# HAVE OUR FORESTS STOPPED GROWING?

## Detecting changes in forest productivity through analyzing 150 years of aboveground biomass accumulation in the White Mountains of New Hampshire

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# ABSTRACT

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**NUENGSIGKAPIAN, P. 1998**. Forest productivity within the northeastern United States is postulated to have suffered overall decline due to net effects of acid and nitrogen deposition, and other recent anthropogenic environmental effects. To determine if these forests have indeed suffered, we compared aboveground tree biomass data from five forested sites located in the White Mountains, NH. We analyzed patterns of long-term biomass accumulation in two unmanaged, even-aged forests using an 81-yr. chronosequence located in West Campton and a 150-yr. chronosequence in Bartlett Experimental Forest (BEF); both chronosequences include repeat measurements. The chronosequences were compared to biomass accumulation trends in Watershed 6 of Hubbard Brook Experimental Forest (HBEF) and to biomass accrued in uneven-aged stands of BEF and old-growth forests in Waterville Valley and Area I of the Bowl Research Natural Area. Aboveground tree productivity increased linearly for 70-80 years in both West Campton (1.79 Mg $ha^{-1}$ $yr^{-1}$; $R^2 = 0.89$) and in even-aged stands of BEF (1.47 Mg $ha^{-1}$ $yr^{-1}$; $R^2 = 0.90$). Aboveground biomass continued to increase in BEF, reached a mean peak biomass of 202 ± 5 Mg $ha^{-1}$ at 110 yr. and leveled off at 162 Mg $ha^{-1}$ at 150 yr. in 1991. Biomass accumulated in old-growth stands of BEF reached mean biomass of 207 ± 5 Mg $ha^{-1}$ in 1991 and the Bowl reached 224 Mg $ha^{-1}$ in 1994. Waterville Valley attained biomass value of 228 Mg $ha^{-1}$ in 1903. We conclude that forest growth in terms of aboveground tree biomass has not diminished significantly as a result of recent environmental effects.

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## Introduction

With our growing concern for the ecological consequences of acid rain, nitrogen deposition and $CO_2$ fertilization, comes an interest in how forest ecosystems have previously responded to and are currently responding to the environmental effects of anthropogenic activities. In regards to acid deposition, researchers currently hypothesize that long-term forest productivity in the northeastern US has diminished due to the leaching of critical cations, such as calcium, out of forest soils (Likens et al. 1996; Hedin and Likens 1996). Several nitrogen scientists currently suggest that nitrogen deposition stimulates plant growth in N-limited forests (Håttenschwiler and Körner 1998; Tamm et al. 1995; Brix 1981). Yet other studies caution that excessive nitrogen inputs can cause nitrogen saturation and severe N:cation imbalance; both of which effects result in forest decline (Van Diljk and Roelofs 1998; Schulze 1989; Rodhe and Rood 1986; Nihlgard 1985).

How and to what degree our forests are responding to atmospheric $CO_2$ increase and global climate change are also uncertain. According to satellite data, plant productivity increased in the northern high latitudes from 1981 to 1991 in response to longer growing seasons (Myneni et al. 1997). Correspondingly, atmospheric-transport GCMs using $CO_2$ data show a large terrestrial sink existing in the northern mid-latitudinal forests (Tans et al. 1990). Controlled experiments and forest growth models also suggest increased plant productivity for systems under elevated $CO_2$ conditions. Mesocosm experiments show a 31% rise in global plant biomass production (Bernston and Bazzaz 1998) and a process-based TEM predicts increase in net primary productivity (<10% increase) for northern and temperate ecosystems under $CO_2$ doubling conditions (Mellilo et al. 1993). Yet, changes in climate or atmospheric $CO_2$ resulting in enhanced plant productivity do not necessarily imply an increase in forest carbon stock. Soil studies in temperate grasslands indicate that increases in carbon stock might result in enhanced soil respiration and decomposition, and correspondingly ensue in a net loss of carbon resources

(Thornley and Cannell 1997). Whether or not overall forest productivity will diminish as a result of human-induced environmental effects is a source of debate. The hypothesized percentage changes in forest response vary, but a current study in the northeastern US does suggest that forest production within this region has experienced an overall decline since the 1940s, due to the net impact of recent environmental effects (Likens et al.1996).

Because no baseline information exists on how our forests would have grown in the absence of human activities, hypotheses on human-induced effects on forest productivity remain speculative. Moreover, interaction of disturbance effects on forest growth presents difficulties in distinguishing the independent impacts of acid deposition, climate change and nitrogen and $CO_2$ fertilization on forest productivity (Innes 1994). To further complicate the issue, forest growth has inherent natural variability. Soil characteristics, habitat type, elevation and site and disturbance history are all known to affect tree and forest growth response.

There is, as of yet, no standard method of determining forest growth. Most research on forest productivity in the past have been carried out in pursuit of characterizing merchantable forest products and majority of scientific studies on forest growth have been concerned with characterizing stand behavior and changes in basal area. It is only recently that scientists have focused on estimating plant productivity through changes in forest biomass. Biomass measurements overtime allow for changes in forest structure to be related to how efficiently available energy is utilized by forest vegetation (Hocker and Early 1983). And since human activity, natural succession and natural disturbances all cause changes in biomass within a stand or a region, the rate of biomass accumulation can be used as an effective means of estimating net ecosystem production and also as a means of describing how forests are responding to synergistic environmental effects. A caution in solely using biomass measurements to study environmental impacts on forest growth, is that biomass can be accumulated in different wood sources. Recent studies on long-term structural changes in vegetation have noted shifts in species composition within northeast forest ecosystems (Leak and Smith 1996; Leak 1996). Identifying trends in species dominance is therefore necessary, if one is to consider whether proposed changes in biomass values are due to overall impact on forest productivity or if they are caused by shifts in species composition.

