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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

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Summary

1. Age-related reductions in stand biomass accumulation are frequently observed in old-growth forests. The phenomenon may be caused by reduced production, increased mortality or both. The relative importance of production and mortality is not well studied, so the mechanisms controlling age-related decline of stand biomass accumulation remain unclear.

2. In this study, conducted in a *Quercus*-dominated deciduous forest in the Northeastern USA, we examined whether age-related decline in stand above-ground biomass (AGB) accumulation could be explained by reduction of above-ground net primary production (NPP) (growth of surviving trees) that may be associated with (i) physiological constraints within individual trees or (ii) changes in stand structure, or by (iii) age-related, increasing tree mortality in stands up to 135 years old. Few previous studies have tested these hypotheses simultaneously within the same forest.

3. We did not find evidence for a reduction in individual tree growth associated with age-related physiological constraints, in terms of foliar carbon assimilation capacity, photosynthesis/respiration balance, nitrogen availability or hydraulic constraints on carbon gain. Over the period of 1937–2006, we did not observe alterations in stand structure, and the above-ground NPP of the *Quercus* forest was generally stable.

4. However, we did find that the primary mechanism driving age-related decline of stand AGB accumulation was biomass loss due to the death of large, dominant trees. Our results indicate that shifts in mortality from the loss of small trees to the loss of large trees, rather than changes in above-ground NPP, drives age-related decline in stand AGB accumulation in this forest.

5. *Synthesis.* We found that within the range of stand development stages analysed, the age-related decline of stand AGB accumulation in a *Quercus*-dominated forest was primarily due to mortality of large, dominant trees and not due to changes in above-ground NPP associated with tree physiology, individual tree growth or stand structure. This result indicates that tree demography and the influence of climate change on disturbances may need to be integrated into models to predict the change of above-ground carbon stock of some old-growth forests.

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Introduction

Forest woody biomass is an important global carbon stock, so it is critical to understand the dynamics of biomass accumulation of forest stands (Cooper 1983). It is generally accepted that the rate of stand biomass accumulation peaks in the early stage of development, usually at the time of canopy closure or peak stand leaf area, and declines thereafter. Such age-related decline in stand biomass accumulation has been widely observed in various empirical studies (Turner & Long 1975; Binkley & Greene 1983; Grier *et al*. 1989; Acker *et al*. 2002; Taylor & MacLean 2005; McMahon, Parker & Miller 2010), potentially reducing the capacity for forests to become sinks for carbon (Hurtt *et al*. 2002).

Stand biomass accumulation is the net result of production and mortality. Therefore, age-related decline of stand biomass accumulation could be attributable to declined production, increased mortality or both. Age-related decline in net primary production (NPP) has been widely observed and studied extensively (see review, Gower, McMurtrie & Murty 1996; Ryan, Binkley & Fownes 1997) and is shown to be primarily responsible for a decline in the rate of stand biomass accumulation in some cases; for example, in Douglas-fir forests of the Pacific Northwest USA, stand biomass accumulation was closely associated to NPP, particularly for early stages of stand development (Grier *et al*. 1989). Alternatively, long-term studies in several old-growth stands have showed that mortality is roughly equal to or higher than production of surviving trees, and thus stand biomass accumulation is close to zero or negative (Grier & Logan 1977; Binkley & Greene 1983; DeBell & Franklin 1987). Given the fact that the production of surviving trees of old-growth stands was in general significantly lower than that of younger stands in these early studies, Ryan, Binkley & Fownes (1997) concluded that 'low net growth rate in old-growth stands apparently results from poor growth (i.e. declining growth of surviving trees), not high mortality'. However, more recent empirical studies have not supported this conclusion. For instance, in some coniferous forests, it was found that mortality could be an equally important or a primary factor that contributed to reduced biomass accumulation in old-growth stands (Acker *et al*. 2002; Taylor & MacLean 2005). In summary, the relative importance of production and mortality in shaping the age-related decline of stand biomass accumulation is not well understood, and the mechanisms responsible for age-related decline in forest biomass accumulation remains uncertain.

The age-related decline of forest stand biomass accumulation is commonly interpreted as the consequence of a large decrease in productivity as forest ageing, but the mechanism causing age-related decline of NPP remains unclear. Numerous hypotheses have been developed to explain the phenomenon as a function of age- or size-dependent physiological constraints leading to reductions in growth of individual trees (see review, Gower, McMurtrie & Murty 1996; Ryan, Binkley & Fownes 1997; Smith & Long 2001; Weiner & Thomas 2001), including (i) photosynthesis–respiration imbalance, (ii) increased nutrient limitation, (iii) increased hydraulic resistance and (iv) reduced allocation to stem production. In addition, Ryan, Binkley & Fownes (1997) and Bond (2000) suggest that genetic changes associated with older meristems may constrain growth of trees as they age, but this has not been experimentally confirmed. Alternatively, age-related decline of forest NPP has also been described as an emergent property of stand dynamics linked to structural change within the forest. Binkley (2004) proposed that near canopy closure, the increasing dominance of large trees would lead to declining resource use efficiency of nondominant trees as the result of intensified competition, and hence reduced stand growth; during further stand development, stand decline was attributed to the inability of larger, older trees to maintain growth, despite their dominance in resource use. Similar hypotheses were also suggested by Smith & Long (2001). Testing these hypotheses is problematic because sufficiently long-term growth data from old forests are rare. Subsequently, most studies addressing stand structure hypotheses can only address a few key expectations (Binkley *et al*. 2002; Binkley 2004; Fernandez & Gyenge 2009).

Mortality of older trees is a stand-level phenomenon that may reduce forest stand biomass accumulation through two pathways. First, intuitively, biomass loss due to mortality reduces living biomass and may be the primary factor to affect forest biomass accumulation. This mechanism has been supported by two recent empirical studies in conifer forests (Acker *et al*. 2002; Taylor & MacLean 2005). Second, mortality could temporarily remove leaf area, and thus decrease NPP. Some studies suggest that mortality does not occur frequently enough to significantly reduce productivity in older forests (Ryan, Binkley & Fownes 1997), but a more recent model simulation indicates that biomass loss due to mortality of larger, older trees, which cannot be compensated for through higher production by smaller trees, may dominate the later stage of forest decline (Berger, Hildenbrandt & Grimm 2004). Overall, more empirical studies are needed to examine the role of mortality in shaping stand biomass accumulation over the age.

Although these major hypotheses associated with age-related decline of stand biomass accumulation have been individually tested for decades in numerous studies, results are not consistent, thereby generating debate among ecologists. One particular knowledge gap is that few studies have examined multiple mechanisms simultaneously within the same forest. In this study, conducted in a *Quercus*-dominated deciduous forest in the Northeastern USA, we examined whether age-related decline of stand above-ground biomass (AGB) accumulation could be explained by reduction in above-ground NPP that

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may be associated with (i) physiological constraints in individual trees (including photosynthesis–respiration imbalance, nutrient limitation, and hydraulic constraint) or (ii) changes in stand structure and canopy dominance; or by (iii) increasing biomass loss due to age-related tree death, recognizing that these mechanisms were not mutually exclusive. Ultimately, we need to understand the mechanisms controlling age-related decline of forest stand biomass accumulation to accurately predict the long-term capacity of forests to sequester carbon in living woody biomass.

Materials and methods

STUDY SITE

Black Rock Forest (BRF) is a 1500 ha preserve in the Hudson Highlands region of New York (41°24′ N, 74°01′ W). It has been managed as a preserve without significant disturbance since 1928. The forest is *Quercus*-dominated (see Appendix S1 in Supporting Information), typical of secondary growth forests that characterize the Northeastern United States (Schuster *et al.* 2008). For the most dominant species *Quercus rubra*, the oldest trees that have been dated by tree-ring analysis are about 150 years old (N. Pederson, pers. comm.). Details of the BRF are reported in Schuster *et al.* (2008). This research was conducted on four *Q. rubra*-dominated neighbouring stands that formed a chronosequence (35-, 70-, 90- and 135-year plots) and eight long-term monitored plots that aged between 98 and 123 years in 2006 and were monitored since 1937 (Fig. 1a, Table S1 in Supporting Information). Although the age span in this study does not cover the entire life span of *Quercus* spp., it is representative of the current status of regenerating *Quercus* deciduous forests in the Northeastern USA (see Fig. S1 in Supporting Information). Tree species composition and estimated living AGB of studied plots are shown in Fig. 1b,c.

