

FORRESTER ET AL: EFFECTS OF BEECH BARK DISEASE ON FOREST BIOMASS

**Effects of beech bark disease on aboveground biomass and species composition in a mature northern hardwood forest, 1985 to 2000<sup>1,4</sup>**

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FORRESTER, J.A., G.G. MCGEE, AND M.J. MITCHELL (SUNY, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210-2778). Effects of beech bark disease on aboveground biomass and species composition in a mature northern hardwood forest, 1985 to 2000.---We examined changes in species composition and aboveground biomass of a maturing, Adirondack northern hardwood forest over a 15-yr period in order to assess the potential effects of beech bark disease on the structure and nutrient cycling processes of the stand. Aboveground biomass of living and dead stems, and annual litter production were estimated in 1985 and 2000 within a 1.96 ha area using total stem inventories ( $\geq 5$  cm dbh). A comparison of species composition and biomass of the forest, as well as mortality and growth rates between the two sampling years are presented. The aboveground biomass of living stems decreased from 209.8 Mg/ha in 1985 to 195.7 Mg/ha in 2000. *Acer rubrum* was the only species to increase in biomass. *Fagus grandifolia* and *Acer saccharum* were the most important species in 1985 and 2000, although *F. grandifolia* increased in importance while *A. saccharum* decreased in importance during this time. Large stems of *F. grandifolia* experienced high mortality rates, but were balanced by ingrowth of smaller stems. In 2000, 58% of *F. grandifolia* exhibited no to minor signs or symptoms of beech bark disease, while 28 and 13% displayed moderate and high signs of infection, respectively. Ninety-nine percent of the uninfected stems were  $< 15$  cm dbh. Although total aboveground biomass decreased during the 15-year period, annual litter production remained constant. Furthermore, the increase in *F. grandifolia* importance value did not substantially alter the lignin content of litter. We conclude that the presence of BBD is hastening the onset of uneven-aged conditions in this second-growth stand but may not lead to large changes in forest nutrient cycling processes based on the lack of change in total lignin content of the leaf litter layer. Currently it appears the canopy will continue to be dominated by shade tolerant species, although the importance of *F. grandifolia* and *A. saccharum* are changing especially with respect to the relative importance of different size classes.

Key words: *Fagus grandifolia*, beech bark disease, aboveground biomass, leaf litter, lignin.

FOOTNOTES:

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<sup>4</sup>Errata: All growth rates presented are **diameter** growth rates ( $\text{mm yr}^{-1}$ ) not **radial** growth rates (as indicated in Table 4 and within the results section). An additional note should appear in the Appendix: Whittaker et al. (1974) suggested use of *Acer spicatum* equation for *A. pensylvanicum*.

Pathogens have been shown to play an integral role in the regulation of forest patterns and processes (Castello et al. 1995). Previous research has documented the effects of chestnut blight (McCormick and Platt 1980), Dutch elm disease (Parker and Leopold 1983), ash yellows (Smallidge et al. 1991), oak wilt (Menges and Loucks 1984), and beech bark disease (Twery and Patterson 1984; Runkle 1990; Krasny and DiGregorio 2001) on tree diameter distributions in eastern deciduous forests. However, changes in biomass accumulation due to introduced pathogens have not been reported. We wished to address specifically whether a pathogen alters the process of biomass accumulation during succession in a northern hardwood forest.

The purpose of our research was to describe changes in the structure, composition and biomass of a mature northern hardwood forest following continued infestation by beech bark disease (BBD; caused by a complex of beech scale, *Cryptococcus fagisuga* Lindinger and fungi *Nectria* spp. on American beech, *Fagus grandifolia* Ehrh.) and to place these results in a local and regional context with respect to changing forest composition. The BBD was introduced in Halifax, N.S. around 1890 and now occurs throughout Canada's Maritime Provinces and the northeastern United States, west to Ohio and south to Virginia (Houston et al. 1979; Houston 1994). The scale and associated fungi spread to the Adirondack region by the 1970s (Houston 1994), and the disease complex entered the "killing front" phase (*sensu* Shigo 1972) in the Adirondacks by the mid-1980s (Krasny and DiGregorio 2001). Adirondack forests are now in the "aftermath" phase of the disease (Shigo 1972, Miller-Weeks 1983). The death or injury of canopy-dominant trees and establishment of root-sprout thickets has markedly altered forest structure.