Currently, patterns of forest production are mostly inferred from chronosequences (Paré and Bergeron 1995; Harcombe et al. 1990). As with all space-for-time techniques, these data are subject to the confounding influence of temporal variability and spatial heterogeneity. Accounts from long-term inventory data may provide time series and independent records of biomass accumulation, but these records are scarce and thus most studies to date have been involved in determining short-term responses to human activities.

In light of these complications, we have compiled and analyzed empirical data from the following five independent, forested sites, located in the White Mountains of New Hampshire: Campton Agricultural Plots, Bartlett Experimental Forest (BEF), Hubbard Brook Experimental Forest (HBEF), Bowl Research Natural Area and Waterville Valley. All data utilized are from forest stands that have been unmanaged since the time of data collection. In order to determine patterns of long-term biomass accumulation, we have presented 81-year and 150-year chronosequences of unmanaged, secondary-growth forests, both of which chronosequences include repeated measures. Using the 150-year chronosequence, we have also attempted to resolve the amount of natural variance on forest growth within this region. Our findings on forest productivity are corroborated by other long-term productivity studies in the region, and tree data from old-growth forests in Waterville Valley (Chittenden 1905) and BEF provide us with estimates of forest productivity in pre-acid rain and pre-nitrogen deposition environments. In summary, this study presents a view of the productivity levels reached by northeastern forests before significant impacts from acid rain, nitrogen deposition and other recent anthropogenic influences, and an account of how these same forest ecosystems have accumulated biomass under the influence of the abovementioned environmental effects.

## Study sites

This study is based on five forested sites located in the northern, western and southern flanks of the White Mountains in New Hampshire; all sites are within 40 km of each other (Fig. 1.). The sites were chosen on the basis of availability of long-term forest data records and compatibility of management histories and environmental conditions (Table 1.). Vegetation throughout the region is characterized as northern hardwoods, with forest cover being a combination of deciduous and coniferous species (scientific species names are from Fernald 1950; Britton and Brown 1970). Predominant deciduous species are beech (*Fagus grandifolia*), sugar maple (*Acer saccharum* March.), yellow birch (*Bepula alleghaniensis* Britt), red maple (*Acer rubrum* L.) and white ash (*Fraxinus americana* L.) Predominant coniferous species include red spruce (*Picea rubrum*), balsam fir (*Abies balsamea* (L.) Mill.) and white pine (*Pinus strobus* L.). The principal study sites for this research are the Campton Agricultural Plots and the Bartlett Experimental Forest (BEF). Forest growth data from the Hubbard Brook Experimental Forest (HBEF), the Bowl Natural Research Area and historic forest-ecosystem records from Waterville Valley (Chittenden 1905) provide context for interpreting how old- and secondary-growth forests in the White Mountains have grown since the turn of the century.

All study sites had sample plots that were comparable in size (Campton: 20x20m; BEF: 30x30m: HBEF: 25x25m; Bowl: 100m$^2$ and 25x25m; Chittenden: 20x20m). It is suggested that plot sizes be kept similar, as studies have shown that extrapolation from sample plots of different dimensions can give highly variable results on estimated weights depending on plot-size and plot-area to plot-edge ratio (Satoo 1982; Young 1973).

## CAMPTON AGRICULTURAL PLOTS

The Campton Agricultural plots were first established as a 70-yr. old-field chronosequence that was used to determine trends in organic matter and nitrogen accumulation in abandoned old-fields (Hamburg 1984). Tree data in terms of diameter-at-breast height (dbh) were first collected in 1978-79 from five sites in West Campton, N.H. Five replicate plots of 20x20m, each with 4 nested subplots of 10x10m, were established in each study site to determine within-site variability. Repeated measurements were made in 1987, 1992 and 1997, resolving uncertainties from confounding temporal and spatial variability. All Campton plots have consistent land-use history, which is characterized by forest clearing between 1800-1840s, agricultural use with row-crop production until the early 1900s, followed by farm abandonment and forest re-growth. The species composition of the old-field forests is dominated by early successional hardwood species in varying combinations of red spruce, sugar maple, oaks and white birch. The plots are mid-elevation, ranging from 470-550m. Soils are well to moderately well-drained spodosols with a sandy, loam texture and are derived from glacial till (Hamburg 1984). The study plots are all located within a 2km$^2$ area of each other and were originally selected in 1978 to reflect environmental conditions of the lower elevations of HBEF's reference watershed (WS-6). Despite efforts to keep the study sites intact, several sites have been impacted since 1979. This study utilized data from portions of three sites that have remained unaltered (Site 3, 5 and 6).

## BARTLETT EXPERIMENTAL FOREST (BEF)

The 1052-ha experimental forest is characterized by mixed-deciduous and coniferous vegetation and is dominated by sugar maple, beech and yellow birch at low elevations and spruce-fir forests at elevations above 650m. Elevation ranges from approximately 200-850m and soils are a coarse-textured, sandy loam spodosol derived from glacial till. Detailed habitat type descriptions have been classified by Leak (1982). The primary environmental characteristics impacting forest growth are habitat type and elevation/ climate complex gradient and the primary disturbances within the BEF were timber management, beech bark disease and damage from the hurricane of 1938 (Leak and Smith 1996). This latter event damaged 9% of deciduous trees and 11% of coniferous trees in the lower and mid-elevations and destroyed 18% and 35% of deciduous and coniferous stems respectively in high elevation forests (Leak et al. 1994).