STUDY DESIGN

We first confirmed the age-related decline of stand AGB accumulation in the BRF by comparing AGB of chronosequence plots and traced the last 70 years of AGB development on long-term plots. Then, we examined whether the observed age-related decline could be explained by (H1) changes in tree physiology related to photosynthesis–respiration balance, nutrient limitation and/or hydraulic constraints; (H2) changing stand structure as reflected by growth dominance or (H3) age-related change in mortality. H1 and H2 mainly affect stand AGB accumulation through reducing NPP, while H3 directly cause biomass loss and may reduce NPP.

H1 was tested based upon six subhypotheses: H1-1: The capacity of foliar carbon fixation decreases with tree age; H1-2: The ratio of photosynthesis to respiration (foliar A/R and whole-tree foliar photosynthesis/woody respiration) decreases with tree age; H1-3: Foliar nitrogen and protein decrease, while carbon to nitrogen ratio (C/N) increases with tree age; H1-4: Hydraulic limitations to carbon gain increase with tree age; H1-5: The AGB growth of individual trees and the growth efficiency (i.e. AGB growth relative to the leaf area sustained) decreases with tree age, given that the physiological constraints examined in H1-1 to H1-4 would finally limit the growth of individual trees (Weiner & Thomas 2001); and H1-6: The canopy annual net foliar exchange decreases with stand age. These subhypotheses were tested by measuring tree physiological characteristics of the dominant tree species, *Q. rubra*, within the stand chronosequence

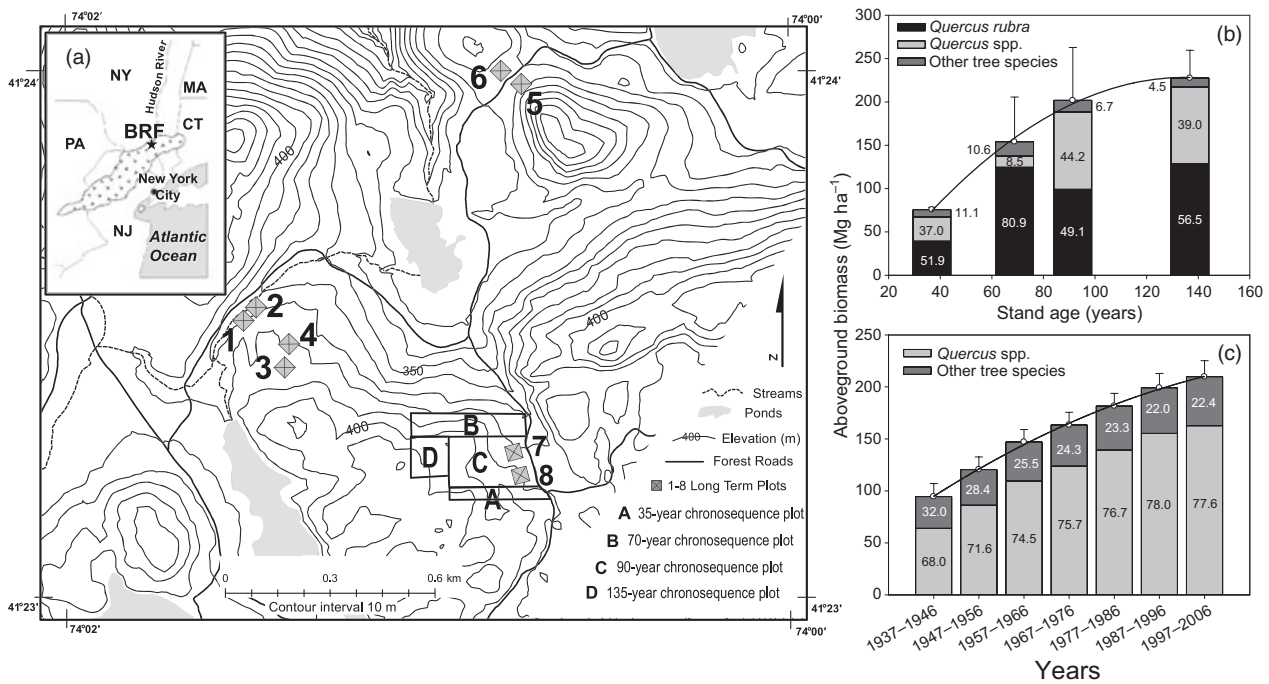


Fig. 1. Map of the Black Rock Forest (BRF) and the above-ground biomass (AGB) of studied plots. (a) map of the BRF showing long-term plots (numbered squares) and stand chronosequence plots (marked with letters). (b) AGB of *Quercus rubra*, other *Quercus* spp. and other tree species is shown for four stand chronosequence plots in 2006. (c) decadal average of AGB of *Quercus* spp. and other tree species in eight long-term plots during 1937–2006. The proportion of AGB (%) is marked for each composition. Error bars indicate the standard error of total AGB ($n = 2$ for stand chronosequence plots and $n = 8$ for long-term plots). The total AGB is fitted with a quadratic curve to show the age-related, declining trend ($R^2 > 0.99$).

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plots. H1-1 was tested by comparing leaf gas exchange parameters and Rubisco activity. To test H1-2, foliar A/R was calculated and the ratio of whole-tree foliar photosynthesis to woody respiration was estimated by the formula (A × total leaf area of the tree)/(stem CO_2 efflux rate × trunk area of the tree) with the area-based stem CO_2 efflux data of 35-, 90- and 135-year plots from (Bowman 2005). H1-3 was examined by measuring foliar nitrogen, carbon and protein components. Tree height, leaf carbon stable isotope ratio ($\delta^{13}C$) and tree Huber value (conducting xylem area: supported leaf area) were combined to assess H1-4. H1-5 was assessed by estimating AGB growth rate utilizing allometric relationships and tree-ring width records. H1-6 was tested by modelling canopy net carbon exchange of studied plots. We did not address allocation hypotheses because this study focused on AGB in the BRF.

H2 was tested with survey data of long-term plots and compared with the prediction (Binkley 2004) that 'the decline in stand-level growth near canopy closure is driven by increasing dominance of larger trees, leading to declining efficiency of resource use of smaller trees; with further stand development,…old trees enter a phase where their growth no longer keeps pace with their increasing dominance of site resources.' A full test of this hypothesis was difficult due to the lack of historical data on resource use efficiency, so we only tested the key expectation that tree growth dominance would initially increase and then subsequently decrease throughout the survey period (1937–2006).

H3 was tested based upon two subhypothesis: H3-1: age-related decline of stand AGB accumulation is mainly caused by increasing mortality biomass loss; H3-2: age-related decline of stand AGB accumulation is mainly caused by increasing mortality-led NPP loss. H3 was addressed by analysing the record of AGB accumulation, above-ground NPP and mortality in long-term plots during 1937–2006. If H3-1 was supported, we predicted that mortality biomass loss would increase with stand development, while above-ground NPP (i.e. growth of the trees that survived the measurement period, Binkley & Arthur 1993) would be stable or increase through time. If H3-2 was supported, we predicted that above-ground NPP would decline over time and be correlated with mortality.