Huntington Forest's Integrated Forest Study (IFS) site provided a unique opportunity to measure changes in aboveground biomass after impacts of BBD because a total stem inventory had been conducted in 1985, just at the time of the advancing killing front and prior to development of the aftermath conditions. We predicted that mortality of large *F. grandifolia* trees due to BBD would result in dramatically decreased *F. grandifolia* and total aboveground biomass, and effectively advance the stand into the "Transitional" forest development stage (*sensu* Bormann and Likens 1979). Furthermore, we expected that decreased live *F. grandifolia* biomass would alter litter quality in a way that could induce changes in nutrient cycling processes in this stand (Lovett et al. 2000). **Methods.** SITE DESCRIPTION. Huntington Forest (HF; 6066 ha), Essex and Hamilton Counties, is located within the Adirondack State Park of New York and is operated by the State University of New York, College of Environmental Science and Forestry. Various

studies have been conducted within Huntington Forest, including the Integrated Forest Study (IFS; Johnson and Lindberg 1992) and the Adirondack Manipulation and Modeling Project (AMMP; Mitchell et al. 1994). The HF is also a National Atmospheric Deposition Program (NADP) and National Trends Network site (NTN). This study was conducted at the existing IFS site, which has been considered an aggrading, even-aged, approximately 100-year-old northern hardwood stand (Mitchell et al. 2002) that, like many Adirondack stands, established following heavy logging and catastrophic fire in the 1890's and early 1900's.

The study site is within the region described by Braun (1950) as the Adirondack Section of the hemlock-white pine-northern hardwoods region. Here, northern hardwoods are dominated by *Acer saccharum*, *F. grandifolia* and *Betula alleghaniensis*, with an important conifer component comprised of *Picea rubens* and *Tsuga canadensis*. Additional species include *Fraxinus americana*, *Prunus serotina*, *Acer rubrum*, and *Tilia americana* (Heimbürger 1934; Braun 1950; nomenclature follows Gleason and Cronquist 1991). Mean annual temperature is 4.4°C with a dormant season mean of 2.8°C and a growing season mean of 14.3°C. Total annual precipitation averages 101 cm (Shepard et al. 1989). The study site's soil is a shallow, Becket bouldery fine sandy loam that is derived from glacial till, overtops a gneiss bedrock and contains a relatively impervious layer at ~60 cm (Somers 1986).

**DATA COLLECTION AND ANALYSIS.** The species, diameter at breast height (dbh) and location of every living and dead stem  $\geq 5.0$  cm dbh within 1.96 ha (49 contiguous 0.04 hectare plots) were recorded in 1985. Tree height in 14 plots also was recorded to develop biomass equations for dominant species. In 2000, we remeasured the dbh of all stems (living and dead)  $\geq 5.0$  cm dbh. Percent cover (0, trace, 10-25, 25-50, 50-75, >75%) of scale and/or canker visible on the bole was estimated for *Fagus grandifolia* stems. In addition, 25, 100-m<sup>2</sup> understory plots were established to estimate the density of stems >1.4 m tall and <5.0 cm dbh.