An initial cruise was carried out in 1931-32 and permanent ¼ acre plots were inventoried for dbh data. These same plots were re-measured in 1939-40 and again in 1991-92. Stand age was established in 1931-32 by tree cores and assumed to be the age of the dominant cohort. Approximately 35% of all inventoried plots were classified in 20-yr. intervals for forest stands of up to 100-120 years old. These stands are even-aged, successional stands that arose from clearcutting in the late 1800s. The other 65% of the inventoried plots constituted stands with trees that were older than 120 years and that had undergone varied cutting histories. These plots had variable tree-age distributions ranging up to 150-190 years (Blum 1961) and were classified as all-aged stands because the details of their origins and past histories were difficult to ascertain (Leak 1986). There were a total of 444 plots inventoried, with 271 plots being managed for various forestry studies and 173 plots being kept as unmanaged units. Our study restricted itself to records from unmanaged plots.

### REFERENCE SITES

The Hubbard Brook Experimental Forest (HBEF) covers approximately 3000 ha, with elevations ranging from 222-1015m. Vegetation is fairly representative of northern New England forests, with sugar maples, paper birch and beech dominating the lower to mid-elevations and red spruce and balsam fir dominating higher elevations. Soils are mostly well-drained spodosols with sandy-loam texture and a thick surface organic layer (Bormann and Likens 1979). Ten of the smaller watersheds in the HBEF have been intensively studied regarding their hydrology, biogeochemistry and ecology. These ten watersheds comprise second-growth forests with a history of cutting in the 1880s and 1910s and with some damage sustained after the 1938 hurricane. Although several watersheds have been treated or cut over the past 32 years, one watershed (WS-6) remains unmanaged and has served as a vegetation reference for the HBEF. Our study overlays published mean biomass figures of WS-6 with our findings in Campton and BEF to demonstrate how biomass has accumulated in second-growth forests within the White Mountains region.

The Bowl Research Natural Area is a 607 ha valley located in the southern flank of the White Mountains. Elevation ranges from 575-915 m and in the mid-1970s, northern hardwoods accounted for 88% of the basal area in the lower elevation range (575-650 m) and 50% of the mid-elevation ranges (650-850 m). The basal area in mid elevations was dominated by red spruce (17%). Red spruce basal dominance increased to 28% in higher elevations, where balsam fir and yellow birch comprised 50% of the basal area (Martin 1977). Area I of the Bowl has never been logged and biomass data from this old-growth stand is included in our study. Only plots below 900m were measured for vegetation data within this area. Data from Waterville Valley (Chittenden 1905) come from fifty 1-acre plots of predominantly virgin forests, of which only several were slightly cut.

## Methods

Aboveground tree biomass values for each individual study were determined using established allometric equations (Whittaker et al. 1979; Freedman et al. 1982; Kinerson and Bartholomew 1977 and Hocker and Early 1983). We favored species-specific equations over general hardwood and softwood equations and applied these to all major tree species and most minor species depending on the availability of equations. The equations used were selected on the basis that they were developed within the northeastern US. Biomass values of uncommon species[1], for which there are no appropriate species-specific equations, were estimated using Monteith (1979) general hardwood and softwood equations. The equations developed for HBEF by Whittaker et al. (1979) provide the best known allometric equations for red spruce, sugar maple, beech and yellow birch in the region and were used to estimate biomass for these species in all our study sites. Freedman et al. equations have been tested by sensitivity analyses (Hamburg 1984) and were used to determine biomass estimates of all other species in Campton. Hocker and Early equations were founded on data records from white pine and mixed-hardwood stands near Durham, N.H. and corroborated by empirical studies in BEF. This source offered the greatest number of species-specific equations and was employed in determining biomass estimates for the BEF inventory data.

Allometric equations using dbh and height as independent variables are based on dimensional analysis and their accuracy has been well demonstrated by Siccama et al. (1994) and Hamburg et al. (1997). Although natural log transformations of diameter provide adequate approximations of bole weight (Baskerville 1972; Tritton and Hornbeck 1982), increased efficiency of prediction can be obtained by using height as an additional predictor of branch weight (Hocker and Early 1983). Since tree heights were not inventoried in our study sites, equations developed by Whittaker et al. (1979) were used to estimate this variable.

As little is known regarding the percentage of total carbon allocated to root biomass (Cairns et al. 1997), only aboveground dry biomass for bole and branch weight was considered in our analyses. Leaf biomass was excluded in our study, as previous studies to which we compared our results, did not include leaves in their biomass analyses. Moreover, leaves are known to be a

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[1] APPENDIX A

small proportion of total tree weight and its omission should not substantially alter biomass estimation (Tritton and Hornbeck 1982).