ABOVE-GROUND BIOMASS

The AGB of 15 of the most abundant species recorded in BRF surveys was estimated from the diameter at breast height (1.3 m D) using allometric regression equations ($AGB = aD^b$, see Table S2 for parameters a and b, Brenneman *et al.* 1978). Allometric studies of *Q. rubra* and *Quercus prinus* in the BRF indicated that these equations were the most accurate among the available ones and were developed in locations with similar site conditions and species composition to the BRF (Schuster *et al.* 2008). For the other 11 less common species, we used the general New-York-State-derived hardwood equation of (Monteith 1979) (see Table S2). Living materials in tree stumps, roots and understorey vegetation were omitted from these formulae. The individual AGB estimates were summed to estimate AGB for each plot.

LEAF PHYSIOLOGY AND CHEMISTRY

In June 2003, 12–23 *Q. rubra* trees were selected for each chronosequence plot. Physiological measurements were conducted on one sunlit upper canopy leaf for each tree. A steady-state response of photosynthesis (A) to internal leaf CO_2 partial pressure (A-C_i Curve) and a respiratory temperature response curve were generated on the same leaf. The photosynthesis (A, 300 μmol mol^{-1} C_i and saturating light) and respiration (R) rates were reported in area-, mass- and nitrogen-based units. The A-C_i curves were fitted to a mechanistic model (Farquhar, Caemmerer & Berry 1980), and respiration–temperature curves were fitted to a modified Arrhenius equation. Parameters including the maximum carboxylation rate of Rubisco (V_{cmax}), RuBP regeneration capacity mediated by maximum electron transport rate (J_{max}), respiration rate at a base temperature (R_0), temperature response coefficient (E_0) and the commonly used Q_{10} were calculated. The leaf material was then used to determine specific leaf area (SLA), protein content, Rubisco activity, leaf nitrogen (on area and mass basis, N_{area} and N_{mass}), C/N and $\delta^{13}C$. The photosynthetic nitrogen use efficiency (PNUE) at A was calculated as the photosynthetic rate per gram of leaf nitrogen. The details of gas exchange measurements, curve fitting and leaf analysis are described in Appendix S1.

The same measurements were repeated in mid-September and late October on a subset of six randomly selected trees in the 35-, 90- and 135-year plots.

TREE CHARACTERISTICS AND TREE-RING GROWTH

For each tree, we measured D, tree height and sapwood area. Foliar biomass was calculated using allometric equations (after Hocker & Earley 1983; see Table S2). Total tree leaf area was estimated for each tree using foliar biomass and SLA. Huber value was calculated as sapwood cross-sectional area per unit leaf area (Tyree & Ewers 1991). Details of these measurements are described in Appendix S1.

A tree core taken low on the trunk was used to age the tree and determine tree growth rate through time. Tree-ring growth was determined for each core, and average AGB growth during 1998–2002 was calculated for each tree using the incremental ring width and the allometric relationship. The AGB growth per unit leaf area was also calculated to compare the growth efficiency between age classes. Age determination was achieved using the cross-dating method, and the long-term AGB accumulation trajectory was determined using the cross-dated ring width and the allometric relationship for 1877–2002. We also calculated the historical AGB growth rate and the relative growth rate (RGR) of AGB, as $(\ln Mass_n - \ln Mass_{n-1})/1$ (year), where $Mass_n$ and $Mass_{n-1}$, respectively, represented tree ABG of the current and the previous year.

CANOPY NET CARBON EXCHANGE

The one-dimensional, multilayer model NEEMo was used to assess the age effect on annual photosynthesis and respiration of the canopy for each stand in the chronosequence (see Appendix S1 and Table S4 for a brief description; Whitehead *et al.* 2004a,b). Stand leaf area index (L) was measured using litter traps and hemispherical photographs (see Appendix S1). The litter trap results were used to calculate the relative contribution of each species (f), while the hemispherical photograph results, which allow adjustment for seasonal variation of L, were used to model canopy carbon exchange.

Daily weather data for 2003 (recorded by the BRF environmental monitoring network) were used in the model to estimate annual gross primary productivity (A_G), annual night-time foliar respiration (R_f) and annual net foliar exchange ($A_N = A_G - R_f$). These values were multiplied by the canopy fraction of *Quercus* spp. (f_Q), assuming that the gas exchange properties of other *Quercus* species were the same as *Q. rubra*. The canopy quantum yield of electron transport (α_{can}), canopy absorbance of photosynthetically active radiation (Q_{can}) and annual canopy light use efficiency (ε_{can}, defined as the molar ratio of A_G to Q_{can}) were calculated. The sensitivities of the model to the

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photosynthetic parameters V_{cmax}, J_{max}, L, R_0 or E_0 were estimated by increasing or decreasing each of these five parameters up to 40% and re-running the model with no changes in values of other parameters.

STAND DOMINANCE

Stand growth dominance was analysed with the growth survey data of 1189 trees within the eight long-term plots from 1937 to 2006, with the number of live trees surveyed for each decade (1937–46 to 1997–2006) ranging between 450 and 817. For each decade, all trees surviving the whole period were ranked by biomass (decadal mean) from the smallest to largest, and then used to estimate the growth dominance: a cumulative curve was plotted with cumulative growth (annual) against cumulative biomass (Binkley 2004; Binkley *et al.* 2006), and a coefficient of growth dominance (CGD) was calculated (defined as the area below the 1 : 1 line minus the area below the growth dominance curve, as a proportion of the area beneath the 1 : 1 line, $-1 < CGD < 1$, Binkley *et al.* 2006). Overall, positive CGD indicate growth dominance, that is. the growth of large trees is greater than their contribution to total stand mass and *vice versa* (termed as reverse dominance).

STAND AGB ACCUMULATION, ABOVE-GROUND NPP AND MORTALITY LOSS

Stand AGB accumulation, above-ground NPP and mortality losses were estimated in the eight long-term plots mentioned earlier. Stand AGB accumulation was estimated as the difference of total living AGB between two observations; mortality loss was defined as the AGB loss of all trees that died during the observation interval and above-ground NPP was the total growth of all surviving trees, including in-growth (trees growing into the smallest inventoried size class) and growth of surviving trees. These variables were estimated for each plot on a decadal basis and presented as annual averages (see Appendix S1).

MORTALITY RATE AND STRUCTURE

Mortality dominance was assessed for the loss of individual and AGB using a similar approach to that used to analyse growth dominance. The number of trees that died in each plot was counted for each decade, and then averaged to obtain an annual mean (individual ha^{-1} $year^{-1}$). Annual tree deaths (of individual or AGB loss) and AGB data of all surveyed trees were then used to plot cumulative curves of mortality and to calculate a coefficient of mortality dominance for individuals (CMD-IND) and biomass (CMD-AGB), respectively, for each decade. The annual mortality (m) and an exponential mortality coefficient (λ) were calculated with the standard approach of $\lambda = \ln(N_0/N_t)/t$ and $m = 1 - e^{-\lambda}$ (Sheil, Burslem & Alder 1995), where N_0 is the number of living trees observed at the beginning of a decade; N_t is the number of trees within the same cohort that survived until the end of the decade; $t = 10$ (years) is the observation interval.

DATA ANALYSIS

A one-way analysis of variance (ANOVA) was used to test the age effect for all variables related to leaf physiology and tree characteristics of the chronosequence. The interactive effects of season and age on leaf physiology were tested using a repeated measurement ANOVA. Significance threshold was set at $P = 0.05$, and data were log or square root transformed to fulfil the assumptions of normality and homoscedasticity. Where significant age effect was detected, Fisher's LSD was used for multiple comparisons among age classes. The long-term trend of tree-ring growth was fitted using linear regression.

The effect of age on stand AGB accumulation, mortality loss and above-ground NPP was analysed with ANCOVA, with plot as a main factor to account for the effect of initial stand age and site quality, and decade as a covariate (with value 1–7) to account for the trend with ageing. This design accounted for the effect of repetitive measurements in each plot while expecting a linear monotonic relationship between variables and stand age. The relationship between AGB accumulation and mortality loss was analysed with ANCOVA, in which AGB accumulation was used as a dependent variable, while plot and mortality were used as a main factor and covariate, respectively. The relationship between above-ground NPP and mortality (of individual or biomass loss) was analysed with the same approach, with above-ground NPP as a dependent variable.

