Forty years of forest measurements support steadily increasing aboveground biomass in a maturing, *Quercus*-dominant northeastern forest

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Forty years of forest measurements support steadily increasing aboveground biomass in a maturing, *Quercus*-dominant northeastern forest[1]

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Eisen, K. (Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853) and A. Barker Plotkin (Harvard Forest, Harvard University, 324 N. Main St. Petersham, MA 01366). Forty years of forest measurements support steadily increasing aboveground biomass in a maturing, *Quercus*-dominant northeastern forest. J. Torrey Bot. Soc. 142(2): 97–112. 2015.—Repeated measurements of permanent plots in northeastern U.S. forests provide an opportunity to assess how stand-level changes impact carbon storage in aboveground biomass over time. We used 42 years of census data for >6000 individual trees in a 2.9- ha permanent plot at the Harvard Forest (Petersham, MA, USA) to determine how changes in stand age, structure, and species composition affect carbon storage in aboveground biomass in a *Quercus-Acer* forest. From 1969 to 2011, the biomass of live trees increased linearly ($R^2 = 0.99$, $p = 0.0002$), from 150 Mg ha^{-1} to 268 Mg ha^{-1}, confirming that this ca. 110-year-old stand is still in the aggradation phase of stand development. Over time, a higher proportion of the stand's biomass occurs in large trees. *Quercus rubra* L. (red oak) accounts for >80 percent of the increase in aboveground biomass due to the rapid growth of dominant stems and low canopy mortality rates. Changes in the biomass of live *Acer rubrum* L. (red maple) stagnated after 1991, in contrast with region-wide increases, while the proportion of total biomass in subordinate *Betula alleghaniensis* Britton (yellow birch), *Betula lenta* L. (black birch), *Fagus grandifolia* Ehrh. (American beech), and *Castanea dentata* (Marshall) Borkh. (American chestnut) increased. In the absence of major canopy disturbance we predict that *Q. rubra* dominance will continue to increase and the stand will steadily accrue carbon for the next century.

Key words: *Acer rubrum*, forest productivity, forest succession, *Quercus rubra*.

The majority of forested ecosystems in the northeastern U.S. are second-growth stands that established following the abandonment of agricultural fields in the mid-to-late 1800s. Over the past half-century, repeated measurements of these forests have documented demographic and ecological changes resulting from succession (Lorimer 1984, Abrams 1998, McEwan et al. 2011), disturbance (Foster 1988, Boose et al. 2001), and land use changes (Foster et al. 1998, Hall et al. 2002).

These permanent plot studies currently provide an opportunity to assess how change in northeastern forests impacts the globally significant carbon sinks documented in the region (Pacala et al. 2001, Goodale et al. 2002). While studies have documented that eastern U.S. forests contain the majority of carbon stored in U.S. forests (McKinley et al. 2011), the processes that generate these sinks are not well understood (Liu et al. 2006). Ecosystem-level measurements of forest-atmosphere exchange (e.g. eddy covariance) can detect changes in net ecosystem exchange on annual-to-decadal time-scales (Barford et al. 2001, Urbanski et al. 2007), but long-term, stand-specific data are needed to relate atmospheric measurements to ecological changes in forests. Furthermore, the capacity for storage may change over decades to centuries with stand-level changes in age, species composition, and structure (Schuster et al. 2008), and these long-term processes are not well represented in current models (Urbanski et al. 2007). Repeated measurements of secondary-growth northeastern forests enable us to investigate how changes in stand dynamics

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may impact carbon storage in trees in these ecosystems (Keeton et al. 2011).

Aboveground biomass in living trees comprises a significant pool of carbon in forests (Fahey et al. 2010), but gains in biomass are expected to change with forest age. Bormann and Likens (1979) proposed that the period of biomass aggradation following a stand-replacing disturbance lasts for approximately 170 years in northeastern U.S. forests, followed by a modest decline to a steady state in which biomass gains would approximately equal losses. Changes in stand demography, including growth rates of older or taller trees (Ryan et al. 1997, Mencuccini et al. 2007), mortality patterns (Xu et al. 2012), and recruitment rates may explain this pattern. In the eastern U.S., recent studies detected linear increases in aboveground biomass in forests 40–125 years old, supporting the predictions of Bormann and Likens (Liu et al. 2006, Urbanski et al. 2007, Fahey et al. 2013; see Battles et al. 2013), although there are still relatively few tests of this hypothesis with permanent plot data.

Because species have differential rates of and capacities for carbon sequestration, changes in species composition as a stand develops can also affect carbon storage in aboveground biomass. One major historical change in eastern US forests is an increase in *Acer rubrum* (red maple; Lorimer 1984, Abrams 1998, McEwan et al. 2011, Thompson et al. 2013). Although relatively uncommon in eastern US forests prior to European colonization, *A. rubrum* increased substantially in northeastern US *Quercus* and *Pinus* dominated forests during the twentieth century (Abrams 1998). Oliver (1975) showed that *Q. rubra* typically attains canopy dominance in stratified stands mixed with *A. rubrum*; however, Lorimer (1984) predicted that *A. rubrum* would become more important in these mixed stands over time. Carbon acquisition by *A. rubrum* can be relatively lower and more sensitive to environmental variation than carbon acquisition by *Quercus* sp. (Turnbull et al. 2001). These physiological differences between *A. rubrum* and *Quercus* sp. suggest that carbon sequestration in aboveground living biomass in secondary forests could decrease as *Acer* increases.

Permanent plot studies allow us to test predictions about how demographic changes in northeastern U.S. forests over time may impact forest productivity and carbon sequestration in aboveground biomass. This study uses data from the Lyford Grid, a 2.9 ha permanent plot in a maturing *Q. rubra-A. rubrum* forest at the Harvard Forest (Petersham, MA, U.S.), to explore these relationships in a second- growth forest. The Lyford Grid dataset includes periodic measurements of more than 6,000 individual living and dead trees over 42 years, capturing forest development from approximately 70 to 110 years after initiation. This site was part of Lorimer's (1984) study of the *A. rubrum* understory in *Q. rubra* forests, in which he predicted increasing *A. rubrum* importance over time. Because the site is representative of the most common forest type in central Massachusetts, it can be used to test two major predictions concerning forest biomass and succession in the region: (1) We expect steady aboveground living biomass accumulation in the Lyford Grid from stand ages 70–110, based on the predictions of Bormann and Likens (1979) and the linear trends in aboveground biomass documented at other New England forests of similar ages (e.g., Urbanski et al. 2007, Fahey et al. 2013), and (2) We expect *Q. rubra* to retain canopy dominance over the 40-year study period, but expect *Acer rubrum* to exhibit relatively greater gains in biomass over time, as predicted by Lorimer (1984).

Materials and Methods. THE LYFORD GRID: SITE DESCRIPTION. The Lyford Grid a is 2.9 ha forest plot dominated by *Q. rubra-A. rubrum* in the Prospect Hill tract at the Harvard Forest (Latitude: +42.53; Longitude: −72.18; Fig. 1). The soil type is a thin glacial till, and the bedrock is gneiss, schist, and granite (Eschman 1966). Soil drainage varies across the site and ranges from poorly to excessively well-drained soils. Elevation rises gradually (from 344 to 356 m) from the southwest portion of the plot to the northeast corner. The climate is cool temperate. Based on data from 1961–1990, July mean temperature is 20.1 °C, January mean temperature is −6.8 °C, and 1066 mm average annual precipitation is distributed evenly throughout the year (Greenland and Kittel 1997).