Aboveground dry biomass values for each study site were plotted against forest age to illustrate biomass accumulation and linear and loglinear regressions on mean biomass values were performed to determine annual productivity rate. With respect to the BEF data set, only even-aged stands were statistically analyzed, as it was not possible to assign stand-ages to the all-aged stands. Because inventories for BEF plots were not always taken during the same calendar year, i.e. some plots were inventoried 1 year apart from others, this resulted in a number of age-classes containing only a few cases. To increase statistical power, we rounded off the ages and grouped data that had no ecological basis for separation. We used residual plots to identify outliers and removed these data points before further analyses. We then tested the significance of age, elevation and soil effects on forest productivity in BEF using general linear factorial models. Natural variability in forest growth was estimated using BEF data exclusively, as this was the only data set large enough to provide a sense of natural variability. 95% confidence intervals were established about mean biomass values of each age class. Natural variation in BEF forest productivity was then estimated by comparing the slopes of regression models on the upper and lower bounds of the 95% confidence intervals. Species contribution to biomass growth was evaluated by following trends in both biomass contribution and relative importance of dominant species. Relative importance values (IV) were defined in terms of relative tree density, frequency and basal dominance. In conclusion, we pooled and overlay biomass accumulation data from Campton, BEF, HBEF, the Bowl Research Area and Waterville Valley to provide an overall picture of how these temperate forest ecosystems have grown over the past 150 years.

## Results

### CAMPTON AGRICULTURAL PLOTS

The initial space-for-time substitution study indicated that the Campton old-fields chronosequence experienced a remarkably linear increase in aboveground biomass accumulation from age 33 to 65 [$R^2$ = 0.98; y-intercept = 0.7], with an average annual aboveground productivity rate of 2.6 ± 0.03 Mg ha$^{-1}$ yr$^{-1}$ (Hamburg 1984). Subsequent measures indicate a leveling off in the rate of biomass accumulation after 65 years, when biomass reached 159 ± 37 Mg ha$^{-1}$. Biomass values increased slightly to 162 ± 16 Mg ha$^{-1}$ at 76 years and then to 166 ± 20 Mg ha$^{-1}$ at 81 years. As a chronosequence, the unaltered study sites (site3, 5 and 6) accrued biomass linearly at a rate of 1.79 Mg ha$^{-1}$ yr$^{-1}$ ($R^2$ = 0.88; y = 35.7) from 33 to 81 years (Fig. 2a; Table 3a). As individual study sites with repeat measures, the younger sites show higher rates of biomass accumulation from 1979 to 1997 than do the older sites (Fig. 2b). Site 3 which was 33 years old in 1979, increased biomass at a linear rate of 2.61 Mg ha$^{-1}$ ($R^2$ = 0.97), while site 5 (47 yr. old in 1979) and site 6 (62 yr.) had annual productivity rates of 1.90 Mg ha$^{-1}$ ($R^2$ = 0.94) and 0.66 Mg ha$^{-1}$ ($R^2$ = 0.53) respectively. Repeat measures also show that biomass values attained by the younger sites in later years are comparable to the biomass of older sites in the initial study. Average standard error of mean for aboveground biomass is 17.5 Mg ha$^{-1}$. For forest stands of ages 47, 62, 63 and 65 yr., the standard errors of mean biomass overlap between the initial chronosequence and the repeated measures. Natural log regression on biomass accumulation against forest age ($R^2$ = 0.94) proved a better fit than a linear regression ($R^2$ = 0.88) on the same data points.

We observed notable increases in aboveground biomass of balsam fir, red maple and white ash, and a decrease in white birch (Table 2d.). Trends in phytosociology are presented in Table 2a-c. Balsam fir regeneration is particularly notable as upward trends are seen in biomass values, basal dominance, tree density and importance values (IV) for the two younger sites and an increase in balsam fir density and IV is observed in the older site 6. Overall tree densities of red maple and white ash are diminishing, while biomass from these species is increasing - this is probably due to stand thinning and increase in basal and canopy dominance of a few robust trees. White birch demise is detected in terms of declining biomass dominance, density and IV. Sugar maple and trembling aspen in the older sites suffered decreases in biomass, tree density and IV.

### BEF EVEN-AGED STANDS

Aboveground biomass in BEF accrued linearly for approximately 70 years ($R^2$ = 0.90; annual productivity rate = 1.47 Mg $ha^{-1}$ $yr^{-1}$; y-intercept = 26.8), reached an apparent peak of 202 ± 5.0 Mg $ha^{-1}$ at 110 years and dropped off slightly after this point (Fig. 3c-d; Table 3b). Natural log regression indicates an annual productivity rate of 3.99 Mg $ha^{-1}$ $yr^{-1}$ for the 150 yr. chronosequence ($R^2$ = 0.82; Fig. 3c). Due to the large number of plots for each age category, the standard errors around mean biomass values for each group were remarkably small, with average SE being 6.6 Mg $ha^{-1}$. As with the Campton Agricultural plots, the younger even-aged stands show a higher rate of biomass accumulation than the older stands (Fig. 3b.). Stands that were 10 years old in 1931 accumulated aboveground biomass at a rate of 1.86 Mg $ha^{-1}$ $yr^{-1}$ from 1931-1991 ($R^2$ = 0.99; y-intercept = 28.4). Productivity rate over the same sixty-year period was slightly lower for stands that were 30 years old in 1931 (1.48 Mg $ha^{-1}$ $yr^{-1}$; $R^2$ = 0.98; y-intercept = 13.7), and notably diminished for stands that were already 70 and 90 years old in 1931 (0.43 Mg $ha^{-1}$ $yr^{-1}$; $R^2$ = 0.93 and 0.11 Mg $ha^{-1}$ $yr^{-1}$; $R^2$ = 0.93 respectively). One exception to this trend is seen in stands that were 50 yr. old at the time of the initial cruise plots. These stands accrued biomass at a rate of 1.70 Mg $ha^{-1}$ $yr^{-1}$ ($R^2$ = 0.96) attaining a mean biomass value of 202 ± 5.0 Mg $ha^{-1}$ when they reached stand age of 110 yr.