Results

AGE-RELATED DECLINE OF STAND ABOVE-GROUND GROWTH

For both stand chronosequence and long-term plots, total stand AGB increased with age with a reducing rate as stands aged (Fig. 1). Mean stand AGB as a function of age was well described using a quadratic equation ($r^2 > 0.99$), confirming an age-related decline of stand AGB accumulation.

LEAF PHYSIOLOGY AND CHEMISTRY

Most gas exchange parameters measured in this study displayed no significant differences among trees of different age classes, with the exception of A and R_N (Table 1). However, A did not decline with tree age as expected, and the age effect on R_N was attributed to the change in leaf nitrogen content (see Results section). The age effect on foliar A/R was not significant, and the mean values of whole-tree foliar photosynthesis/wood respiration generally showed an increasing trend with age. Thus, these results did not support the prediction of H1-1 and H1-2 that A and A/R would decrease with tree age.

There was a significant age effect on leaf N_{mass} and C/N, but the trend was opposite to the prediction of H1-3 that leaf nitrogen and C/N, respectively, decrease or increase with tree age; leaves from the youngest age class displayed lowest N_{mass} (and highest C/N) (Table 1). Although the difference in leaf protein concentration was significant among stands, the magnitude of this difference seemed too small (2.4%) to be biologically relevant.

Tree height peaked at *c.* 24 m, and height growth was not substantial after 70 years. Huber values decreased with tree age, indicating hydraulic exacerbation. The leaf $\delta^{13}C$ showed no change among age classes, indicating unchanged water use efficiency (Table 1). These results provide a strong counter argument for hydraulic limitation to carbon gain (H1-4).

Most observed physiological parameters showed seasonal fluctuation throughout 2003, but the effect of age and age × season was not significant for any parameter (see Table S3).

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Table 1. Tree age effect on physiological parameters and leaf characteristics of upper canopy leaves

Parameters	Age stage and mean tree age (year)				
	35-year 36.8 (0.6) (n = 12)	70-year 68.8 (0.6) (n = 12)	90-year 91.4 (0.7) (n = 23)	135-year 136.8 (1.9) (n = 13)	P (ANOVA)
Photosynthesis and respiration					
V_{cmax} (20 °C, μmol m^{-2} s^{-1})	38.8 (3.6)	29.8 (3.2)	32.7 (2.5)	36.2 (4.8)	0.19
J_{max} (20 °C, μmol m^{-2} s^{-1})	75.8 (6.8)	58.7 (4.9)	62.7 (4.0)	79.7 (6.8)	0.06
A (20 °C, μmol m^{-2} s^{-1})	11.1 (1.1)^{b}	7.4 (0.8)^{a}	8.4 (0.7)^{ab}	9.4 (0.8)^{ab}	**0.03**
A_{mass} (20 °C, μmol kg^{-1} s^{-1})	134 (15)	91.8 (10.3)	105.5 (8.8)	108.7 (8.4)	0.19
Photosynthetic nitrogen use efficiency (20 °C, μmol gN^{-1} s^{-1})	6.8 (0.8)	3.7 (0.4)	4.4 (0.4)	4.6 (0.4)	0.07
Rubisco activity (μmol m^{-2} s^{-1})	11.7 (1.3)	12.9 (0.9)	13.4 (0.7)	13.6 (0.8)	0.68
Q_{10} (15–25 °C)	1.98 (0.09)	2.07 (0.07)	2.12 (0.08)	2.04 (0.15)	0.76
E_0 (kJ mol^{-1})	48.3 (2.9)	51.4 (2.2)	52.7 (2.5)	49.4 (4.5)	0.71
$R_{0\ area}$ (10 °C, μmol m^{-2} s^{-1})	0.79 (0.08)	0.7 (0.06)	0.69 (0.05)	0.77 (0.06)	0.60
$R_{0\ mass}$ (10 °C, μmol kg^{-1} s^{-1})	9.1 (1.0)	8.7 (0.7)	8.4 (0.6)	8.9 (0.8)	0.91
$R_{0\ N}$ (10 °C, μmol gN^{-1} s^{-1})	0.45 (0.05)	0.34 (0.02)	0.35 (0.02)	0.38 (0.04)	0.07
R_{area} (20 °C, μmol m^{-2} s^{-1})	1.54 (0.12)	1.46 (0.11)	1.42 (0.07)	1.52 (0.06)	0.72
R_{mass} (20 °C, μmol kg^{-1} s^{-1})	18 (1.5)	18.2 (1.2)	17.5 (0.8)	17.8 (1.0)	0.96
R_N (20 °C, μmol gN^{-1} s^{-1})	0.89 (0.07)^{b}	0.70 (0.03)^{a}	0.72 (0.04)^{a}	0.75 (0.04)^{ab}	**0.05**
A/R (20 °C, area)	7.7 (1.4)	5.5 (0.8)	6.0 (0.5)	6.1 (0.4)	0.32
A/R (20 °C, whole tree)*	36.1 (12.4)	–	42.0 (12.1)	199.0 (89.7)	–
Nitrogen and protein					
N_{area} (g m^{-2})	1.77 (0.11)	2.08 (0.08)	1.98 (0.07)	2.06 (0.08)	0.18
N_{mass} (%)	2.06 (0.1)^{a}	2.55 (0.08)^{b}	2.43 (0.05)^{b}	2.38 (0.05)^{ab}	**< 0.001**
C/N (g g^{-1})	28.4 (1.2)^{b}	23.3 (0.6)^{a}	24.0 (0.4)^{a}	24.8 (0.5)^{a}	**< 0.001**
Protein (mg mL^{-1})	58.2 (0.1)^{a}	59.6 (0.1)^{b}	59.2 (0.2)^{ab}	58.3 (0.3)^{a}	**< 0.001**
Hydraulic limitation					
Tree height (m)	14.4 (0.7)^{a}	23.3 (0.8)^{bc}	20.5 (0.7)^{b}	24.0 (1.0)^{c}	**< 0.001**
Huber value (cm^2 m^{-2})	0.180 (0.017)^{c}	0.103 (0.009)^{b}	0.094 (0.009)^{b}	0.060 (0.009)^{a}	**< 0.001**
$\delta^{13}C$ (‰)	−26.5 (0.2)	−26.1 (0.1)	−26.4 (0.1)	−26.6 (0.1)	0.34
Above-ground growth					
Total above-ground biomass (kg)	96 (14)^{a}	447 (38)^{b}	772 (68)^{c}	2405 (222)^{d}	**< 0.001**
Growth 1998–2002 (kg $year^{-1}$)	3.6 (0.5)^{a}	11.0 (1.8)^{b}	16.4 (1.8)^{b}	27.6 (2.3)^{c}	**< 0.001**
Growth per leaf area 1998–2002 (g m^{-2} $year^{-1}$)	85.8 (8.0)	68.7 (8.5)	70.8 (7.3)	56.3 (5.0)	0.14

Values shown are means ± SE. ANOVA results (P-values) are shown, and means are compared by LSD for variables with significant age effect ($P < 0.05$ in bold font), and values followed by the same letter are not significantly different.
*Calculated as (A × total leaf area of the tree)/(stem CO_2 efflux rate × trunk area of the tree) with area-based stem CO_2 efflux rate from (Bowman 2005). ANOVA was not performed because only mean and error were reported for stem CO_2 efflux. Standard error in the table was calculated with the approach of error analysis.

TREE GROWTH

The AGB of individual trees and the annual growth rate of AGB per tree (1998–2002 average) all increased with age class (Table 1). After adjusting the growth rate with the total leaf area, the age effect became insignificant, indicating the growth efficiency was not different between the age classes.