The Lyford Grid's land-use history includes an early period of typically complex ownership and activity followed by few changes over the last 70 years. The forest was cleared and used as pasture during European settlement, then grew back to *Pinus strobus* Douglas ex D. Don (white pine) after 1840. The old-field *P. strobus*

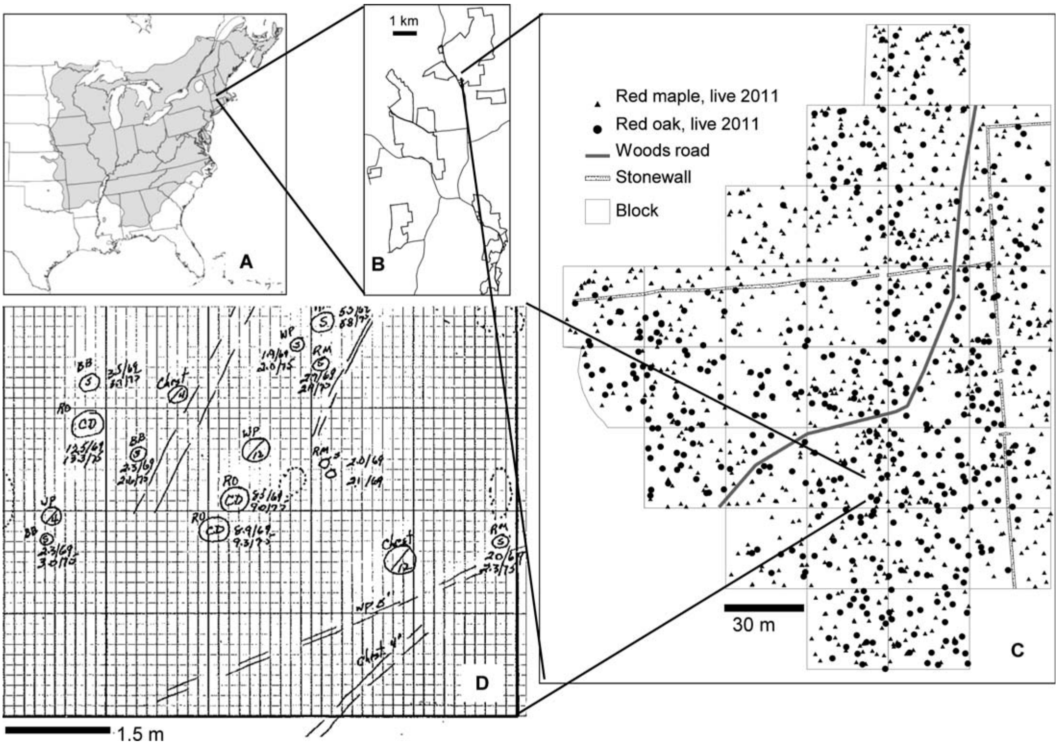

FIG. 1. (A) Range of *Q. rubra* in North America (source is http://esp.cr.usgs.gov/data/little/, Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr.). (B) Harvard Forest tracts in Petersham, MA. (C) The 2.9 ha Lyford Grid, showing the subset of censused trees that were live read oak (*Q. rubra*) and red maple (*A. rubrum*) stems in 2011; Sample portion (approximately 50m^2) of one of Lyford's original large-scale maps, (D) showing live tress (open circles), dead trees (circles with a slash), downed stems, and boulders (dotted ovals).

was cut intensively in the late 1890's and the present even-aged, mixed-hardwood forest initiated around 1900. The Harvard Forest conducted moderate forest improvement and thinning activities in the early 1900s. In 1938, a major hurricane severely damaged 10% of the stand, followed by limited salvage harvesting. Since then, there has been little management activity in the study area. Pest and pathogen disturbances include the chestnut blight (*Cryphonectria parasitica*) in the 1910s, which reduced overstory chestnut to small sprouts, and a major gypsy moth (*Lymantria dispar*) outbreak in 1981 (MassGIS 1997, Pederson 2005), which preferentially defoliated *Quercus* and *Betula* species. Based on tree cores collected in 2002–2003 (Pederson 2005), the approximate stand age was 110 years in 2011.

PERMANENT PLOT ESTABLISHMENT AND CENSUSES. Walter Lyford established the study area in the 1960s. He mapped and censused all trees greater than 5 cm diameter at breast height (DBH; 1.37 m) in 1969. The plot was remeasured in 1975 and again over the period from 1987–1992. For the purposes of this study, this group of measurements will be referred to as the 1991 census (6 blocks were censused in 1987, 13 in 1991, and 13 in 1992). Additional remeasurements were undertaken in 2001, and in 2011. At each census, the species, DBH, and canopy class (scored as dominant, codominant, intermediate, and suppressed) were recorded for all living stems. Canopy classes were defined as follows: dominant trees received full sunlight from the top and sides; codominant trees received full sunlight from the top and partial sunlight from the sides; intermediate trees received partial sunlight from the top and sides; suppressed trees received partial sunlight from the top (Smith et al. 1997). In some cases, particularly with trees censused in 1987, canopy class assignments are missing; these were inferred based on canopy classes for that tree in the prior and subsequent census. For fewer than 15 trees per census, we were unable to infer a canopy class. The locations of trees that had grown to be greater than 5 cm DBH since the last measurement were mapped and added to the dataset. Two methods were used to assign coordinates to stems that had been recruited into the 5 cm and above diameter class. For stems located within approximately 1.5 m of a known point (either another tree or the edge of a block), coordinates were interpolated in the field. When this method was not feasible, the INTERPNT method of triangulation (Boose et al. 1998) was used.

Dead stems were tracked over the study and trees previously observed as either living or dead that could no longer be located were scored as "gone." Lyford also mapped soil drainage class based on detailed examinations of the soil. The original large-scale map data (1:60) were converted to a GIS database after the 1991 census. All raw data are available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data-archive), dataset HF032 (Foster et al. 1999).

DATA ANALYSIS. The biomass of living stems was calculated using previously published allometric equations that estimate biomass from DBH (Appendix). When multiple published equations were available for a species, the equation developed at the site closest to the Harvard Forest was selected. When multiple equations developed in New England were available, the equation that had the largest sample size and a range of diameters that best matched the Lyford Grid dataset was used. An equation developed to model the biomass of hardwoods was used for *Castanea dentata* (American chestnut) and for species designated as "unknown" (5 stems from 1969–1991).

To investigate temporal trends and relationships among stand characteristics over time, data were analysed in R version 2.15.1 (R Core Team 2012). A linear model was fit to the aboveground biomass of all living trees over time. The residuals from the linear model were randomly distributed. The contribution of a species to total aboveground biomass in living stems was calculated as the biomass of the species divided by the total biomass. We split the trees into two categories, to examine differing trends in growth and species composition within the vertical structure of the stand. We included the dominant and codominant canopy classes as "canopy" because both receive direct sunlight, and the intermediate and suppressed classes as "subordinate" because they receive little or no direct sunlight. To analyze changes in the stand structure over time, we compared diameter distributions from 1969 and 2011 using a two-sample two-sided Kolmogorov-Smirnov test. The ks.boot function in the Matching package (Sekhon 2011) was used because the function executes a bootstrapped version of the univariate Kolmogorov-Smirnov test that corrects for distributions that are not perfectly continuous.

Annual average mortality rates were calculated as: $M = 1-(S/N_0)^{(1/y)}$, where S is the number of survivors, N_0 is the original number of stems, and y is the number of years between samples (Runkle 2000). Annual average recruitment rates were calculated using the same formula, except that S was the number of living stems at the start of a period (N_0) plus the number of recruits from that period.

Results. OVERALL TRENDS IN BIOMASS AND STAND STRUCTURE. From 1969 to 2011, the aboveground biomass of living trees increased linearly (Fig. 2A). Although stand density decreased from 1284 stems ha^{-1} in 1969 to 836 stems ha^{-1} in 2011 and resulted in a continual input of relatively small-diameter dead wood, the growth of living trees comprised the largest component of the overall increase in biomass (Fig. 2B). Most of the biomass increase was in the canopy, which added 2.6 ± 0.5 Mg ha^{-1} yr^{-1} and increased from 111.9 Mg ha^{-1} in 1969 to 223.0 Mg ha^{-1} in 2011 ($R^2 = 0.90$, $p = 0.01$; Fig. 3A; Table 1). Biomass in the subordinate level increased slightly, from 36.2 Mg ha^{-1} in 1969 to 45.4 Mg ha^{-1} in 2011 ($R^2 = 0.10$, $p = 0.60$; Fig. 3A; Table 1).

The diameter distributions of live trees in the Lyford Grid in 1969 and 2011 indicate that biomass became concentrated in larger stems over this period (Fig. 4A). These distributions were significantly different (two-sided two-sample Kolmogorov-Smirnov test; $D = 0.19$, $p < 2.2 \times 10^{-16}$). In 1969, stems less than 40 cm DBH comprised 80 percent of all biomass in living stems; in 2011, the percentage of biomass in this size class was 40 percent.