95% Confidence intervals were drawn around the mean biomass for each age-class and regressions were run on the upper and lower bounds of the 95% confidence values (Fig. 3e).

Natural log regressions on the upper bounds indicated a productivity rate of 2.38 Mg $ha^{-1}$ $yr^{-1}$ for stands in the high biomass content range, and a productivity rate of 2.53 Mg $ha^{-1}$ $yr^{-1}$ for stands in the low biomass range. This difference in biomass accumulation rates suggests that approximately 6% of difference in production is due to natural variability. Shifts in relative biomass dominance of hardwoods and softwoods were also observed. Biomass contribution of softwoods increased from 15.1% to 25.3% between 1931 and 1991, whilst that of hardwoods declined from 84.9% to 74.7% over the same period of time.

### BEF ALL-AGED STANDS

Biomass values in uneven-aged stands ranged from 52 to 246 Mg $ha^{-1}$ in 1931 and 91 to 289 Mg $ha^{-1}$ in 1991 (Fig. 4a). The reason for this large range in stand biomass can be explained by the fact that not all stands in the all-aged plots are fully stocked; this situation being especially true in sites at higher elevations and with shallow soils. The mean biomass of the uneven-aged stands in 1931 is 147.0 ± 3.9 Mg $ha^{-1}$. This mean biomass value rises only slightly after the 1938 hurricane, reaching 152.0 ± 4.5 Mg $ha^{-1}$ in 1939 and increases to 206.5 ± 4.5 Mg $ha^{-1}$ by 1991. Despite the large range in biomass values observed in each data inventory, the large number of plots ($N$ >90) result in small standard errors (mean SE = 4.3 Mg $ha^{-1}$; Fig. 4b). Elevation and impact of soils were found to have significant impact on biomass production (Elev: $p = 0.000$; soils: $p < 0.038$). Age could not be determined and was therefore not factored into statistical analyses. Average hardwood biomass dominance decreased slightly from 84.8% to 81.4% between 1931 and 1991, while that of softwoods increased from 15.2% to 18.6%.

### 150 YEARS OF BIOMASS ACCUMULATION IN THE WHITE MOUNTAINS

Biomass and production trends observed in the Campton Agricultural plots, BEF even-aged stands and HBEF WS-6 were strikingly similar. Forest production in all three areas seem to have leveled off or slowed down considerably at similar productivity rates after the stands had reached the ages of 60-80 years. Fig. 5 presents an overlay of biomass and production values for individual even-aged stands within Campton, BEF and HBEF WS-6 for 150 years after cutting. Biomass values for each age class in Campton fall within the range and standard deviation of biomass values for the same age categories in BEF. Biomass values for HBEF WS-6 are somewhat higher, but the accumulation trend of a linear increase, followed by a leveling off at approximately 80 years, is similar to the trends seen in Campton and BEF. We also observe that the mean biomass value attained by all-aged stands in BEF by 1991 is similar to the biomass value of Area 1 of the Bowl in 1974 and approaching values achieved by Waterville Valley in 1903 and the Bowl in 1994 (Fig. 6).

## Discussion

Biomass accumulation trends observed in Campton and HBEF WS-6 follow models of ecosystem biomass accretion, where biomass rises to a steady state with time and with no indication that ecosystem-biomass peaks before declining to an asymptotic level, a phenomenon explained by continuous regeneration and mortality within the forest system (Peet 1981). The BEF chronosequence does indicate that a biomass peak was reached at 110 years. As this biomass peak was attained by the stands that were 50 yr. old in 1931, we suggest that these plots had reached a stage of stand development where episodic mortality, due to the hurricane of 1938, caused post-disturbance biomass accumulation to exceed steady state before falling to an equilibrium (Peet 1981). All three study sites have also attained comparable biomass values between 60-80 years. Although mean biomass values of HBEF WS-6 are on the higher end of biomass values reached by the BEF even-aged stands, they are still within the range of biomass values attained by BEF stands of similar age-classes. Slight differences in biomass between the study sites for might also be an artifact of how the age-classes were designated within each study area. As the age-classes in BEF were classified in 20-year intervals, the 110-yr. old BEF stands could be considered comparable in age to the 80-yr. old forest in HBEF WS-6.

Similarity in patterns of biomass and production in the study sites are observed in spite of differences in latitude and elevation, heterogeneity of soils, local weather patterns and geological environments. However, biomass values attained by all three study areas are conservative compared to the biomass peaks predicted for the northeast region by JABOWA, a forest growth model that has been applied to vegetation in HBEF WS-6 (Bormann and Likens 1994). Forest-age at which peak or equilibrium biomass is attained by these secondary-growth forests is also earlier than that predicted by the forest growth model.

Apparent decline in biomass and production might be explained through shifts in species composition (Horn 1974) or nutrient limitation (Vitousek and Reiners 1975). Decline in biomass has been observed in other areas where there is a shift in biomass contribution from deciduous to coniferous species (Bormann and Sidle 1990), a phenomenon that is occurring in Campton and BEF. Clearly, production trends in the even-aged stands are insufficient for establishing whether or not forest growth, in terms of biomass accumulation, has indeed decreased as a result of recent anthropogenic influences. Biomass values from old growth and virgin forests in Chittenden (1903), the Bowl Research Area and the all-aged stands from BEF however, help us resolve this issue (Fig. 6). At 100-150 years, the BEF even-aged stands had already reached biomass values that were comparable, if not greater than, the BEF all-aged stands in 1931, which at this time had age distributions ranging from ~150-190 years. These all-aged stands had not yet reached a biomass peak in 1931 and continued to accumulate biomass, reaching a mean biomass value of 206.5 ± 4.5 Mg ha$^{-1}$ in 1991, when they would have reached stand-ages of ~210-250 years. The BEF all-aged stands by this time are seen to approximate the structure and level of productivity achieved by the reference old-growth forests of the Bowl (Area 1) and Waterville Valley.