Biomass was estimated using equations developed specifically for the site and other published equations (Appendix 1). Separate equations were developed for each tree species using dbh as the dependent variable. Equations used to estimate biomass of dead stems were based on the bole only (components for leaves and branches were excluded). We recognize that there may be some potential error in using the biomass equation for foliage for those *F. grandifolia* with substantial BBD since they may have less foliage than the uninfected trees for which the equation was developed. Tree mortality rates (% / yr) were calculated as exponential decays following Runkle (1990) and Sheil et al. (1995):

$$\text{Mortality rate} = [1 - (S/N_0)^{(1/ny)}] * 100\%$$

where **S** represents the number of survivors, **N<sub>0</sub>** is the original number of stems and **ny** indicates the number of years between samplings. Growth rates were calculated as the differences of the 2000 and 1985 diameters for each tree divided by the number of years between samplings. Paired t-tests were performed to evaluate the difference in living and dead biomass between sampling periods. Biomass means and variances were calculated from values measured on each of the 49 0.04-ha plots. In order to examine whether the statistically significant changes in foliar biomass were potentially significant for biogeochemical processes (e.g., litter decay rates, forest floor nitrification rates), we estimated the total lignin content of leaf litter for 1985 and 2000 using percent lignin

concentrations from Melillo et al. (1982) for the four most important species in the stand.

**Results.** Aboveground living biomass (stems  $\geq 5.0$  cm dbh) decreased 7% from 209.8 Mg ha<sup>-1</sup> (Table 1; p-value = 0.03) in 1985 to 195.7 in 2000. *Acer saccharum* and *Populus grandidentata* exhibited a 10% and 100% decline respectively in living aboveground biomass. Live biomass of *F. grandifolia*, *B. alleghaniensis*, and *A. rubrum* did not change significantly (p>0.05). *Fagus grandifolia* and *A. saccharum* remained the two most abundant and dominant species in 2000, although *F. grandifolia* increased in importance (from 42% to 48% IV) and *A. saccharum* decreased in importance throughout the stand (35% to 29% IV; Table 2). Although mortality of *F. grandifolia* was highest for large stems (Table 3, Fig. 1), the importance of this species increased due to the many new individuals that entered the smaller size classes thereby increasing the species' total density from 352 to 411 stems ha<sup>-1</sup>. *Fagus grandifolia* also experienced faster radial growth rates than the other dominant species during the 15 yr study period (Table 4). This faster radial growth was likely enhanced by the greater contribution of individuals from smaller size classes. *Acer saccharum* density and basal area declined, with the highest mortality in the smaller size classes (5-20 cm dbh; Fig. 1).

Changes in foliar biomass followed the same pattern as the total aboveground biomass (Table 1), with *A. saccharum* and the total foliar biomass decreasing within the stand over the 15 yr period. Due to the substantially higher lignin content of *F. grandifolia* litter (24.1%) versus the other dominant species (*A. saccharum*, 10.1%; *A. rubrum* 10.1%, *Betula*, 14.5%; Melillo et al. 1982) and the lack of change in *F. grandifolia* foliar biomass, the average (weighted by mass of component species) lignin content of the hardwood leaf litter at the HF remained relatively constant (19.0% in 1985 versus 18.3% in 2000).

The aboveground biomass of dead stems more than doubled during the study period interval (18.3 Mg ha<sup>-1</sup> in 1985 to 40.6 Mg ha<sup>-1</sup> in 2000; Table 1). *Fagus grandifolia* and *A. saccharum* together represented the largest portion of the dead biomass (63% in 1985 and 73% in 2000). Biomass of dead *A. saccharum* more than tripled and *F. grandifolia* almost doubled from 1985 to 2000 (p-values of 0.0016 and 0.0346, respectively).

Fifty-eight percent of living *F. grandifolia* exhibited no (21%) to minor (<10% of scale or canker; 37%) signs of BBD, while 28% and 13% displayed moderate (>10% but <50% of scale or canker) to high (>50% of either scale or canker) symptoms of disease respectively in 2000. Ninety-nine percent of the uninfected stems were <15 cm dbh.

The density of stems <5.0 cm dbh in 2000 was 3952 stems ha<sup>-1</sup>, the majority of which were *F. grandifolia* and *Viburnum alnifolium* (3124 and 708 stems ha<sup>-1</sup>, respectively; Table 5). *Acer saccharum* stems <5.0 cm dbh were absent from the study plots.