Average annual recruitment rates increased from 0.3 percent from 1969 to 1975 to 1.3 percent from 2001 to 2011 (Table 2). However, biomass in recruits decreased overall over the study period, from 2.66 Mg ha^{-1} (1969–1975) to 1.61 Mg ha^{-1} (2001–2011). Average

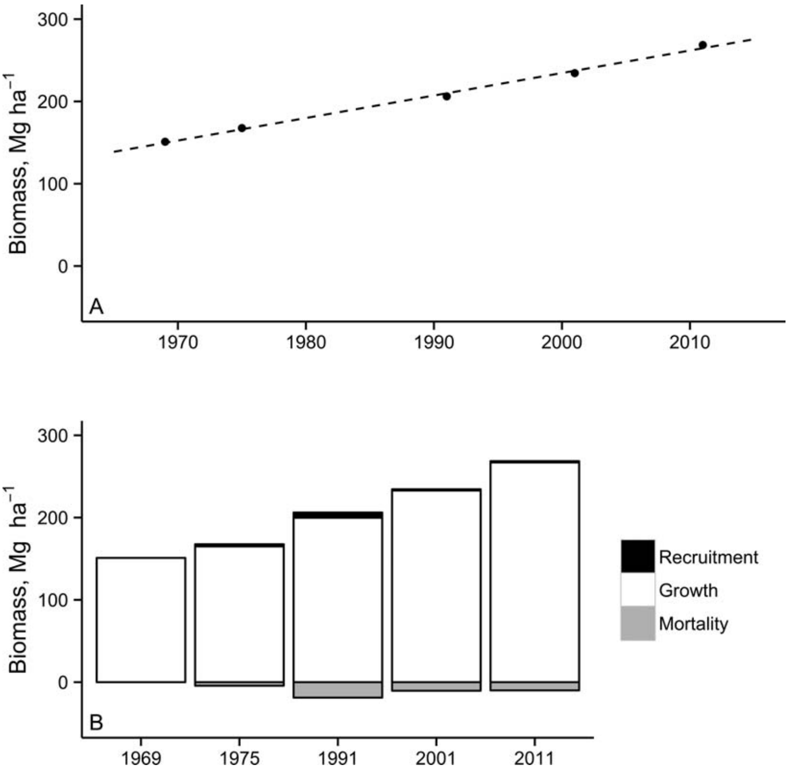

FIG. 2. (A) Aboveground biomass in living individuals increased linearly (y = 2.74x − 5235.84; R^2 = 0.99; p = 0.00013) from 1969 to 2011 (stand age ~70–110 years). (B) Aboveground biomass at each census partitioned into recruitment of new individuals (black), growth (white), and mortality (grey). Growth added 2.76 ± 0.58 Mg ha^{-1} yr^{-1}, recruitment 0.29 ± 0.13 Mg ha^{-1} yr^{-1}, and mortality −1.03 ± 0.15 Mg ha^{-1} yr^{-1}.

annual mortality in the canopy ranged from 0.4 percent from 1969 to 1975 to 0.7 percent from 1975 to 1991 (Table 3). Average annual mortality in the subordinate level was higher and decreased over time, from 3.8 percent from 1969 to 1975 to 2.4 percent from 2001 to 2011 (Table 3).

SPECIES-LEVEL DYNAMICS. *Q. RUBRA*. *Q. rubra* dominated forest biomass, and became more important over time. Aboveground biomass in living *Q. rubra* more than doubled from 90.7 Mg ha^{-1} in 1969 to 185.0 Mg ha^{-1} in 2011, while the biomass in all other living trees increased 48 percent from 56.4 Mg ha^{-1} to 83.4 Mg ha^{-1} (Table 1). *Q. rubra* growth comprised the majority of forest-wide increases over the study period, ranging from 78 percent of the total biomass increment (1991–2001) to 87 percent (1969–1975). *Q. rubra* density decreased from 244 stems ha^{-1} in 1969 to 145 stems ha^{-1} in 2011, while its share of the total biomass increased from 60.2 to 68.9 percent.

The diameter distributions of live *Q. rubra* in 1969 and 2011 were significantly different (two-sided two-sample Kolmogorov-Smirnov test; $D = 0.59$, $P < 2.2 \times 10^{-16}$; Fig. 4B). In 2011, stems larger than 40 cm DBH comprised 80 percent of all *Q. rubra* live biomass, versus 29 percent in 1969. Biomass in *Q. rubra* stems increased in the canopy (Fig. 3B; Table 1) and the annual mortality rate in the canopy was very low and consistently less than 0.4 percent (Table 3). In contrast, biomass in subordinate *Q. rubra* decreased with an annual mortality rate of subordinate *Q. rubra* consistently greater than 6 percent (Table 3; Fig. 3C). There was no recruitment of *Q. rubra* stems into the stand after 1991 (Table 2).

A. RUBRUM. Biomass in *A. rubrum* increased 34 percent over the study period, from 33.9 Mg ha^{-1} in 1969 to 45.5 Mg ha^{-1} in 2011 (Table 1) while *A. rubrum*'s contribution to biomass growth declined from 19 percent of the total (1969–1975) to 2 percent (2001–2011). *A. rubrum* density decreased from 693

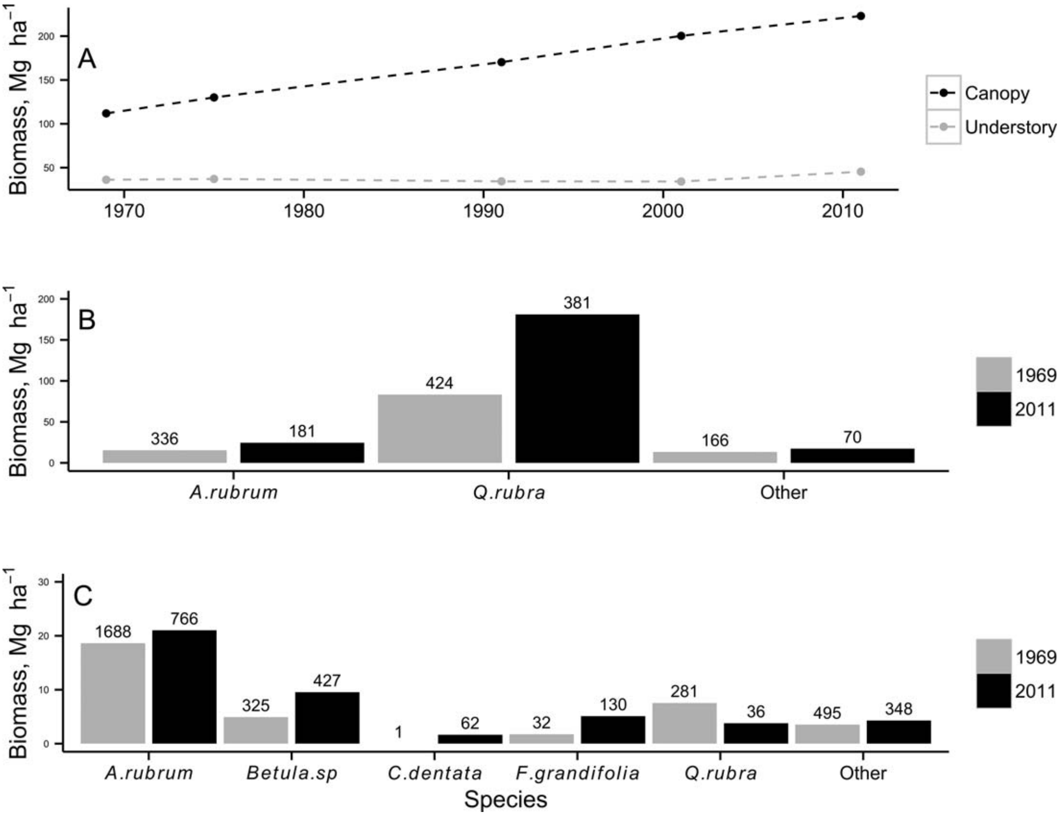

FIG. 3. (A) Aboveground biomass in living stems in the canopy (black) and the subordinate level (grey), (B) and biomass in the canopy, (C) and subordinate level by species. The values above the bars in panels B and C indicate the number of stems that comprise the biomass represented in each bar.

stems ha^{-1} in 1969 to 330 stems ha^{-1} in 2011 and its share of the total biomass decreased from 22.6 to 17.0 percent.

The diameter distributions of live *A. rubrum* in 1969 and 2011 were significantly different (two-sided two-sample Kolmogorov-Smirnov test, $D = 0.34$, $P < 2.2 \times 10^{-16}$; Fig. 4C). In 1969, stems less than 20 cm DBH comprised 63 percent of all *A.rubrum* live biomass; in 2011, the percentage of biomass in this size class was 29 percent. *A. rubrum* biomass in the canopy increased from 15.3 Mg ha^{-1} in 1969 to 26.8 Mg ha^{-1} in 2001, and then slightly declined to 24.5 Mg ha^{-1} in 2011. Subordinate biomass increased slightly from 18.6 to 21.0 Mg ha^{-1} from 1969 to 2011 (Table 1). *A. rubrum* recruitment increased from 1969 to 1991, then decreased from 1991 to 2011 (Table 2). *A. rubrum* mortality in the canopy increased overall from 0.1 percent annually from 1969 to 1975 to 0.8 percent from 2001 to 2011, while subordinate *A. rubrum* mortality ranged from 2.4 percent annually from 1975 to 1991 to 3.0 percent from 1969 to 1975 (Table 3).