In conclusion, we observed that natural variance in biomass production accounts for approximately 6% of differences seen in biomass accumulated in the Bartlett region. This implies that changes in productivity of less than 6% will be difficult if not impossible to detect within this site and possibly this region. We also conclude that it is not apparent if overall productivity in terms of biomass production has suffered as a result of recent anthropogenic influences, as biomass values reached by the older even-aged stands today are comparable to values attained by old-growth forests before WWII industrialization. This is not to suggest that these forests have not been impacted, but rather to caution the use of biomass as an indicator of forest health, as a decline in the dominance of one tree species might favor the increase in the dominance of another. It is also important not to assume that biomass values of Waterville Valley in 1905 or BEF uneven-aged stands in 1931 are representative of biomass values attained by other forest stands in the northeast in the early 1900s. Still the issue of spatial heterogeneity are to a certain extent resolved with the BEF data, as the even-aged stands seem to be reaching the biomass values and production rates of the old-growth stands within the same forest region. Considering the productivity rates attained by all our study sites, it is unlikely that biomass values will extend past mean biomass values of 200-220 Mg/ ha in the near future.

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## ***List of Tables, Figures and Appendices.***

Table 1. Study site characteristics.

| *Site* | **Area (ha)** | **Age (yr.)** | **Elevation (m)** | **History/ Site Char.** | **Managed, M Unmanaged, UM** | **Data Records** |
|---|---|---|---|---|---|---|
| *Bartlett* [2] | 1052 | Old-growth;<br>2nd-growth: 10 – 150 yr. | 200-850 | Commercially logged from 1870; Pastureland. Estd. as experimental forest in 1929 | M, UM | 1931-32<br>1939-40<br>1991-92 |
| *Bowl Area I* [3] | | Old-growth 35-200> | 575-915 | Old-growth forest | UM | 1974<br>1994 |
| ***Campton*** [4] | Sites located within 2km area | 33-81 | 470-550 | Agricultural, plowed old Fields | UM | 1978<br>1987<br>1992<br>1997 |
| ***Hubbard Brook*** | | | | | | |
| *WS-6* | 13.23 | 87 | 540-780 | Selectively cut ~1909 Heavy cutting in 1917 | UM | 1965<br>1977<br>1982<br>1987<br>1992<br>1997 |

**Table 2a. Basal area of tree species in sites 3, 5 and 6 of Campton Agricultural Chronosequence (m2 per ha).**

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[2] Data Courtesy of Bill Leak and Marie-Louise Smith, USFS in Durham, N.H.

[3] Data Courtesy of Wayne Martin, USFS, HBEF.

[4] Data Courtesy of Steve Hamburg, Brown University.

***Site 3***

| | *original measurement* | *repeat measures* | | |
|---|---|---|---|---|
| *Forest Age/ yr.* | *30-35* | **39-44** | **44-49** | **49-54** |
| *Species* | | | | |
| Balsam fir | 1.1 | 1.3 | 1.9 | 2.9 |
| Red Spruce | 1.5 | 1.4 | 1.0 | 0.8 |
| White pine | 9.6 | 10.7 | 13.4 | 10.7 |
| Aspen | 1.0 | 1.3 | . | . |
| Sugar maple | 0.1 | 0.2 | 0.1 | 0.4 |
| Red maple | 9.3 | 12.2 | 13.1 | 14.4 |
| White ash | 0.7 | 1.2 | 1.6 | 1.6 |
| White birch | . | . | . | . |
| **Total** | 25.2 | 30.4 | 31.7 | 31.5 |

***Site 5***

| *Forest Age/ yr.* | *45-50* | **53-58** | **58-63** | **63-68** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 1.3 | 2.5 | 3.6 | 5.5 |
| Red Spruce | 0.1 | 0.1 | 0.1 | 0.4 |
| White pine | 1.8 | 2.5 | 3.1 | 4.3 |
| Aspen | 10.1 | 7.3 | 7.4 | 6.1 |
| Sugar maple | 2.8 | 4.7 | 2.8 | 3.7 |
| Red maple | 6.4 | 6.6 | 9.8 | 10.8 |
| White ash | 2.6 | 2.4 | 2.8 | 3 |
| White birch | 1.2 | 2.1 | 1.5 | 0.6 |
| **Total** | 28.1 | 28.9 | 32.0 | 36.2 |

***Site 6***

| *Forest Age/ yr.* | *60-65* | **73-78** | **78-83** |
|---|---|---|---|
| *Species* | | | |
| Balsam fir | 8.9 | 8.2 | 7.4 |
| Red Spruce | 6.8 | 4.8 | 5.5 |
| White pine | 0.3 | 0.9 | 0.4 |
| Aspen | 2 | 1.5 | 1.7 |
| Sugar maple | 0.6 | 0.4 | 0.3 |
| Red maple | 13.1 | 14.4 | 17 |
| White ash | . | . | 0.1 |
| White birch | 1.1 | 1.4 | . |
| **Total** | 34.1 | 33.3 | 33.7 |

Forest Ages that are underlined and italicized indicate original measurements in 1979.
Forest Ages that are in bold indicate repeat measurements.