The cross-dated tree-ring-width chronology indicated a decline in annual increment associated with age (Fig. 2a). It is evident that trees of different ages were incorporated into the chronology at different times (Fig. 2b). As individual trees possess a natural age-related decline in ring width (Fritts 1976), incorporation of trees of different ages into the chronology at different times will likely result in enhanced variability in ring width and underestimate the declining trend in time of the chronology. Subsequently, the actual decline in annual increment associated with age may be more significant than shown in Fig. 2a.

The relative growth rate decreased exponentially over the tree age (Fig. 2c). However, these declines did not offset the AGB accumulation (Fig. 2b) and annual AGB growth (Fig. 2c) of older trees. Overall, annual AGB growth increased through the first 130 years. Declining growth rates since the 1990s occurred in all four age classes (data not shown), so the trend was mainly attributed to environmental conditions rather than age effect. Therefore, we reject H1-5 that the AGB growth of individual trees and growth efficiency decrease with age.

CANOPY NET CARBON EXCHANGE

The four stands had similar L ranging between 2.0 and 2.4, suggesting canopy closure before or near 35 years of age. The

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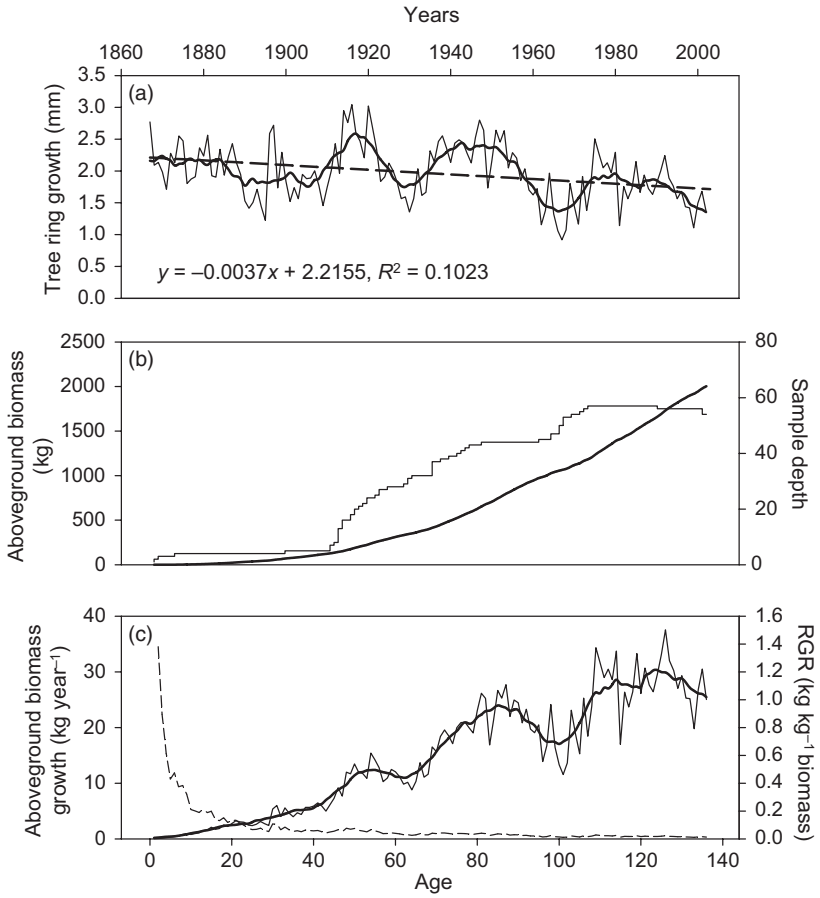


Fig. 2. Tree-ring-width chronology and above-ground growth. (a) thin solid line, the average raw tree-ring width; bold solid line, 11-year moving average; bold dashed line, long-term tree-ring-width growth trend (equation and R^2 are shown). (b) sample depth (thin solid line) of tree-ring-width data and above-ground biomass accumulation trajectory (bold solid line) calculated based on tree-ring-width chronology and allometric relationship. (c) annual above-ground growth (solid line) and relative growth rate (dashed line) of the studied trees in the oldest plot. The bold solid line shows 11-year moving average of annual above-ground growth.

fraction of the total leaf area of *Quercus* spp. in the canopy was also similar among the stands (73–79%). A_N ranged between 2.35 and 3.09 Mg C ha^{-1} (Table 2). In general, canopy carbon fluxes of *Quercus* (A_G, R_f, A_N) showed no clear trend associated with stand age, and R_f/A_G was generally constant (0.65–0.72). Parameters related to light use efficiency (α_{can}, Q_{can} and ε_{can}) were also similar among these stands. Sensitivity analyses suggest that A_N was more sensitive to photosynthetic and respiratory parameters (V_{cmax}, J_{max}, R_0, E_0) than to L (see Fig. S2). Therefore, we reject H1-6 that canopy annual net foliar exchange decreases with stand age.

STAND GROWTH DOMINANCE

Monitored trees in long-term plots constantly exhibited cumulative growth curves that were very close to the 1 : 1 line (Fig. 3a–g) and CGD close to 0 (−0.06–0.006) (Fig. 3h), suggesting no growth dominance throughout the 70-year time span. A generally consistent pattern was observed for individual plots, despite higher variability due to smaller sample size (data not shown). Therefore, we reject H2 that tree growth dominance would initially increase and subsequently decrease with stand development.

STAND ABOVE-GROUND BIOMASS PRODUCTIVITY

The above-ground NPP of the long-term plots ranged between 2950 and 4060 kg ha^{-1} year^{-1} during the 70-year measurement span and appeared to be plot specific (plot effect $P = 0.004$, ANCOVA). The absence of decade and plot × decade effects indicated a stable decadal status during 1937–2006 in all plots. The AGB accumulation in long-term plots generally decreased as stands aged ($P = 0.0003$, ANCOVA, Fig. 4a). This trend was accompanied by increasing biomass loss due to mortality over time ($P < 0.0001$, ANCOVA, Fig. 4a). Plot effects and plot by decade interactions were not significant for either of these two variables.

Stand AGB accumulation and mortality loss (two independently estimated variables) exhibited a negative linear relationship ($P < 0.0001$, ANCOVA), with a coefficient close to −1 (−1.047, Fig. 4b), suggesting that AGB accumulation was predominantly determined by biomass loss due to mortality. This pattern appeared consistent among the plots (plot × mortality loss, $P = 0.83$, ANCOVA). These results support H3-1: that mortality loss would increase with stand development, while net above-ground productivity would be stable through time. Although the AGB accumulation and mortality displayed

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Table 2. Leaf area index, canopy composition and canopy carbon flux model results (carbon fluxes and light use efficiency) of four stands with different age

Canopy info. or model results	Stand			
	35-year	70-year	90-year	135-year
L (canopy photo, $n = 12$)	2.16 (0.11)	2.05 (0.07)	2.44 (0.11)	2.36 (0.09)
f_Q (%)	78.7	73.6	76.2	73.2
A_G (Mg C ha^{-1})	9.01	7.53	8.56	8.38
R_f (Mg C ha^{-1})	5.92	5.18	6.16	5.78
R_f/A_G	0.66	0.69	0.72	0.69
A_N (Mg C ha^{-1})	3.09	2.35	2.40	2.60
α_{can} (mol C mol^{-1} PAR)	0.0360	0.0357	0.0374	0.0359
Q_{can} (%)	62	62	62	61
ε_{can} (mol C mol^{-1} Q)	0.0156	0.0140	0.0152	0.0159

Values shown are mean ± SE.

large temporal variability during 1987–2006, they generally fit the negative 1 : 1 relationship, and hence the variability does not counteract the overall pattern. In contrast, above-ground NPP was not correlated to annual mortality ($P = 0.73$, ANCOVA) or mortality biomass loss ($P = 0.54$), and the pattern was consistent among plots ($P = 0.80$ for plot × annual mortality, $P = 0.83$ for plot × mortality biomass loss, ANCOVA). This result, together with the constant above-ground NPP, does not support our H3-2 that age-related decline of stand biomass accumulation is mainly caused by increasing mortality-led NPP loss.