OTHER SPECIES. Biomass in species other than *Q. rubra* and *A. rubrum* accounted for 13.4 Mg ha^{-1} in 1969 and 17.3 Mg ha^{-1} in 2011 in the canopy; these species comprised 12 percent of canopy biomass in 1969 and 8 percent in 2011 (Fig. 3B; Table 1). Combined *Betula alleghaniensis* (yellow birch) and *B. lenta* (black birch) biomass in the canopy ranged from 5.5 to 6.5 Mg ha^{-1} across the study period. *C. dentata* was absent from the canopy, and *Fagus grandifolia* (American beech) canopy biomass increased from 0.9 Mg ha^{-1} in 1969 to 2.7 Mg ha^{-1} in 2011. Other species accounted for 7.0 Mg ha^{-1} in canopy biomass in 1969 and 9.0 Mg ha^{-1} in 2011.

These species were more abundant in the subordinate level (Fig. 3C; Table 1). They accounted for 10.1 Mg ha^{-1} of subordinate

Table 1. Biomass in the canopy and subordinate level of the Lyford Grid, in Mg ha^{-1}. Total values are slightly greater than the sum of canopy and subordinate components in some cases because of live stems missing canopy class data. Unassigned stems totaled less than 1% of the total stems and biomass in any year.

	1969	1975	1991	2001	2011
Acer rubrum					
Canopy	15.3	17.5	23.5	26.8	24.5
Subordinate	18.6	19.6	19.3	18.1	21.0
Total	34.1	37.3	43.5	44.9	45.5
Betula alleghaniensis & *B. lenta*					
Canopy	5.4	6.1	6.2	6.4	5.6
Subordinate	4.9	5.4	5.9	7.3	9.5
Total	10.4	11.5	12.2	13.7	15.1
Castanea dentata					
Canopy	0.0	0.0	0.0	0.0	0.0
Subordinate	0.0	0.0	0.2	0.6	1.7
Total	0.3	0.0	0.2	0.6	1.7
Fagus grandifolia					
Canopy	0.9	1.3	1.4	3.2	2.7
Subordinate	1.7	1.8	3.4	3.7	5.1
Total	2.6	3.1	5.1	6.9	7.8
Quercus rubra					
Canopy	83.2	98.0	132.2	155.8	181.2
Subordinate	7.5	7.3	3.1	1.8	3.8
Total	90.8	105.3	135.6	157.6	185.0
Other[3]					
Canopy	7.0	7.3	6.9	8.1	9.0
Subordinate	3.5	3.0	2.5	2.7	4.3
Total	11.4	10.3	9.5	10.8	13.3
Total					
Canopy	111.9	130.1	170.3	200.3	223.0
Subordinate	36.2	37.1	34.4	34.2	45.4
Total	149.6	167.4	206.2	234.5	268.4

[3] Other species include *Acer pensylvanicum, A. saccharum, Alnus incana, Amelanchier* sp.*, Betula papyrifera, B. populifolia, Fraxinus americana, Hamamelis virginiana, Nyssa sylvatica, Picea rubens, Pinus strobus, Populus grandidentata, Prunus serotina, Quercus alba, Quercus velutina, Tsuga canadensis, Ulmus* sp.

biomass in 1969 and increased to 20.6 Mg ha^{-1} in 2011; they comprised 28 percent of subordinate biomass in 1969 and 45 percent in 2011. Over this period, subordinate *B. alleghaniensis* and *B. lenta* increased from 4.9 Mg ha^{-1} to 9.5 Mg ha^{-1}. *F. grandifolia* increased from 1.7 Mg ha^{-1} to 5.1 Mg ha^{-1}, while *C. dentata* increased from less than 0.1 to 1.7 Mg ha^{-1}.

Recruitment of these species generally increased over the study period (Table 2). *B. alleghaniensis* and *B. lenta* recruitment increased from 0.8 percent from 1969 to 1975 to 1.8 percent from 2001 to 2011. *C. dentata* recruitment increased from zero from 1969–1975 to an average annual rate of 10.4 percent from 2001 to 2011, while *F. grandifolia* also increased from 0.9 percent average annual recruitment (1969–1975) to 3.9 percent (2001–2011). Recruitment in all other species increased over the study period from 0.7 to 5.7 percent average annual recruitment.

Mortality did not increase or decrease consistently across these species (Table 3). The annual average mortality rate of *B. alleghaniensis* and *B. lenta* was approximately 1 percent in the canopy and the rate in the subordinate level decreased from 2.2 to 1.3 percent from 1969 to 2011. *F. grandifolia* mortality increased in the canopy from 0.0 (1969–2001) to 2.5 percent (2001–2011) and in the subordinate level from 0.0 (1969–1991) to 1.3 percent (2001–2011). Mortality of *C. dentata* generally increased from 3.0 percent (1969–1975), which resulted in the absence of the species in 1975, to 4.3 percent (2001–2011). Mortality rates among all other species in the canopy ranged from 1.1 percent (1991–2001) to 2.6 percent (1969–1975); subordinate mortality among these species generally decreased

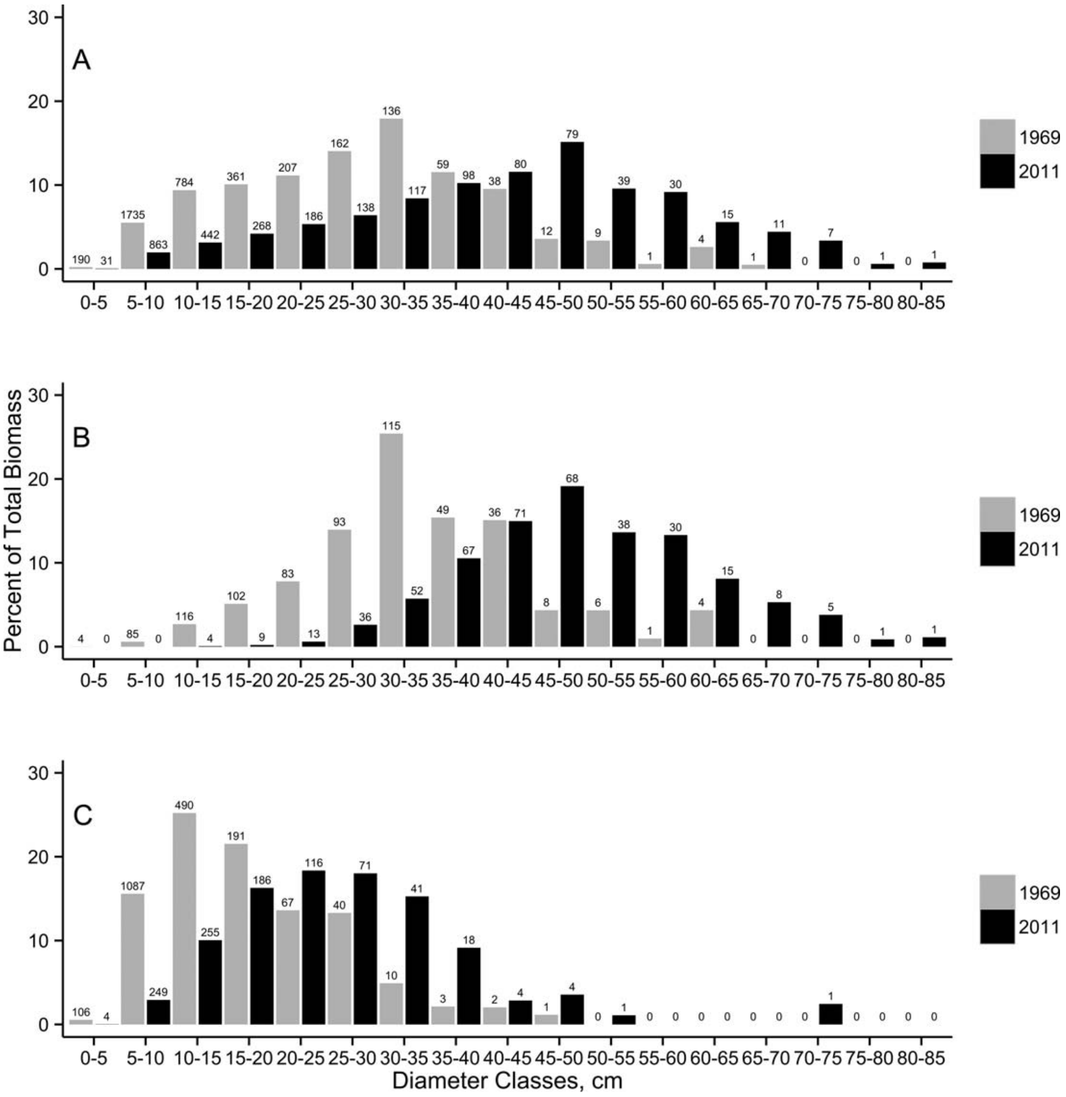

FIG. 4. (A) The percent of total biomass of all living trees, (B) red oaks, (C) and red maples in 1969 (grey) and 2011 (black) by diameter classes. Numbers at the top of each bar indicate the number of individual trees in that diameter class and year.

over time from 7.5 percent (1975–1991) to 2.2 percent (2001–2011).