**Table 2b.** **Tree density in sites 3, 5 and 6 of Campton Agricultural Chronosequence (# trees per ha).**

***Site 3***

| *Forest Age/ yr.* | *30-35* | **39-44** | **44-49** | **49-54** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 263 | 244 | 319 | 438 |
| Red Spruce | 144 | 119 | 81 | 63 |
| White pine | 307 | 213 | 238 | 125 |
| Aspen | 88 | 56 | 0 | 0 |
| Sugar maple | 150 | 138 | 94 | 81 |
| Red maple | 2388 | 1431 | 1100 | 925 |
| White ash | 263 | 156 | 156 | 131 |
| **Total** | 3650 | 2394 | 2013 | 1800 |

***Site 5***

| *Forest Age/ yr.* | *45-50* | **53-58** | **58-63** | **63-68** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 433 | 858 | 1208 | 1491 |
| Red Spruce | 42 | 58 | 150 | 158 |
| White pine | 25 | 25 | 25 | 17 |
| Aspen | 383 | 242 | 217 | 192 |
| Sugar maple | 1000 | 825 | 450 | 550 |
| Red maple | 592 | 483 | 608 | 558 |
| White ash | 167 | 125 | 133 | 133 |
| White birch | 58 | 42 | 17 | 8 |
| **Total** | 2733 | 2767 | 2983 | 3458 |

***Site 6***

| *Forest Age/ yr.* | *60-65* | **73-78** | **78-83** |
|---|---|---|---|
| *Species* | | | |
| Balsam fir | 612 | 1303 | 1954 |
| Red Spruce | 377 | 318 | 323 |
| White pine | 16 | 15 | 8 |
| Aspen | 38 | 18 | 23 |
| Sugar maple | 78 | 70 | 31 |
| Red maple | 433 | 322 | 323 |
| White birch | 12 | 12 | 23 |
| **Total** | 1598 | 2258 | 3085 |

Forest Ages that are underlined and italicized indicate original measurements in 1979.
Forest Ages that are in bold indicate repeat measurements.

**Table 2c. Importance values of tree species in sites 3, 5 and 6 of Campton Agricultural Chronosequence.**

***Site 3***

| *Forest Age/ yr.* | *30-35* | **39-44** | **44-49** | **49-54** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 8 | 9 | 14 | 16 |
| Red Spruce | 7 | 8 | 8 | 6 |
| White pine | 20 | 19 | 24 | 19 |
| Aspen | 6 | 6 | . | . |
| Sugar maple | 6 | 6 | 7 | 6 |
| Red maple | 38 | 38 | 37 | 38 |
| White ash | 7 | 7 | 6 | 8 |
| Others | 8 | 7.6 | 5.3 | 7.5 |

***Site 5***

| *Forest Age/ yr.* | *45-50* | **53-58** | **58-63** | **63-68** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 11 | 17 | 21 | 23 |
| Red Spruce | 2 | 3 | 6 | 6 |
| White pine | 5 | 6 | 6 | 7 |
| Aspen | 20 | 15 | 14 | 11 |
| Sugar maple | 21 | 19 | 12 | 12 |
| Red maple | 20 | 17 | 21 | 19 |
| White ash | 9 | 8 | 8 | 8 |
| White birch | 6 | 6 | 3 | 2 |
| Yellow birch | 2 | 2 | 2 | 2 |
| Others | 4 | 7 | 7 | 10 |

***Site 6***

| *Forest Age/ yr.* | *60-65* | **73-78** | **78-83** |
|---|---|---|---|
| *Species* | | | |
| Balsam fir | 27 | 32 | 35 |
| Red Spruce | 19 | 13 | 15 |
| White pine | 3 | 3 | 1 |
| Aspen | 7 | 4 | 4 |
| Sugar maple | 6 | 4 | 2 |
| Red maple | 27 | 24 | 26 |
| White birch | 4 | 4 | 2 |
| Others | 7 | 16 | 15 |

Forest Ages that are underlined and italicized indicate original measurements in 1979.

Forest Ages that are in bold indicate repeat measurements.

**Table 2d.** **Species specific aboveground biomass in sites 3, 5 and 6 of Campton Agricultural Chronosequence (Mean +/- SE/ Mg per ha)**

***Site 3***

| *Forest Age/ yr.* | *30-35* | **39-44** | **44-49** | **49-54** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 3.9 | 4.8 | 6.7 | 11.4 |
| Red Spruce | 6.3 | 5.7 | 4.6 | 3.3 |
| White pine | 26.6 | 31.9 | 43 | 34.9 |
| Aspen | 3.4 | 5.3 | 0.1 | 0 |
| Sugar maple | 0.5 | 0.7 | 0.4 | 1.9 |
| Red maple | 34.5 | 51.1 | 57.7 | 65.7 |
| White ash | 2.8 | 5.8 | 8.1 | 8.5 |
| **Total** | 80.7+/-4 | 108+/-5 | 123+/-10 | 128+/-11 |

***Site 5***

| *Forest Age/ yr.* | *45-50* | **53-58** | **58-63** | **63-68** |
|---|---|---|---|---|
| *Species* | | | | |
| Balsam fir | 4.7 | 8.3 | 11.5 | 16.7 |
| Red Spruce | . | 0.2 | 0.4 | 1.5 |
| White pine | 8 | 7.9 | 10.4 | 16.5 |
| Aspen | 39.7 | 31 | 32.2 | 22.1 |
| Sugar maple | 18.8 | 24.1 | 15.5 | 16.5 |
| Red maple | 30 | 29.5 | 44.9 | 50.7 |
| White ash | 11.5 | 15.7 | 19.3 | 20.7 |
| White birch | 11.9 | 12.5 | 9.1 | 3.3 |
| Yellow birch | 1.6 | 2.4 | 1.3 | 4.8 |
| **Total** | 126+/-15 | 133 +/- 20 | 148 +/- 29 | 159 +/- 37 |