**Discussion.** We predicted that BBD would cause elevated mortality rates and a subsequent decline in biomass of *F. grandifolia* in this maturing, even-aged stand. For the overall stand, we believed that BBD might inhibit continued biomass accumulation associated with the aggrading phase of Bormann and Likens' (1979) biomass accumulation model, and hasten the onset of the transition phase of stand development.

expected *F. grandifolia* mortality to be highest within the larger size classes because larger stems are more susceptible to the disease (Houston 1975). As predicted, mortality was highest among the larger diameter stems, but due to recruitment of many smaller

diameter stems, the biomass of *F. grandifolia* and of the stand decreased only minimally. Alternatively, compositional shifts from early to late-successional species and an unexplained decline in *A. saccharum* contributed more to biomass decline than the effect of the pathogen.

Due to competitive trade-offs between *F. grandifolia* and *A. saccharum* noted from previous studies of the codominants (Canham 1988; Poulson and Platt 1989), we expected to see the importance of *A. saccharum* increase within the stand. Typically, *F. grandifolia* and *A. saccharum* are the most shade-tolerant species in the understory and compete to fill canopy gaps created by the death of a stem. Although *A. saccharum* has faster growth rates in canopy openings (Poulson and Platt 1989), it has shorter longevity than *F. grandifolia* beneath the closed canopy, so tends to be more successful filling canopy gaps under high frequencies of gap formation. We felt BBD would create such a condition within the IFS stand, however the high mortality rate of *A. saccharum* stems <20 cm dbh has virtually eliminated the competition for *F. grandifolia*. The mortality rate of *A. saccharum* in this stand (2.1% for stems  $\geq 10$  cm dbh) is slightly higher than the mean rate reported from stands in the “Adirondack New England Mixed Forest North American Maple Project” plots (1.1%; Allen et al. 1999), but lower than rates observed in PA (3.5%; Horsley et al. 2000) and predicted for the Adirondack Park (3.0%; Manion and Griffin 2001). Horsley et al. (2000) found that “sugar maple decline” was associated with an interaction between low levels of Mg and stress caused by defoliation. Although no marked changes in the Mg solute concentrations in soil solution have been found (Mitchell et al., 1992; Mitchell et al., unpublished data), further investigation into the changes in soil chemistry at this site would be interesting and may provide information on the role of acidic deposition in a regional decline of *A. saccharum*.

The change in biomass measured over the 15 yr period of this study is interesting when placed in the context of Bormann and Likens’ (1979) biomass accumulation model for northern hardwoods. That model suggested the occurrence of a transition stage (beginning at approximately 180-200 years) in which live biomass reaches a maximum and then, as canopy dominant trees begin to senesce and die, begins to decline to a lower, constant level in the steady-state (old growth) phase. The Huntington Forest IFS site may be entering the transition phase earlier than was hypothesized by Bormann and Likens. If the IFS site was entering the transition phase during the period of this study, then the observed live biomass should be greater than forests in the steady-state phase. This was not the case. Live biomass estimates from this study were lower than those reported from some studies of other northern hardwood old-growth forests, but similar to those reported for Hubbard Brook, NH (Table 6). Therefore, although gaps are clearly being created by canopy-dominant beech trees at this site, biomass accumulation does not appear to have reached its expected maximum. Consequently, while BBD may be hastening the creation of gaps by canopy-dominant trees at this site, it may be simultaneously delaying the onset of the hypothesized peak in biomass accumulation that would mark the onset of the transition phase.

Alternatively, BBD may result in biomass accumulation patterns in which the hypothesized transition phase is never manifested. Gap creation appears to have begun in this stand prior to the expected peak in biomass accumulation. Therefore, since an uneven-aged stand structure has already been established at this site, if the stand recovers from the BBD-induced biomass decline and once again begins to increase biomass in the

future, it is likely that biomass will increase asymptotically to the steady-state rather than passing through a transition state. Several other forest types have been shown to demonstrate logistic-asymptotic biomass accumulation curves that lack the maximum associated with a transition stage followed by slight decrease to steady state conditions (Peet 1981).