Discussion. LARGE *Q. RUBRA* DRIVE STEADY BIOMASS GAINS. Five censuses of the Lyford Grid over the past 42 years indicate that the forest has steadily gained aboveground biomass (Fig. 2A), supporting Bormann and Likens' (1979) model prediction that stands aged 70–110 years remain in the biomass aggradation phase. This finding is consistent with observations from other even-aged forests in the region (Fig. 5A), including permanent plots at the oak-dominated Harvard Forest EMS site (Urbanski et al. 2007) and at the Arnot Forest northern hardwoods in central New York (Fahey et al. 2013). However, oak-dominated permanent plots in eastern New York's Black Rock Forest showed that live aboveground biomass levelled off around age 100 (Schuster et al. 2008, Xu et al. 2012), and biomass growth approached steady state in northern hardwoods stands only 65 years old at Hubbard Brook in New Hampshire (Battles et al. 2013). Because of the region-wide history of forest clearing, there are few permanent plot data available to

Table 2. Number of recruited stems and average annual recruitment rates for each census interval.

	1969–1975	1975–1991	1991–2001	2001–2011
A. rubrum				
Number	17	186	60	34
Rate	0.1	0.6	0.4	0.3
Betula alleghaniensis & *B. lenta*				
Number	19	124	82	84
Rate	0.8	1.8	1.9	1.8
C. dentata				
Number	0	8	24	47
Rate	0	13.9	14.9	10.4
F. grandifolia				
Number	2	29	38	47
Rate	0.9	5.5	4.5	3.9
Q. rubra				
Number	3	12	0	0
Rate	0.1	0.1	0.0	0.0
Other species				
Number	24	117	110	135
Rate	0.7	1.8	5.6	5.7
Total				
Number	65	476	314	347
Rate	0.3	0.8	1.2	1.3

extend the age axis of the biomass development curve beyond around 120 years (Fig. 5A). Using a chronosequence, Keeton et al. (2011) found that biomass approached maximum values in northern hardwoods stands with dominant tree ages of approximately 350 to 400 years (Fig. 5B). Biomass of northeastern forests will not increase indefinitely, but these findings suggest that the timing of an age-related decline in aboveground biomass growth may depend on other stand-level processes, and exogenous disturbance and stress (Luyssaert et al. 2008).

Increasing dominance of large *Q. rubra* stems drives the currently observed increase in aboveground biomass in the Lyford Grid. Over the study period, *Q. rubra* biomass doubled, while all other species increased by about 40 percent and *A. rubrum* increased at an even slower rate (34 percent). Over time, *Q. rubra* biomass became increasingly concentrated in a few large stems (Fig. 4B). Between 1969 to 1991, a major decline in subordinate *Q. rubra* was likely the result of competition and the 1981 gypsy moth outbreak. No *Q. rubra* recruited into the plot after 1991, consistent with low *Quercus* regeneration across eastern North America (McEwan et al. 2011).

The low mortality and high growth rates of the existing canopy trees indicate that *Q. rubra* could retain dominance for a long time as the forest ages, despite low recruitment. Pederson (2005) observed that average growth rates of *Q. rubra* stems in southern New England increased with age, in stands with trees up to 200–300 years old. Because the 110-year-old *Q. rubra* stems in the Lyford Grid may continue to live and grow steadily for another century, oak dominance provides a mechanism for the maintenance of high productivity in aging forests.

This study corroborates findings in tropical (Slik et al. 2013) and temperate (Lutz et al. 2012) forests that large-diameter trees dominate forest gains in aboveground biomass and actively fix large quantities of carbon (Stephenson et al. 2014). Concentrating biomass in fewer, larger trees does make the forest more vulnerable to biomass losses from stochastic or disturbance-related mortality. For example, central New England is vulnerable to major hurricane disturbance (return interval ~150 years; Boose et al. 2001), and susceptibility to blowdown increases with tree size (Foster 1988). In a ca. 130-year-old *Quercus* forest in New York, Xu et al. (2012) found that despite a consistent low (2 percent) mortality rate, over time 'biomass

Table 3. Numbers of trees dying between censuses, and average annual mortality rates by species and canopy class for each census interval.

	1969–1975	1975–1991	1991–2001	2001–2011
A. rubrum				
Canopy				
Number	2	32	23	20
Rate	0.1	0.7	0.9	0.8
Subordinate				
Number	279	482	322	226
Rate	3.0	2.4	3.2	2.8
B. alleghaniensis & *B. lenta*				
Canopy				
Number	4	14	4	5
Rate	1.1	1.6	0.8	1.1
Subordinate				
Number	40	70	34	48
Rate	2.2	1.6	1.4	1.3
C. dentata				
Canopy				
Number	0	0	0	0
Rate	–	–	–	–
Subordinate				
Number	1	0	4	10
Rate	3.0	–	6.7	4.3
F. grandifolia				
Canopy				
Number	0	0	0	2
Rate	0	0	0	2.5
Subordinate				
Number	0	0	4	11
Rate	0	0	0.7	1.3
Q. rubra				
Canopy				
Number	2	21	3	8
Rate	0.1	0.3	0.1	0.2
Subordinate				
Number	96	149	35	16
Rate	6.8	6.5	6.8	6.4
Other species				
Canopy				
Number	12	21	5	8
Rate	2.6	2.2	1.1	2.0
Subordinate				
Number	165	276	55	52
Rate	6.7	7.5	3.0	2.2
Total				
Canopy				
Number	20	88	35	443
Rate	0.4	0.7	0.5	0.6
Subordinate				
Number	581	977	468	363
Rate	3.8	3.1	2.8	2.4

loss increased because more large trees died, which is simply because there were more large trees in stands as stands aged.' Runkle (2013) found that mortality increased with larger stem size in an old-growth forest in Ohio. As yet, this process is not evident in the Lyford Grid. Annual mortality rates for the entire forest hovered around 2 percent throughout the study period, but stems in the canopy had average annual mortality rates that were consistently lower than 1 percent and exhibited no increase over time. Mortality of *Q. rubra*, which comprises the majority of stems in the canopy, decreased over the study period.

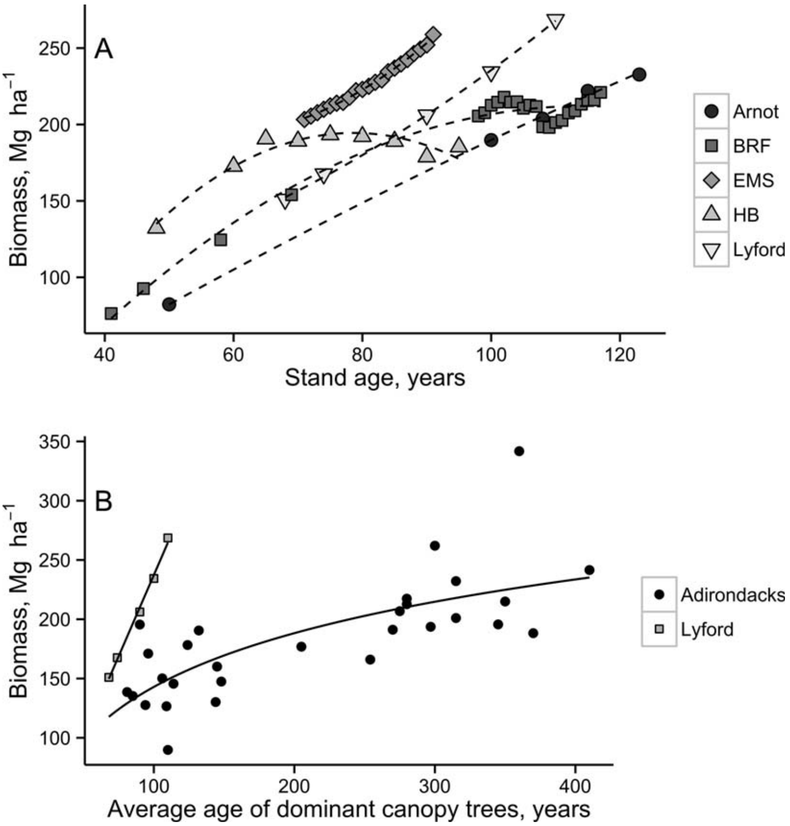

FIG. 5. (A) Aboveground live biomass in relation to approximate stand age for oak-maple and northern hardwoods forests in the northeastern U.S. Permanent plots at the Arnot Forest (circles; Fahey et al. 2013), Black Rock Forest (BRF, squares; Schuster et al. 2008, Schuster unpublished data), in the EMS footprint at the Harvard Forest (diamonds; Urbanksi et al. 2007, Goldman et al. 2014), Hubbard Brook W6 (HB, upright triangles; Battles et al. 2013), and the Lyford Grid at the Harvard Forest (inverted triangles). (B) Biomass of mature and old-growth northern hardwood forest plots relative to average age of dominant canopy trees in the Adirondacks, NY (circles; Keeton et al. 2007, Keeton et al. 2011), compared to the biomass of the Lyford Grid (squares).