MORTALITY STRUCTURE

The number of tree deaths in long-term plots decreased from about 30 trees ha^{-1} year^{-1} in 1937–46 to about 15 trees in 1997–2006; meanwhile, the annual mortality remained constant at about 2% without a clear decadal trend (1.8–2.4%; see Fig. S3a). At such low mortality rate, the exponential mortality coefficient was almost the same as annual mortality. The deviation of annual tree deaths, annual mortality and exponential mortality coefficient among plots (the ratio of standard error to mean) decreased during the first 20–30 years of the survey and remained relatively stable thereafter, indicating reduced variability regarding individual mortality rate as stands aged (see Fig. S3b).

The individual cumulative mortality curves were constantly far beyond the 1 : 1 line (Fig. 3a–g) with CMD-IND in the range of −0.65 to −0.89 without showing a clear temporal trend (Fig. 3h), indicating strong reverse dominance and limited changes in the structure of individual mortality (i.e. the distribution of dead trees over tree size was relatively constant) over time. In contrast, AGB mortality cumulative curves were beyond the 1 : 1 line during 1937–76 (CMD-AGB = −0.3 to −0.4), but moved towards the 1 : 1 line during subsequent decades, and CMD-AGB increased to 0.02 during 1997–2006 (Fig. 3). These trends suggested that as stands aged, AGB mortality shifted from predominantly young, small trees to large, dominant trees. This shift in mortality was not due to an increase in the proportion of large trees that die, but rather because stands were composed of more large trees (indicated by increased average AGB of individual trees) and higher proportion of stand AGB were stored in larger trees that are subject to mortality loss over time (see Fig. S4). In other words, biomass loss increased because more large trees died, which is simply because there were more large trees in stands as stands aged.

Discussion

We found an age-related decline of stand AGB accumulation in a *Quercus*-dominated forest and examined three possible mechanisms. This decline was not likely to be caused by mechanisms that decreased above-ground NPP. We did not find evidence for reduced individual tree growth associated with age-related physiological constraints (decreased foliar/canopy carbon fixation capacity and photosynthesis/respiration balance, decreased nitrogen availability or increased hydraulic constraints on carbon gain) or alterations in stand structure that may reduce stand resource use efficiency, or increased mortality-led productivity loss. However, we found that increased biomass loss due to tree mortality was the primary cause of the age-related decline of stand AGB accumulation in the BRF. As stands aged, annual mortality and the structure of individual mortality did not change. In older stands with proportionately more large trees and fewer small trees, maintenance of the individual mortality rate and structure led to a shift of mortality AGB loss from small trees to large, dominant trees over time. As a result, the effect of tree mortality on AGB loss increased as stand age increased, and subsequently, the death of large trees was the primary mechanism driving age-related decline of stand biomass accumulation. This mechanism substantially explains age-related decline of stand biomass accumulation in the BRF during the first *c*. 130 years of growth, which is typical of modern regenerating eastern deciduous forest in the United States. Additional studies would be required to examine whether the same mechanism applies to older forests of this type or whether different mechanisms shape age-related forest stand growth during the late stages of stand development.

PHYSIOLOGICAL CONSTRAINTS OF TREE GROWTH AND STAND PRODUCTIVITY DECLINE

Age- or size-related decrease in growth of individual trees could decrease stand-level productivity, and thus lead to decline of forest biomass accumulation. Physiological constraints that may reduce the growth of older trees have been widely addressed, but few general insights have been gained. Resource-led (e.g. nutrient, water) physiological constraints on photosynthesis, which can reduce tree growth (see reviews of (Bond 2000; Niinemets 2002), appeared common, but increasing AGB growth in older trees has also been observed (Johnson & Abrams 2009; Sillett *et al*. 2010). Our study exam-

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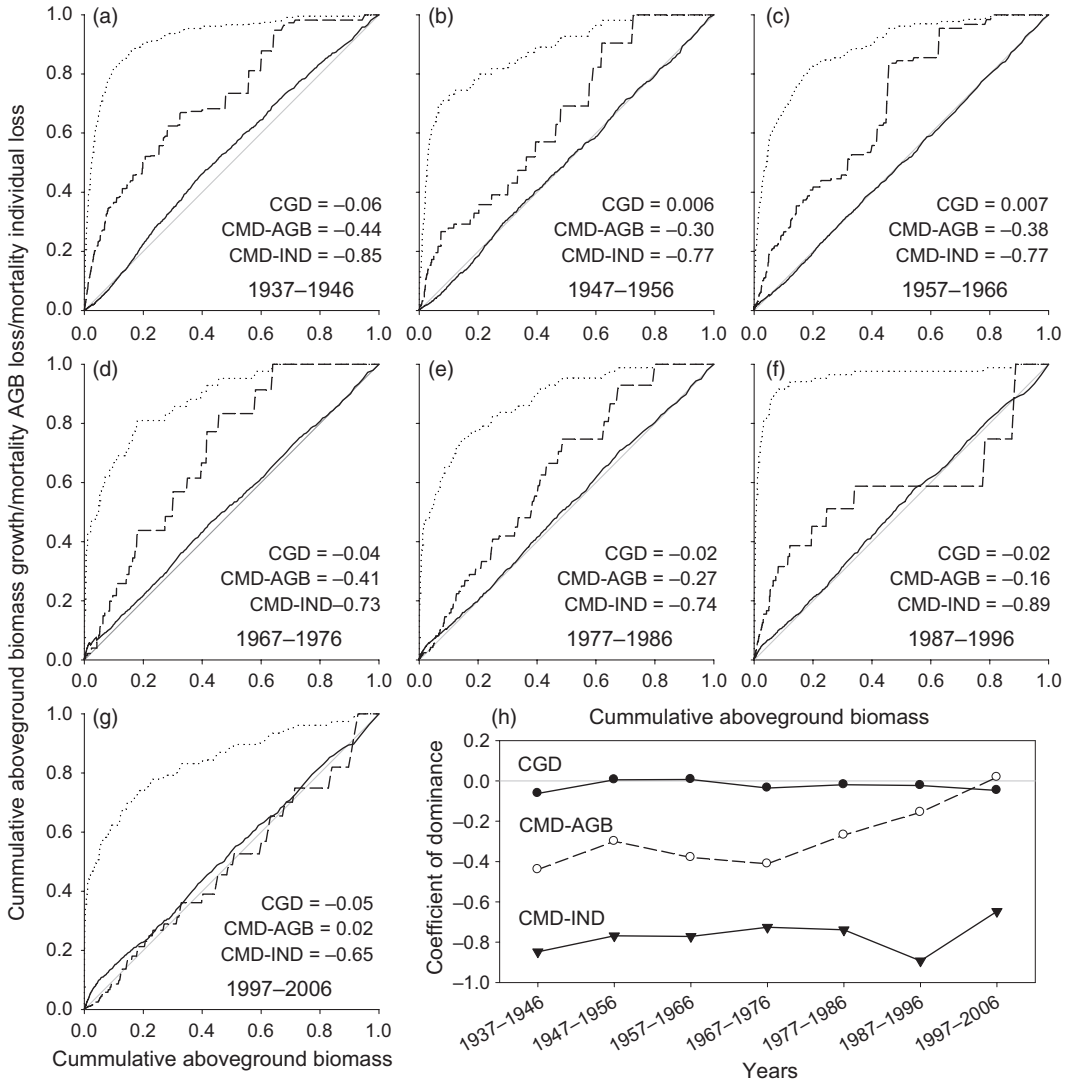