Because of the presence of BBD in northern hardwood forests it may be impossible to ever adequately test the Bormann and Likens biomass accumulation model. To date, several biomass estimates have been made for aggrading stands on the rising limb of the biomass curve, as well as for others in the steady-state developmental stage (Table 6). However, no studies have reported live biomass for stands in eastern North America that established following catastrophic disturbance and have developed undisturbed for ~200 years. Since few, if any, northern hardwood forests are expected to remain unaffected by BBD, the developmental trends of current aggrading stands will be complicated by BBD effects.

Although BBD has affected the structural characteristics of the forest, the lack of change in the estimated lignin content of the IFS litter layer indicates that the disease may not greatly alter nutrient dynamics in this stand. Leaf litter lignin content is believed to be an important regulator of litter decomposition rates and forest floor nitrification rates (Lovett et al. 2000). If BBD had induced substantial changes in litter quality (e.g., through an increase in sugar maple litter and accompanying decrease in lignin content) then possible changes in biogeochemical pathways might be expected. Future research should investigate how biogeochemical pathways may be altered by BBD.

Our observation is that BBD has hastened the onset of uneven-aged conditions in this second-growth stand. Currently it appears the canopy will continue to be dominated by shade tolerant species, although the importance of *F. grandifolia* is increasing relative to *A. saccharum*. The slow death of canopy trees and lack of soil disturbance caused by BBD does not appear to offer recruitment opportunities to shade intolerant and mid-tolerant species. In order to clarify possible changes in nutrient cycling processes due to BBD, and problematic aspects of forest stand development due to the lack of study sites to complete critical segments of eastern deciduous forest chronosequences, it is vital that long-term studies of sites such as the Huntington Forest IFS stand continue.

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Table 1. Percent change from 1985 to 2000 in (a) total aboveground living (foliar+branch+bole wood+bole bark) and dead (bole wood+bole bark) biomass ( $\text{Mg ha}^{-1}$ ) for stems  $\geq 5.0$  cm dbh and (b) foliar biomass at the Huntington Forest IFS site. P-values indicate the degree of difference in biomass between the time periods.

a. Total aboveground									
Species	Living				Dead				
	1985	2000	% Change	p-value	1985	2000	% Change	p-value	
<i>Acer saccharum</i>	94	85	-10	0.04	5	16	+235	0.001	
<i>Fagus grandifolia</i>	59	58	-1	0.82	7	13	+99	0.03	
<i>Acer rubrum</i>	25	27	+7	0.27	2	3	+59	0.40	
<i>Betula alleghaniensis</i>	24	23	-5	0.43	4	4	+14	0.66	
<i>Populus grandidentata</i>	4	0	-100	0.05	1	4	+270	0.07	
TOTAL <sup>a</sup>	210	196	-7	0.03	18	41	+122	<0.0001	

b. Foliar				
Species	1985	2000	% Change	p-value
<i>Acer saccharum</i>	1.4	1.3	-11	0.02
<i>Fagus grandifolia</i>	1.2	1.2	+1	0.78
<i>Acer rubrum</i>	0.3	0.4	+6	0.42
<i>Betula alleghaniensis</i>	0.8	0.7	-8	0.21
TOTAL	4.1	3.9	-6	0.04

<sup>a</sup>Includes species that contributed  $<2.0 \text{ Mg ha}^{-1}$  (*Populus tremuloides*, *Prunus serotina*, *Abies balsamea*, *Picea rubens*, *Acer pensylvanicum*, *Tsuga canadensis*).

Table 2. Species importance values (IV=[rel den + rel ba]/2), density and basal area of living stems  $\geq 5.0$  cm dbh in 1985 and 2000 at the Huntington Forest IFS site.