Canopy dynamics will be a major focus in future censuses.

CHANGING SUBORDINATE DOMINANCY OVER 42 YEARS. Previous studies predicted that *A. rubrum* would come to dominate the canopy of eastern US forests following disturbance and the death of stems in the canopy (Lorimer 1984, Abrams 1998), because of its ability to function as both an early and a late successional species (Drury and Runkle 2006). Contrary to our expectation that *A. rubrum* would become a more important contributor to stand biomass over the study period, its biomass has grown slowly for the past 20 years relative to many other species. Perhaps *A. rubrum* growth is limited as it is squeezed between the persistent *Q. rubra* canopy and recruitment of *Betula* and *Fagus*. *A. rubrum* recruitment increased from 1969 to 1991, but then decreased from 1991 to 2011, and mortality increased over time (Table 2, 3). Tree-ring data from the site show that biomass increment of individual *A. rubrum* stems over the past century peaked in the 1970s, followed by slow growth since 1980 (Pederson 2005). These trends indicate that *A. rubrum* is unlikely to become a canopy dominant in this forest, despite its ubiquity.

These findings are in concordance with other site-specific studies of *Quercus*-dominant forests at the Harvard Forest (Urbanski et al. 2007) and in the region (Schuster et al. 2008), but contrast sharply with the well-documented, region-wide trend that shows shifting species dominance from *Quercus* to *Acer* over the past decades and centuries (McEwan et al.

2011, Thompson et al. 2013). *A. rubrum* volume exceeds *Q. rubra* in Massachusetts (Butler 2013) and across the eastern U.S. (McEwan et al. 2011). The reasons for the regional versus site difference are likely multifaceted, and are an intriguing avenue for further investigation. One possible explanation is that little timber harvesting has occurred at the Lyford Grid and other permanent plot sites over the past half-century. In contrast, moderate-intensity timber harvesting is widespread through the region, and *Q. rubra* is commonly harvested (McDonald et al. 2006). Low regeneration and recruitment of *Q. rubra* then could lead to its declining importance relative to the opportunistic *A. rubrum*.

While less numerous than *A. rubrum*, four other species have become increasingly prominent in the subordinate level. *B. alleghaniensis, B. lenta, F. grandifolia*, and *C. dentata* comprised 18 percent of the subordinate biomass in 1969, and doubled to comprise 36 percent in 2011. Rates of recruitment for these species generally increased across the study period. The reappearance of *C. dentata* is unexpected, given its absence from the plot in 1975. Because almost all *C. dentata* stems are less than 10 cm DBH, and the pathogen *Cryphonectria parasitica* is widespread, these stems will likely continue to die back and resprout over time, never reaching the canopy. *B. lenta*, which shares a generalist strategy with *A. rubrum*, has shown strong recruitment throughout the region (Orwig and Foster 1998, Faxla-Raymond et al. 2012, Barker Plotkin et al. 2013) as part of stand understory reinitiation, or after major disturbance. Increasing *F. grandifolia*, a late successional species, has also been observed in *Quercus* forests of similar age to the Lyford Grid (Goebel and Dix 1996, Schuster et al. 2008).

Changing species composition in the subordinate level of the Lyford Grid may impact carbon storage in aboveground biomass if canopy disturbances over the next 10–100 years allow *Betula*, *Fagus*, and *Acer* to ascend to the canopy and impede the initiation of a new cohort of *Quercus* or other species. The carbon sequestration consequences of a shift in overstory composition from *Quercus* to *Betula-Fagus-Acer* depend on whether *Quercus* has an inherently higher growth capacity than these other species. Due to their high photosynthetic capacities, water-use efficiencies, and photosynthetic nitrogen-use efficiencies in wet and dry environments, *Quercus* can exhibit greater carbon acquisition relative to *A. rubrum* (Turnbull et al. 2001, Turnbull et al. 2002). How these differences scale up to the forest stand is less clear, and suggest a need for a larger synthesis of permanent plot and regional (e.g. Jenkins et al. 2001) studies.

Conclusions. We leveraged 42 years of periodic re-measurements of living and dead trees in the Lyford Grid permanent plot to examine forest biomass development. The stand steadily accrued carbon in aboveground, living biomass as the stand matured from 70 to 110 years old, providing empirical support for Bormann and Likens' (1979) long-standing model of live biomass accumulation over time, for the range of stand ages addressed by the data. Increasing dominance of *Q. rubra* in the forest canopy drives the observed linear increase in aboveground biomass. Contrary to predicted dynamics, *A. rubrum* importance declined over the past 20 years, while subordinate *B. lenta* and *alleghaniensis*, *F. grandifolia*, and *C. dentata* increased. These changes in the subordinate level of the forest have not affected overall live, aboveground forest biomass because canopy trees account for 75–82 percent of the total biomass in the plot, but they may ascend to the canopy when overstory *Q. rubra* is lost to gap dynamics or major disturbances. Dominant *Q. rubra* stems can continue to accrue biomass even after reaching 150–300 years of age, so if current low mortality of *Q. rubra* continues, we predict that the Lyford Grid and other older *Quercus*-dominant forests in the region may continue to add carbon in aboveground biomass for another century. This and other permanent plot studies ground ecosystem-level measurements of forest carbon uptake and can improve predictions of how forest biomass accumulation will change in the future.

Literature Cited

ABRAMS, M. D. 1998. The red maple paradox. BioScience 48: 355–364.

BARFORD, C. C., S. C. WOFSY, M. L. GOULDEN, J. W. MUNGER, E. H. PYLE, S. P. URBANSKI, L. HUTYRA, S. R. SALESKA, D. FITZJARRALD, AND K. MOORE. 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294: 1688–1691.

BARKER PLOTKIN, A., D. FOSTER, J. CARLSON, AND A. MAGILL. 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology 94: 414–423.

Battles, J. J., T. J Fahey, C. T. Driscoll, J. D. Blum, and C. E. Johnson. 2013. Restoring soil calcium reverses forest decline. Envir. Sci. Tech. Lett. DOI: 10.1021/ez400033d.

Boose, E. R., E. F. Boose, and A. L. Lezberg. 1998. A practical method for mapping trees using distance measurements. Ecology 79: 819–827.

Boose, E. R., K. E. Chamberlain, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. Ecol. Monogr. 7: 27–48.

Bormann, F. H. and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, 253 p.

Butler, B. J. 2013. Massachusetts' forest resources, 2012. Res. Note NRS-189. Newtown Square, PA: USDA Forest Service, Northern Research Station. 3 p.

Drury, S. A. and J. R. Runkle. 2006. Forest vegetation change in southeast Ohio: Do older forests serve as useful models for predicting the successional trajectory of future forests? Forest Ecol. Manag. 223: 200–210.

Eschman, D. F. 1966. Surficial geology of the Athol Quadrangle, Worcester and Franklin Counties, Massachusetts. US Government Printing Office.

Fahey, T. J., P. B. Woodbury, J. J. Battles, C. L. Goodale, S. P. Hamburg, S. V. Ollinger, and C. W. Woodall. 2010. Forest carbon storage: ecology, management, and policy. Front. Ecol. Environ. 8: 245–252.

Fahey, T. J., R. E. Sherman, and D. A. Weinstein. 2013. Demography, biomass and productivity of a northern hardwood forest on the Allegheny Plateau. J. Torrey Bot. Soc. 140: 52–64.

Faxla-Raymond, N., A. E. Patterson, W. S. F. Schuster, and K. L. Griffin. 2012. Oak loss increases foliar nitrogen, δ15N and growth rates of *Betula lenta* in a northern temperate deciduous forest. Tree Physiol. 32: 1092–1101.

Foster, D. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U.S. J. Ecol. 76: 105–134.

Foster, D., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems 1: 96–119.