Fig. 3. Growth and mortality dominance of all monitored trees in long-term plots (1937–2006). The dominance curve (a–g) plots the cumulative increment distribution of above-ground growth or mortality (y) as a function of the cumulative above-ground biomass (AGB) distribution (x). The coefficient of growth dominance (CGD, solid line) and mortality dominance of AGB (CMD-AGB, dashed line) and individuals (CMD-IND, dotted line) are shown for each decade (a–g) and summarized in j. The 1 : 1 and coefficient of dominance = 1 lines are shown in grey solid line for reference.

ined whether the growth of individual *Q. rubra* trees declined with age (H1-5) and tested hypotheses of potential physiological constraints: unbalanced carbon gain and respiration (H1-1, H1-2, H1-6), nutrient (nitrogen) limitation (H1-3) and hydraulic constraints (H1-4) (Gower, McMurtrie & Murty 1996). None of these hypotheses were supported for *Q. rubra* between 35 and 135 years old in the BRF, commensurate with observations of increasing basal area and biomass growth with increasing tree age in *Quercus* spp.(Schuster *et al.* 2008; Johnson & Abrams 2009), suggesting the pattern may be common for this important genus. Another potential physiological mechanism affecting the growth of older trees is the biomass allocation pattern, which was not tested in this study. High above-ground growth and growth efficiency of older trees observed in this study may be partially attributable to increasing biomass allocation to stems over time. Given the potential importance of biomass allocation, this should be addressed in further studies in the BRF.

Pioneering studies on forest stand development suggested that age-related decline of forest productivity was due to reduced photosynthesis to respiration ratios, primarily due to increased respiration over time. More recent empirical evidence rejected this hypothesis (Ryan, Binkley & Fownes 1997; Ryan *et al.* 2004); we also reject this hypothesis. Within the same stand chronosequence, a stand-level model shows that the percentage of woody-tissue respiration was relatively constant at 10% of gross primary production (GPP) and was not affected by stand age (9.7%, 11.8% and 10.6% of GPP, respectively, for 35-, 90- and 135-year stands, Bowman 2005). In summary, responses of *Q. rubra* at the BRF are consistent with

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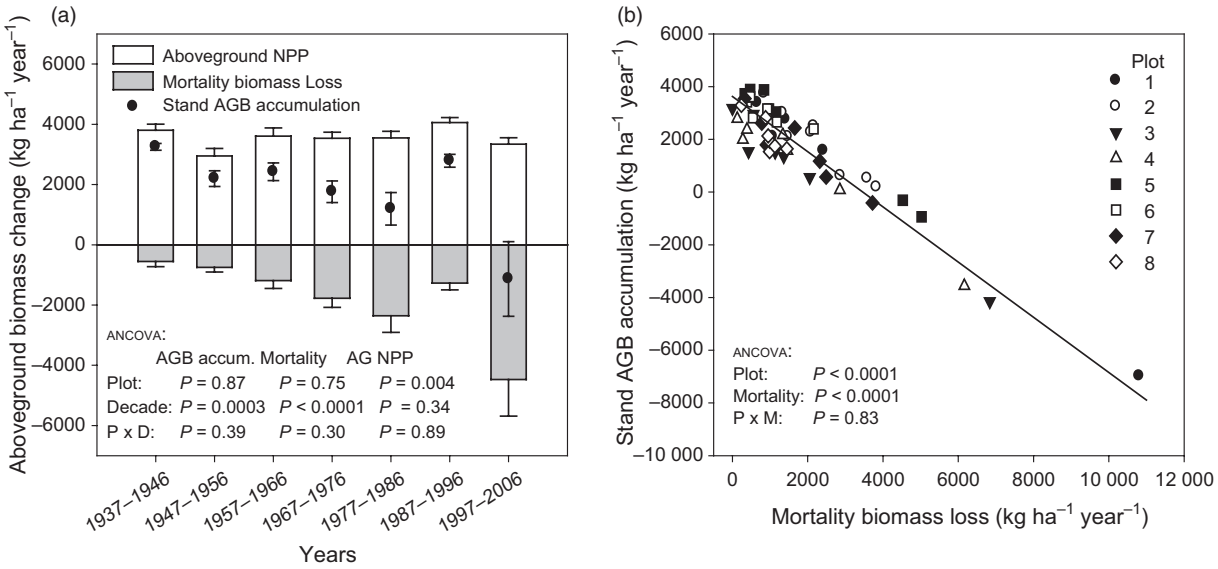


Fig. 4. Annual average of stand AGB accumulation, mortality loss and above-ground net primary production (NPP) of each decade during 1937–2006 are shown (a). Above-ground NPP and mortality loss are respectively presented in white and grey vertical bars as mean ± SE. Stand AGB accumulation is shown by the solid circle (mean ± SE). ANCOVA results (*P*-values) are shown for the effect of plot, decade and plot × decade. The relationship between stand AGB accumulation and mortality loss is shown for each plot (b). ANCOVA results (*P*-values) are shown for the effect of plot, mortality (covariate) and plot × mortality.

other studies, suggesting a minimal role for reduced photosynthesis and increased respiration as the cause of age-related decline of forest stand production.

Support for the nutrient and hydraulic limitation hypotheses is equivocal. In some cases, reduced nutrient availability may contribute to declining growth of older forests, but this response is not universal (Ryan, Binkley & Fownes 1997). Similarly, hydraulic limitation of gas exchange in taller (usually older) trees, although commonly observed, is not consistently supported (Ryan, Phillips & Bond 2006). In particular, the link between hydraulic limitation of carbon assimilation and tree growth is rarely studied (n.b. Barnard & Ryan 2003; Ryan *et al*. 2004). Therefore, these mechanisms for age-related forest stand productivity decline may be case-specific (e.g. species, season and site). In our study, these two mechanisms did not limit individual tree growth of *Q. rubra* and forest NPP, perhaps due to specific biological features of *Q. rubra*; for example, compared with more widely studied coniferous species, the relatively fast litter nutrient mobilization rate in *Quercus* forests may eliminate the nutrient limitation, as found in a study contrasting *Pinus sylvestris* and *Quercus robur* (Yuste *et al*. 2005). Furthermore, *Q. rubra* may adjust its growth pattern to alleviate hydraulic limitation. Hydraulic limitation has been suggested to be a function of tree size, especially tree height (Mencuccini *et al*. 2005; Martinez-Vilalta, Vanderklein & Mencuccini 2007; Abdul-Hamid & Mencuccini 2009), and support for the hydraulic limitation hypothesis has predominantly been observed in tall trees. In contrast, *Q. rubra* in this study shifted from vertical height growth to horizontal girth growth and crown expansion (data not shown) after 70 years. This transition in growth direction may minimize hydraulic limitation imposed by the length of the hydraulic path and gravitational potential. Similarly, *Quercus* spp. have a host of adaptations to drought such as waxy xeromorphic leaves, low water potential for stomatal closure and high photosynthetic rates in dry conditions, which together may limit hydraulic constraints at the whole-tree and stand level (Turnbull *et al*. 2001). More specifically, vessel elements in angiosperms such as *Q. rubra* are generally more specialized than tracheids in conifers for the efficient conduction of water (Hacke, Sperry & Pittermann 2005), yet much of the support for the hydraulic limitation hypothesis was obtained from coniferous stands (Ryan, Phillips & Bond 2006). Finally, nitrogen and hydraulic limitations may be moderated by nitrogen deposition and CO_2 fertilization (Phillips, Buckley & Tissue 2008), and the role of these stimulatory effects of global change phenomenon deserves further study.

AGE-RELATED STAND STRUCTURE CHANGE

Binkley *et al*. (2006) proposed a four-phase dynamic of forest growth dominance and suggested the pattern plays a role in the age-related decline of forest productivity; this hypothesis has been tested and supported by a few studies (Binkley *et al*. 2002; Binkley 2004; Fernandez & Gyenge 2009). However, we did not observe growth dominance and its phase-switch during the past 70 years in the BRF. Although factors accounting for this sustained 'evenness' in the relationship between tree size and growth are not clear, it is not entirely surprising because species-specific dynamics of dominance have been observed and similar patterns was shown in *Populus tremuloides* in the Rocky Mountains (Binkley *et al*. 2006). The cause of the phenomenon in *P. tremuloides* stands was attributed to clonal characteristics (Binkley *et al*. 2006), but this mechanism is not

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likely to apply to nonclonal, seed-reproduced oaks such as *Q. rubra* in BRF.