***Site 6***

| *Forest Age/ yr.* | *60-65* | **73-78** | **78-83** |
|---|---|---|---|
| *Species* | | | |
| Balsam fir | 36.6 | 31.6 | 24.9 |
| Red Spruce | 29.6 | 20.9 | 31.7 |
| White pine | 1.1 | 2.6 | 1.1 |
| Aspen | 9.4 | 7.5 | 8.2 |
| Sugar maple | 3.5 | 1.8 | 1.6 |
| Red maple | 70.1 | 76.4 | 92.2 |
| White birch | 9.7 | 8.9 | 0 |
| **Total** | 165+/-24 | 162+/-15 | 166+/-20 |

Forest Ages that are underlined and italicized indicate original measurements in 1979.
Forest Ages that are in bold indicate repeat measurements.

Table 3a. Aboveground biomass accumulation for Campton chronosequence (Mean ± SE/ Mg per ha).

**Campton Agricultural Chronosequence**
(even-aged forests)

| *Forest Age/ yr.*[5] | **33** | **42** | **47** | **52** | **55** | **57** | **60** | **62** | **63** | **65** | **76** | **81** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Wood biomass/ Mg per ha* | | | | | | | | | | | | |
| Original data | 81± 5 | | 126± 15 | | | 151± 11 | | 165± 24 | 173± 14 | 171± 14 | | |
| Repeated measures | | 108±5 | 123± 10 | 129± 11 | 133±20 | | 148± 29 | | | 159± 37 | 162± 16 | 166± 20 |

Table 3b. Aboveground biomass values for even-aged stands in Bartlett Experimental Forest (Mean ± SE/ Mg per ha).

**Bartlett Experimental Forest**
(even-aged forests)

| *Forest Age/ yr.* | **10** | **20** | **30** | **40** | **50** | **60** | **70** | **80** | **90** | **100** | **110** | **130** | **150** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *No. of plots* | 4 | 4 | 27 | 28 | 34 | 31 | 13 | 6 | 29 | 1 | 31 | 7 | 1 |
| *Wood biomass/ Mg per ha* | 41±13 | 73±17 | 64 ± 2 | 71 ± 3 | 99± 5 | 113± 4 | 140±9 | 124± 11 | 149±4 | 156 | 202± 5 | 150± 11 | 162 |

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[5] Forest age is presented here as the mid-point of each age-range

## APPENDIX A

### ALLOMETRIC EQUATIONS USED TO CALCULATE ABOVEGROUND LIVING TREE BIOMASS

### Equations developed by Freedman et al. (1982) followed the form:

$$\boxed{W = C*e^{[A + B \ln (D^2 * H)]}}$$

W : aboveground biomass in kg
D : dbh of tree in cm
H : height of tree in m

| *Species* | *Code* | **A** | **B** | **C** |
|---|---|---|---|---|
| Balsam fir | BF | -2.6169 | 0.8597 | 1.03 |
| Red maple | RM | -2.9178 | 0.9052 | 1.01 |
| White-gray birch | WB | -2.8747 | 0.9089 | 1.03 |
| Trembling aspen | ASP | -3.2992 | 0.9333 | 1.02 |

### Equations developed by Hocker and Early (1983) followed the form:

$$\boxed{WT = e^{(A + B \ln D * H)}}$$

WT : bole and branch weight in g
D : dbh in cm
H : height in m

| *Species* | *Code* | **A** | **B** |
|---|---|---|---|
| Basswood | BW | 4.10 | 1.18 |
| Eastern hemlock | EH | 4.55 | 1.26 |
| Gray birch | GB | 2.81 | 1.59 |
| Hop hornbeam | HH | 3.36 | 1.47 |
| Mountain maple | MM | 2.60 | 2.19 |
| Paper birch | PB | 3.71 | 1.38 |
| Pin cherry | PC | 3.32 | 1.44 |
| Red maple | RM | 3.54 | 1.40 |
| Red oak | RO | 3.62 | 1.45 |
| Striped maple | SM | 3.50 | 1.44 |
| Witch hazel | WH | 3.28 | 1.49 |
| White pine | WP | 3.88 | 1.29 |

### Equations developed by Kinerson and Bartholomew (1977) followed the form:

$$\begin{aligned} St &= e^{(2.379 + 1.565 * \ln D * H)} \\ Br &= e^{(1.733 + 2.656 * \ln D * H)} \\ Fo &= e^{(-0.952 + 2.586 * \ln D * H)} \end{aligned}$$

St : stem wood and bark biomass in g
Br : branch wood and bark biomass in g
Fo : foliage biomass in g
D : dbh in cm
H : height in m

### Equations developed by Whittaker et al. (1974) followed the form:

$$WT = 10^{[A + B * \log10 (PV)]}$$

WT : aboveground dry biomass in g
PV : parabolic volume in $cm^3$

| ***Species*** | *Code* | *A* | *B* |
|---|---|---|---|
| Sugar maple | SM | -0.0201 | 0.9768 |
| Beech | BE | 0.1733 | 0.9526 |
| Yellow birch | YB | 0.0974 | 0.9615 |
| Red spruce | RS | 0.8219 | 0.7966 |