Foster, D., A. Barker Plotkin, and W. Lyford. 1999. Lyford Mapped Tree Plot at Harvard Forest since 1969. Harvard Forest Data Archive: HF032. doi:10.6073/pasta/a122491ac0b3b83ff6a916430 6ab064b

Goebel, P. C. and D. M. Hix. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. Forest Ecol. Manag. 84: 1–21.

Goldman, E., S. Wofsy, and J. W. Munger. 2014. Archived Data: Ecological measurements to complement eddy-flux measurements at Harvard Forest, http://atmos.seas.harvard.edu/lab/data/nigec-data.html. Accessed 26 February 2014.

Goodale, C. L., M. J. Apps, R. A. Birdsey, C. B. Field, L. S. Heath, R. A. Houghton, J. C. Jenkins, G. H. Kohlmaier, W. Kurz, S. Liu, G.-J. Nabuurs, S. Nilsson, and A. Z. Shvidenko. Forest carbon sinks in the Northern Hemisphere. Ecol. Appl. 12: 891–899.

Greenland, D. and T. Kittel. 1997. A climatic analysis of long-term ecological research sites. http://intranet2.lternet.edu/sites/intranet2.lternet.edu/files/documents/Scientific%20Reports/Climate%20and%20Hydrology%20Database%20Projects/CLIMDES.pdf

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. J. Biogeogr. 29: 1319–1335.

Jenkins, J. C., R. A. Birdsey, and Y. Pan. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. Ecol. Appl. 11: 1174–1193.

Keeton, W. S., C. D. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecol. Appl. 17: 852–868.

Keeton, W. S., A. A. Whitman, G. C. McGee, and C. L. Goodale. 2011. Late- successional biomass development in northern hardwood-conifer forests of the Northeastern United States. Forest Sci. 57: 489–505.

Liu, J., S. Liu, and T. R. Loveland. 2006. Temporal evolution of carbon budgets of the Appalachian forests in the U.S. from 1972 to 2000. Forest Ecol. Manag. 222: 191–201.

Lorimer, C. G. 1984. Development of the red maple understory in Northeastern oak forests. Forest Sci. 30: 3–22.

Lutz, J. A., A. J. Larson, M. E. Swanson, and J. A. Freund. 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PLoS One 7: e36131. Doi:10.1371/journal.pone.0036131.

Luyssaert, S., E. D. Schulze, A. Börner, A. Knohl, D. Hessenmöller, B. E. Law, P. Ciasis, and J. Grace. 2008. Old-growth forests as global carbon sinks. Nature 455: 213–215.

MassGIS (Massachusetts Office of Geographic Information). 1997. MassGIS data – insect infestation (BUGS). Website (http://www.mass.gov/anf/research-and-tech/it-serv-and- support/application-serv/office-of-geographic-information-massgis/datalayers/insect- infestation-bugs.html). Downloaded 5 August 2003.

McDonald, R. I., G. Motzkin, M. S. Bank, D. B. Kittredge, J. Burk, and D. R. Foster. 2006. Forest Harvesting and Deforestation Relationships over Two Decades in Massachusetts. Forest Ecol. Manag. 227: 31–41.

McEwan, R. W., J. M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34: 244–256.

McKinley, D. C., M. G. Ryan, R. A. Birdsey, C. P. Giardina, M. E. Harmon, L. S. Heath, R. A. Houghton, R. B. Jackson, J. F. Morrison, B. C. Murray, D. E. Pataki, and K. E. Skog. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. Ecol. Appl. 21: 1902–1924.

Mencuccini, M., J. Martinez-Vilata, H. A. Hamid, E. Korakaki, and D. Vanderklein.

2007. Evidence for age- and size-mediated controls of tree growth from grafting studies. Tree Physiol. 27: 463–473.

OLIVER, C. D. 1975. The development of northern red oak (*Quercus rubra L.*) in mixed species, even-age stands in central New England. Doctoral Thesis, Yale University.

ORWIG, D. A. AND D. R. FOSTER. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J. Torrey Bot. Soc. 125: 60–73.

PACALA, S. W., G. C. HURTT, D. BAKER, P. PEYLIN, R. A. HOUGHTON, R. A. BIRDSEY, L. HEATH, E. T. SUNDQUIST, R. F. STALLARD, P. CIAIS, P. MOORCROFT, J. P. CASPERSEN, E. SHEVLIAKOVA, B. MOORE, G. KOHLMAIER, E. HOLLAND, M. GLOOR, M. E. HARMON, S.-M. FAN, J. L. SARMIENTO, C. L. GOODALE, D. SCHIMEL, AND C. B. FIELD. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. Science 292: 2316–2320.

PEDERSON, N. A. 2005. Climatic Sensitivity and Growth of Southern Temperate Trees in the Eastern US: Implications for the Carbon Cycle. Doctoral Dissertation, Columbia University.

R CORE TEAM. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, AU.

RUNKLE, J. R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology 81: 554–567.

RUNKLE, J. R. 2013. Thirty-two years of change in an old-growth Ohio beech-maple forest. Ecology 94: 1165–1175.

RYAN, M. G., D. BINKLEY, AND J. H. FOWNES. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27: 213–262.

SCHUSTER, W. S. F., K. L. GRIFFIN, H. ROTH, M. H. TURNBULL, D. WHITEHEAD, AND D. T. TISSUE. 2008. Changes in composition, structure and aboveground biomass over seventy-six years (1930–2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. Tree Physiol. 28: 537–549.

SEKHON, J. S. 2011. Multivariate and Propensity Score Matching Software with Automated Balance Optimization: The Matching Package for R. J. Stat. Softw. 42: 1–52.

SLIK, J. W. F., G. PAOLI, K. MCGUIRE, I. AMARAL, J. BARROSO, M. BASTIAN, L. BLANC, F. BONGERS, P. BOUNDJA, C. CLARK, M. COLLINS, G. DAUBY, Y. DING, J. DOUCET, E. ELER, L. FERREIRA, O. FORSHED, G. FREDRIKSSON, J. GILLET, D. HARRIS, M. LEAL, Y. LAUMONIER, Y. MALHI, A. MANSO, E. MARTIN, K. MIYAMOTO, A. ARAUJO-MURAKAMI, H. NAGAMASU, R. NILUS, E. NURTJAHYA, A. OLIVEIRA, O. ONRIZAL, A. PARADA-GUTIERREZ, A. PERMANA, L. POORTER, J. POULSEN, H. RAMIREZ-ANGULO, J. REITSMA, F. ROVERO, A. ROZAK, D. SHEIL, J. SILVA-ESPEJO, M. SILVEIRA, W. SPIRONELO, H. TER STEEGE, T. STEVART, G. E. NAVARRO-AGUILAR, T. SUNDERLAND, E. SUZUKI, J. TANG, I. THEILADE, G. VAN DER HEIJDEN, J. VAN VALKENBURG, T. VAN DO, E. VILANOVA, V. VOS, S. WICH, H. WOLL, T. YONEDA, R. ZANG, M. ZHANG, AND N. ZWEIFEL. 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Global Ecol. Biogeogr. 22: 1261–1271.

SMITH, D. M., B. C. LARSON, M. J. KELTY, AND P. M. S. ASHTON. 1997. The practice of silviculture: applied forest ecology, 9th edition. John Wiley, NY.

STEPHENSON, N. L., A. J. DAS, R. CONDIT, S. E. RUSSO, P. J. BAKER, N. G. BECKMAN, D. A. COOMES, E. R. LINES, W. K. MORRIS, N. RÜGER, E. ÁLVAREZ, C. BLUNDO, S. BUNYAVEJCHEWIN, G. CHUYONG, S. J. DAVIES, Á. DUQUE, C. N. EWANGO, O. FLORES, J. F. FRANKLIN, H. R. GRAU, Z. HAO, M. E. HARMON, S. P. HUBBELL, D. KENFACK, Y. LIN, J.-R. MAKANA, A. MALIZIA, L. R. MALIZIA, R. J. PABST, N. PONGPATTANANURAK, S.-H. SU, I.-F. SUN, S. TAN, D. THOMAS, P. J. VAN MANTGEM, X. WANG, S. K. WISER, AND M. A. ZAVALA. 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature. doi:10.1038/nature12914.

THOMPSON, J. R., D. N. CARPENTER, C. V. COGBILL, AND D. R. FOSTER. 2013. Four centuries of change in Northeastern United States forests. PLoS One 8: e72540.

TURNBULL, M. H., D. WHITEHEAD, D. T. TISSUE, W. S. F. SCHUSTER, K. J. BROWN, AND K. L. GRIFFIN. 2001. The response of leaf respiration to temperature and leaf characteristics in three deciduous tree species differs at sites with contrasting water availability. Tree Physiol. 21: 571–578.