The absence of growth dominance in our observations may be related to the timing of dominance phase-switch. Binkley (2004) stated that growth dominance would occur just prior to canopy closure generating stand-level growth decline, while decline during further stand development was attributed to the development of reverse dominance. However, there is limited information about the age at which these shifts occur and the length of the transition periods between phases. In *Eucalyptus saligna* monoculture plantations, the occurrence, peak and offset of growth dominance were observed at 2, 10 and 20 years, respectively (Binkley *et al.* 2003); in contrast, a reversal of growth dominance was not observed until >150 years for *Pinus contorta* stands (Binkley *et al.* 2006). Unfortunately, our long-term results do not cover the very young and very old stages of stand development, during which changes in stand structure may affect stand growth.

INCREASED MORTALITY AS A MECHANISM FOR AGE-RELATED DECLINE OF STAND BIOMASS ACCUMULATION

Forest stand growth is the sum of above-ground NPP and mortality biomass loss. Therefore, decreased stand biomass accumulation may primarily be due to reduced NPP or to increased mortality biomass loss. Ryan, Binkley & Fownes (1997) concluded that reduced productivity rather than increased mortality was the cause of reduced net growth rate of older forest. This conclusion has been challenged by some more recent studies that observed mortality as a significant cause of age-related decline of stand biomass accumulation in conifer forests (Acker *et al.* 2002; Taylor & MacLean 2005). In this study, the constant above-ground NPP and negative 1 : 1 relationship between stand AGB accumulation and mortality loss indicated that age-related decline of stand AGB accumulation in the BRF was predominantly determined by increasing mortality loss rather than reduced above-ground NPP. Thus, the results in the BRF confirm that mortality could play an important role in generating age-related decline of stand biomass accumulation, primarily due to the loss of large, dominant trees.

In the BRF, relatively consistent above-ground NPP maintained the forest as a carbon sink over the past 70 years and we did not find any correlation between above-ground NPP and mortality, suggesting mortality-led loss of NPP did not significantly affect stand biomass accumulation. Two factors may contribute to the maintenance of above-ground NPP. First, old-growth forests can maintain productivity if they have sufficiently high tree densities (Luyssaert *et al.* 2008); tree density in BRF generally remained stable from the 70-year stand onward (see Table S1) or after 1950s in long-term plots (Schuster *et al.* 2008). Therefore, abundant new recruitments or growth of previously suppressed trees may compensate for the loss of productivity due to the mortality of older trees. Second, above-ground NPP may be stimulated by recent environmental changes so that the commonly observed age-related decline was negated (Boisvenue & Running 2006; Phillips, Buckley & Tissue 2008; McMahon, Parker & Miller 2010). In addition to elevated CO_2 concentration, possible growth stimulating effects in BRF include a 1.0 °C increase in mean air temperature over the 20th century and a mean annual deposition of 6–7 kg N ha^{-1} (NADP 2007). Further study of these factors may reveal their influence on wood NPP over time.

It is notable that the *Quercus*-dominated forest in the BRF exhibited high mortality rates during 1997–2006 (associated with droughts, see discussion), in contrast to the low mortality in 1987–96. This variability suggests that the observed mortality may be environmentally driven and therefore not solely age-related; however, this does not undermine our conclusion that age-related decline of stand AGB accumulation was predominantly driven by mortality loss. Overall, the mortality and stand AGB accumulation of these two decades still adhere to the general 1 : 1 negative relationship that fits the entire survey record (i.e. for 1987–96, high stand AGB accumulation was primarily due to low mortality and *vice versa* for 1997–2006). Interestingly, mortality may function very differently from the broadly studied and accepted physiological constraints on NPP in terms of shaping forest stand biomass accumulation. The influence of age- or size- related physiological constraints on NPP may have inherently low variability because age and size increment in trees are continual and irreversible. Furthermore, the influence of physiological variability on NPP is ultimately limited by maximum potential tree growth, which is $<2\%$ of the whole-tree biomass of large trees (Fig. 2c). By contrast, tree mortality acts as a cumulative probability over time and is subject to environmental and stochastic factors. In particular, for older forests, a considerable proportion of biomass would exist in a small number of large, dominant trees and death events that have high impact on stand growth would only happen intermittently. Such inherent stochastic behaviour suggests that mortality as a mechanism to reduce biomass accumulation of forest stands must be evaluated using long-term trend analyses because short-term studies may easily be biased by intermittent events. Subsequently, the covariance between mortality and stand growth should be emphasized as well as the temporal trend.

As forests age, the major cause of tree mortality shifts from competition for resources to ageing and exposure to disturbances (Taylor & MacLean 2005). In contrast to some physiological growth models (sigmoidal growth of individual tree), increasing growth of individual trees has been observed in old-growth *Quercus* and other common tree species in the eastern USA (Johnson & Abrams 2009); our results of tree-ring analysis and allometric estimation of tree biomass in the chronosequence plots support these observations. Therefore, we postulate that for these species like *Q. rubra*, tree mortality associated with size-related exposure to disturbances, rather than reduced growth of individual trees over time, can generate forest stand biomass accumulation decline over time. In addition, significant disturbance-driven tree mortality may happen before physiological/genetic constraints on growth occur and thus shape the stand AGB accumulation. In *Abies* and *Picea*

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forests in New Brunswick, Canada, mortality was indicated as the major reason for stand decline with more than 60% due to wind-throw, stem- or top-breakage and insects (Taylor & MacLean 2005). In the BRF, periods of slower or negative stand AGB accumulation were also associated with insect outbreaks and droughts (Schuster *et al.* 2008). The variability of mortality observed during the 1987–2006 time period may be related to the favourable decade of 1987–96 followed by several significant droughts since 1999, accompanied by substantial tree death during 1999–2005 (Schuster *et al.* 2008). It is notable that disturbances are subject to many stochastic factors, and their frequency and intensity have large temporal and spatial variability. Stochastic disturbance events make the influence of mortality on forest productivity significantly more difficult to detect (Foster *et al.* 2010). Compared with deaths of seedlings and small trees, disturbance-driven deaths of dominant trees are rare, variable, high-impact events, whose variability simply cannot be incorporated into chronosequence studies and would confound surveys with insufficient time spans; for example, in our study, no clear trends in stand growth or the relationship between mortality and stand growth decline would be observed based on observations during any 20- to 30-year period.

In northern temperate forests, the rate of change in tree biomass and the factors generating that change are of primary importance in assessing current and near-future carbon stocks (Houghton 2005). To predict the change of carbon stock in old-growth forests with mortality as a primary determinant of stand biomass accumulation, we suggest that model studies include tree demography, as well as the influence of stochastic factors and climate change on disturbances that are associated with tree death; for example, climate models project increasing frequency and/or intensity of disturbances, such as fire, pest and disease outbreak, and extreme weather events in some regions (Easterling *et al.* 2007). These factors are likely to increase tree mortality, and thus decrease carbon stock in AGB of older forests, but have not been well modelled. Future studies on these topics will improve our capability to infer forest living biomass as carbon sources or sinks in the terrestrial biosphere.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods.

Table S1. Plot information.

Table S2. Parameters of tree equations.

Table S3. Age and seasonal effect on physiological parameters and leaf characteristics.

Table S4. Parameters of canopy model.

Figure S1. Forest stand ages within the Highlands Region.

Figure S2. Annual canopy carbon fluxes in response to changes in model parameters.

Figure S3. Tree mortality in long-term plots and the deviation of mortality among plots.

Figure S4. Changes of tree size distribution, average tree AGB and cumulative AGB.

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