Species	IV (%)		Density (stems ha <sup>-1</sup> )		Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	
	1985	2000	1985	2000	1985	2000
<i>Fagus grandifolia</i>	42	48	352	411	9	9
<i>Acer saccharum</i>	35	30	193	132	12	10
<i>Betula alleghaniensis</i>	11	10	50	39	4	4
<i>Acer rubrum</i>	10	10	40	32	4	4
<i>Populus grandidentata</i>	1	0	3	0	1	0
<i>Picea rubens</i>	1	1	5	10	<1	<1
<i>Prunus serotina</i>	<1	1	2	2	<1	<1
<i>Populus tremuloides</i>	<1	<1	1	1	<1	<1
<u><i>Abies balsamea</i></u>	<1	<1	2	2	<1	<1
<i>Acer pensylvanicum</i>	<1	<1	2	2	0	0
<i>Tsuga canadensis</i>	<1	<1	1	1	0	0
<i>Prunus pensylvanica</i>	0	<1	0	2	0	0
TOTAL			649	633	29	27

Table 3. Tree mortality rates ( % / year ) by species and size class at the Huntington Forest IFS site.

SIZE CLASS (cm dbh)	ALL SPECIES	<i>Fagus</i> <i>grandifolia</i>	<i>Acer</i> <i>saccharum</i>	<i>Betula</i> <i>alleghaniensis</i>	<i>Acer rubrum</i>
ALL stems	1.7	1.1	2.7	1.7	1.7
5-10	1.5	0.6	7.0	- <sup>a</sup>	100
10-15	1.3	0.4	4.1	1.2	7.1
15-20	1.3	0.6	2.7	4.5	0
20-25	2.0	2.5	1.1	1.0	3.0
25-30	2.0	2.4	2.0	1.6	1.9
30-35	2.3	4.5	1.2	1.9	2.5
35-40	1.6	3.8	1.5	1.6	0
40-45	1.4	2.7	1.5	0.9	0.5
45-50	2.0	7.1	1.0	2.2	0
50-55	1.5	7.1	0	-	0
55-60	1.2	-	0	-	-
>60	4.5	-	5.9	-	-

<sup>a</sup> Hyphen indicates <1 stem present in size class.

Table 4. Radial growth rates (mm yr<sup>-1</sup>) of species from 1985 to 2000 in the Huntington Forest IFS site.

Species	Number of trees	Growth	
		(mm yr <sup>-1</sup> )	Standard error
<i>Acer rubrum</i>	58	2.4	0.20
<i>Picea rubens</i>	6	2.1	0.92
<i>Populus tremuloides</i>	1	2.1	-
<i>Tsuga canadensis</i>	1	1.9	-
<u>Fagus grandifolia</u>	591	1.9	0.05
<i>Betula alleghaniensis</i>	76	1.8	0.11
<i>Acer pensylvanicum</i>	2	1.7	0.13
<i>Prunus serotina</i>	3	1.5	0.19
<i>Acer saccharum</i>	256	1.5	0.07
<i>Abies balsamea</i>	3	1.3	0.73

Table 5. Composition of stems  $\geq 1.4$  and  $< 5.0$  cm dbh in the Huntington Forest IFS site in 2000.

Species	Density (stems ha <sup>-1</sup> )
<u>Fagus grandifolia</u>	3416
<i>Viburnum alnifolium</i>	1172
<i>Fraxinus americana</i>	84
<i>Picea rubens</i>	48
<i>Acer pensylvanicum</i>	8
<i>Acer rubrum</i>	4
<i>Acer saccharum</i>	0
ALL SPECIES	4732

Table 6. Comparison of basal area and aboveground biomass reported from some North American northern hardwood forests. An asterisk denotes studies that reported basal area and biomass.

Forest Age and Location	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Biomass (Mg/ha)	Reference
<b>Mature</b>			
New York	25-34	196-236	McGee et al. 1999; Yorks 2001*; current study*
New Hampshire	26	198	Likens et al. 1994*
Michigan	31-47	230-267	Rutkowski and Stottlemeyer 1993*; Fisk et al. 2002*
<b>Old-growth</b>			
Massachusetts	25-38	-	Dunwiddie and Leverett 1996
Northern Ontario	25-29	179 & 209	Morrison 1990*
Michigan	27-52	262- 325	Mroz et al. 1985*; Frelich and Lorimer 1991; Fisk et al. 2002*
New York	28-40	-	McGee et al. 1999
New Hampshire	32-35	209-225	Martin and Bailey 1999*

