and near or total failure in odd years. Qualitative phenological data from HWF indicate that the even-year beechnut cycle also occurred from 1984-1989 (R. Masters, unpublished data). However, without quantitative data it is difficult to compare nut production before and after BBD infestation (i.e., what is termed “good” today may have been “poor” in the 1950’s). It is possible that between-trap variation in seed production (based on individual trees above each trap) may obscure trends over time.

However, our data indicate higher beechnut production since 1994. This is true on both the mixed and hardwood plots, although the trends are more pronounced on the hardwood site where there are more beech. With loss of sugar maple from the canopy and lack of replacement, sugar maple seeds as a food source will continue to decline, which may affect small mammals and other seed predators. In contrast, production of more beechnuts could be beneficial to black bears (*Ursus americanus*), deer, blue jays (*Cyanocitta cristata*), and the myriad other wildlife species dependent on this major source of energy in the northern hardwood forest.

Predictions of declining nut production have not yet proved correct; on the contrary, nut production over the duration of the study appeared to increase over time. One possible explanation for this that is the cohort of beech trees that grew up in the presence of BBD are now large enough for nut production. These younger beech may be viable despite the stress of BBD and may continue to produce nuts, if not further stressed by pathogens or other disturbances. Alternately, perhaps there are so many small to medium size beech trees that the cumulative result of their fruiting results in more nuts/ha than the forest of fifty years ago that contained only a few large beech.

On both managed and unmanaged stands on HWF, beech have been decimated by BBD. In a summary of forest measurements on Continuous Forest Inventory plots located at 400 m intervals throughout HWF, Sage (1996) reported that between 1965 and 1980, nearly 80% of the beech >41 cm dbh died from BBD. After 1980, most large beech were dead or in decline, and mortality of 25-38 cm dbh trees increased. There was limited mortality of trees <25 cm dbh, but crown dieback or yellowing and stem defect occurred on 40% of trees. Our study indicates that the smaller beech have begun to die. Similar results were reported in a separate study on HWF (Forrester et al. 2003). Adirondack beech increased in volume but decreased in density (Didier 2003) since 1968. Indeed, BBD was the primary cause of mortality for beech trees >30 cm dbh in the Adirondacks (Manion and Griffin 2001).

Nearly 40 years after the arrival of BBD, the northern hardwood forest in the central Adirondacks continues to undergo major changes in structure and composition. Our study site may be analogous to other unmanaged, mature forests, including portions of the state-owned Adirondack Forest Preserve. Comparison of this study area to similar sites not yet affected by BBD would explain the contribution of BBD to changing forest conditions. It is important to understand beechnut production both at local and rangewide scales; therefore, we recommend adoption of a simple, regionwide nut production survey. As the Killing Front of BBD continues to move westward, such a survey would illuminate the impact of BBD on wildlife populations.

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