TURNBULL, M. H., D. WHITEHEAD, D. T. TISSUE, W. S. F. SCHUSTER, K. J. BROWN, V. C. ENGEL, AND K. L. GRIFFIN. 2002. Photosynthetic characteristics in canopies of *Quercus rubra*, *Quercus prinus* and *Acer rubrum* differ in response to soil water availability. Oecologia 130: 515–524.

URBANSKI, S., C. BARFORD, S. WOFSY, C. KUCHARIK, E. PYLE, J. BUDNEY, K. MCKAIN, D. FITZJARRALD, M. CZIKOWSKY, AND J. W. MUNGER. 2007. Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest. J. Geophys. Res. 112: G02020.

XU, C. Y., M. H. TURNBULL, D. T. TISSUE, J. D. LEWIS, R. CARSON, W. S. F. SCHUSTER, D. WHITEHEAD, A. S. WALCROFT, J. LI, AND K. L. GRIFFIN. 2012. Age-related decline of stand biomass accumulation is primarily due to mortality and not to reduction in NPP associated with individual tree physiology, tree growth or stand structure in a *Quercus*-dominated forest. J. Ecol. 100: 428–440.

Appendix
Supporting Material for Biomass Calculations

Table 1. Allometric equations.

Species	Equation	Source, location, range, number
Acer pensylvanicum (Striped maple)	BM = (e^(7.227 + 1.6478 * ln(D / 2.54)) / 1000	Jenkins et al. (2004) after Young et al. (1980) ME; 1–3 cm; *n* = 12
Acer rubrum (Red maple)	BM = 0.1262 * D^2.3804	Ter-Mikaelian and Korzukhin (1997) after Young et al. (1980) ME; 3–66 cm; *n* = 62
Acer saccharum (Sugar maple)	BM = 0.1008 * D^2.5735	Ter-Mikaelian and Korzukhin (1997) after Brenneman *et al.* (1978) WV; 5–50 cm; *n* = 119
Alnus incana (Alder sp.)	BM = 0.2612 * D^2.2087	Ter-Mikaelian and Korzukhin (1997) after Young *et al.* (1980) ME; 3–9 cm; *n* = 30
Amelanchier sp. (Shadbush)	BM = [64.180 * (D^2.322)] / 1000	Ohmann et al. (1976) MN; *n* = 45
Betula alleghaniensis (Yellow birch)	BM = 0.1684 * D^2.4150	Ter-Mikaelian and Korzukhin (1997) after Whittaker et al. (1974) NH; 1–63 cm; *n* = 14
Betula lenta (Black birch)	BM = 0.0629 * (D^2.6606)	Ter-Mikaelian and Korzukhin (1997) after Brenneman et al. (1978) WV; 5–51 cm; *n* = 8
Betula papyrifera (Paper birch)	BM = 0.0612 * (D^1.6287)	Ter-Mikaelian and Korzukhin (1997) after Young et al. (1980) ME; 3–51 cm; *n* = 51
Betula populifolia (Gray birch)	BM = 0.1564 * (D^2.3146)	Ter-Mikaelian and Korzukhin (1997) after Young et al. (1980) ME; 3–23 cm; *n* = 30
Castanea dentata (American chestnut)[1]	BM = 0.45 * (e^(0.95595 + 2.4264 * ln(D / 2.54))	Wartluft (1977) WV, 2–25 cm, *n* = 200
Fagus grandifolia (American beech)	BM = 0.1967 * (D^2.3916)	Ter-Mikaelian and Korzukhin (1997) after Whittaker et al. (1974) NH; 1–63 cm; *n* = 14
Fraxinus americana (White ash)	BM = (exp^(7.1148 + 1.3707*ln(D / 2.54))) / 1000	Young *et al.* (1980) ME; 0–3 cm; *n* = 12
Hamamelis virginiana (Witch hazel)	BM = (38.111 * (D)^2.900) / 1000	Smith and Brand (1984) after Telfer (1969) Canada; 0–4 cm; *n* = 21
Nyssa sylvatica (Black gum)	BM = (10^(1.1468 + 1.4806 * log10(D^2)) / 1000	Jenkins et al. (2004) after Williams and McClenahan (1984) OH; 0–7 cm; *n* = 38
Picea rubens (Red spruce)	BM = (10^(2.1735 + 2.1936 * log10(D))) / 1000	Siccama *et al.* (1994) NH; 3–38 cm; *n* = 15
Pinus strobus (Eastern white pine)	BM = 0.0696 * (D^2.4490)	Ter-Mikaelian and Korzukhin (1997) after Young *et al.* (1980) ME; 3–66 cm; *n* = 35
Populus grandidentata (Largetooth aspen)	BM = 0.0785 * (D^2.4981)	Ter-Mikaelian and Korzukhin (1997) after Perala and Alban (1994) MI; 3–45 cm; *n* = 57
Prunus serotina (Black cherry)	BM = 0.0716 * (D ^2.6174)	Ter-Mikaelian and Korzukhin (1997) after Brenneman et al. (1978) WV; 5–51 cm; *n* = 26
Quercus alba (White oak)	BM = 0.0579 * (D^2.6887)	Ter-Mikaelian and Korzukhin (1997) after Brenneman et al. (1978) WV; 5–50 cm; *n* = 29

Table 1. Continued.

Species	Equation	Source, location, range, number
Quercus rubra (Red oak)	$BM = 0.1130 * (D^{2.4572})$	Ter-Mikaelian and Korzukhin (1997) after Brenneman et al. (1978) WV; 5–50 cm; $n = 24$
Quercus velutina (Black oak)	$BM = 0.0904 * (D^{2.5143})$	Ter-Mikaelian and Korzukhin (1997) after Bridge (1979) RI; 7–27 cm; $n = 27$
Tsuga canadensis (Eastern hemlock)	$BM = 0.0991 * (D^{2.3617})$	Ter-Mikaelian and Korzukhin (1997) after Young et al. (1980) ME; 3–51 cm; $n = 36$
Ulmus sp. (Elm)	$BM = 0.0825 * (D^{2.468})$	Perala and Alban (1994) MI; 4–29 cm; $n = 14$
Unknown species[1]	$BM = 0.45 * (e^{(0.95595 + 2.4264 * \ln(D / 2.54))})$	Wartluft (1977) WV; 2–25 cm; $n = 200$

[1] The equations used for *Castanea dentata* (American chestnut) and the unknown species are general hardwood equations.

BM: Biomass (in kg).
D: DBH (in cm).
Range: Diameters of trees used to develop equation.
Number: Number of trees used to develop equation.

Literature Cited

BRENNEMAN, B. B., D. J. FREDERICK, W. E. GARDNER, L. H. SCHOENHOFEN, AND P. L. MARSH. 1978. Biomass of species and stands of West Virginia hardwoods. Proceedings, Central Hardwood Forest Conference II; West Lafayette, IN. p. 159–178.

JENKINS, J. C., D. C. CHOJNACKY, L. S. HEATH, AND R. A. BIRDSEY. 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. USDA Forest Service Northeastern Research Station GTR-319.

OHMANN, L. F., D. F. GRIGAL, AND R. B. BRANDER. Biomass estimation for five shrubs from northeastern Minnesota. Research Paper NC-133. North Central Forest Experiment Station, Forest Service, USDA.

SICCAMA, T. G., S. P. HAMBURG, M. A. ARTHUR, R. D. YANAI, F. H. BORMANN, AND G. E. LIKENS. 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook Experimental Forest. Ecology 75: 246–248.

SMITH, W. B. AND G. J. BRAND. 1983. Allometric biomass equations for 98 species of herbs, shrubs, and small trees. Research Note NC-299. North Central Forest Experiment Station, Forest Service, USDA.

TELFER, E. S. 1969. Weight-diameter relationships for 22 woody plant species. Can. J. Bot. 47: 1851–1855.

TER-MIKAELIAN, M. T. AND M. D. KORZUKHIN. 1997. Biomass equations for sixty-five North American tree species. Forest Ecol. Manag. 97: 1–24.

WHITTAKER, R. H., F. H. BORMANN, G. E. LIKENS, AND T. G. SICCAMA. 1974. The Hubbard Brook ecosystem study: Forest biomass and production. Ecol. Monogr. 44: 233–254.

WILLIAMS, R. A. AND J. R. MCCLENAHEN. 1984. Biomass prediction equations for seedlings, sprouts, and saplings of ten central hardwood species. Forest Sci. 30: 523–527.

YOUNG, H. E., J. H. RIBE, AND K. WAINWRIGHT. 1980. Weight tables for tree and shrub species in Maine. Life Sciences & Agriculture Experiment Station Miscellaneous Report 230. 86 p.