Appendix 1. Biomass equations used to predict aboveground biomass in 1985 and 2000 in Huntington Forest IFS site. The equation from Briggs et al. 1989 and Briggs, unpublished is  $y = b_1 + b_2 D^2$ , where  $y$  = dry weight (kg) and  $D$  = dbh (cm); Young et al. 1980 used  $y = e^{(b_1 + b_2 \ln D)}$  where  $y$  = dry weight (lb) and  $D$  = dbh (in); Whittaker et al. 1974 used  $\log y = b_1 + b_2 \log D$ , where  $y$  = dry weight (g) and  $D$  = dbh (cm).

<i>Species</i>	dbh	Component	$b_1$	$b_2$	Reference	
<i>Fagus grandifolia</i>	≥10	Foliage	0.43	0.00971	Briggs et al. 1989	
		Branch	-5.81	0.14948		
		Bole wood	-17.15	0.40381		
		Bole bark	-0.06	0.02584		
	<10	Foliage	0.06	0.1094	Briggs, unpublished	
		Branch	0.09	0.6585		
		Bole wood	-1.37	2.4277		
		Bole bark	-0.20	0.3119		
<i>Acer rubrum</i>	≥10	Foliage	-0.11	0.00709	Briggs et al. 1989	
		Branch	-2.62	0.09665		
		Bole wood	-48.29	0.40732		
		Bole bark	-3.53	0.05941		
	<10	Foliage	-0.03	0.0965	Briggs, unpublished	
		Branch	0.79	0.9438		
		Bole wood	-0.45	2.1621		
		Bole bark	0.00	0.5218		
<i>Acer saccharum</i>	≥10	Foliage	-0.24	0.009957	Briggs, unpublished	
		Branch	46.85	$b_2=4.992$ $b_3=0.235355$		$y = b_1 + b_2 D + b_3 D^2$
		Bole wood	-33.74	0.476107		
		Bole bark	-3.64	0.054305		
	<10	Foliage	0.00	0.0669	Briggs, unpublished	
		Branch	0.20	2.1313		



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	Bole wood	-0.66	1.1922	
	Bole bark	-0.04	0.1471	
<i>Betula alleghaniensis</i>	Foliage	-1.5337150	1.978348	Young et al. 1980
	Branch	-0.8257923	2.379461	
	Bole	0.75123020	2.341190	
<i>Populus</i> sp.	Foliage	-1.7819340	2.076605	
	Branch	-1.659575	2.524430	
	Bole	0.1729552	2.670926	
<i>Tsuga canadensis</i>	Foliage	-0.6185584	2.030049	
	Branch	-1.775095	2.703338	
	Bole	0.2607714	2.3666161	
<i>Picea rubens</i> and <i>Prunus serotina</i> <sup>a</sup>	Foliage	-0.7980554	2.138061	
	Branch	-1.351318	2.338385	
	Bole	0.3960433	2.374645	
<i>Prunus pensylvanica</i>	Foliage	-1.20785700	2.037966	
	Branch	-0.62594580	1.919658	
	Bole	0.57936450	2.298775	
<i>Abies balsamea</i>	Foliage	-1.64523300	2.450614	
	Branch	-2.20596000	2.460493	
	Bole	0.34870420	2.411658	
<i>Acer pensylvanicum</i>	Foliage	1.0687	1.7983	Whittaker et al. 1974
	Branch	0.8976	3.1640	
	Bole wood	1.8772	2.3364	
	Bole bark	1.2469	2.1133	

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<sup>a</sup>Note: Monteith (1979) suggested use of *Picea* equation for *Prunus serotina*.

## Figure Captions

Fig. 1. Tree (>5.0 cm dbh) mortality rates by species and size class between 1985 and 2000 at the Huntington Forest, IFS site.

Fig. 2. Diameter distribution of living *Fagus grandifolia* in 1985 and 2000 at the Huntington Forest IFS site.

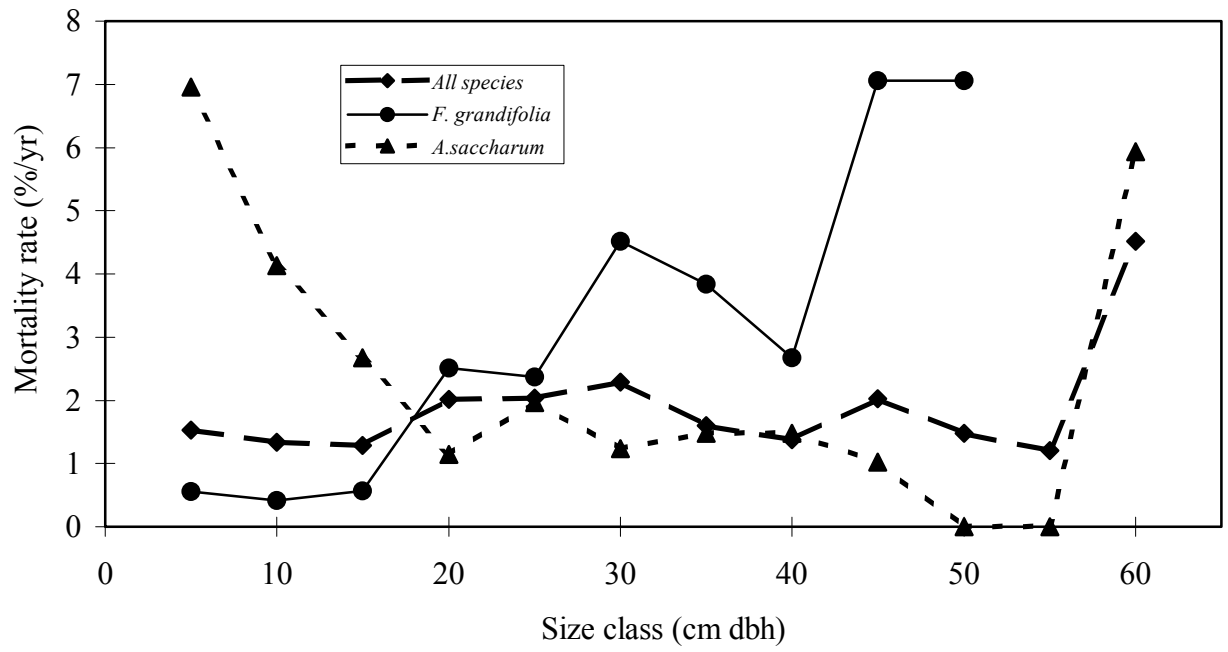


Fig. 1.

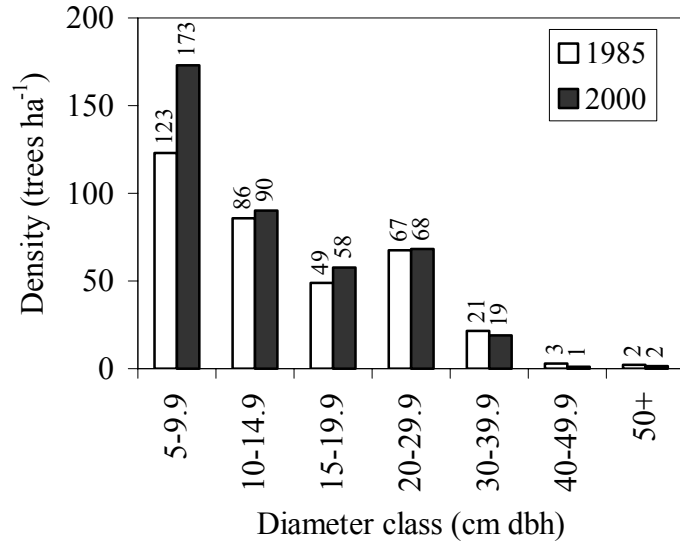


Fig. 2.