



Original article

Pattern and dynamics of biomass stock in old growth forests: The role of habitat and tree size



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ARTICLE INFO

Article history:

Received 14 December 2015

Received in revised form

12 June 2016

Accepted 15 June 2016

Available online 25 June 2016

Keywords:

Forest dynamics

Carbon sequestration

Tree size

Growth

Mortality

Spatial variation

ABSTRACT

Forest ecosystems play a fundamental role in the global carbon cycle. However, how stand-level changes in tree age and structure influence biomass stock and dynamics in old-growth forests is a question that remains unclear.

In this study, we quantified the aboveground biomass (AGB) standing stock, the coarse woody productivity (CWP), and the change in biomass over ten years (2004–2014) in a 25 ha unmanaged broad-leaved Korean pine mixed forest in northeastern China. In addition, we quantified how AGB stock and change (tree growth, recruitment and mortality) estimations are influenced by the variation in habitat heterogeneity, tree size structure and subplot size.

Our analysis indicated that Changbai forest had AGB of 265.4 Mg ha⁻¹ in 2004, and gained 1.36 Mg ha⁻¹ y⁻¹ between 2004 and 2014. Despite recruitment having better performance in nutrient rich habitat, we found that there is a directional tree growth trend independent of habitat heterogeneity for available nutrients in this old growth forest. The observed increases in AGB stock (~70%) are mainly attributed to the growth of intermediate size trees (30–70 cm DBH), indicating that this forest is still reaching its mature stage. Meanwhile, we indicated that biomass loss due to mortality reduces living biomass, not increment, may be the primary factor to affect forest biomass dynamics in this area.

Also, spatial variation in forest dynamics is large for small sizes (i.e. coefficient of variation in 20 × 20 m subplots is 53.2%), and more than 90 percent of the inherent variability of these coefficients was predicted by a simple model including plot size. Our result provides a mean by which to estimate within-plot variability at a local scale before inferring any directional change in forest dynamics at a regional scale, and information about the variability of forest structure and dynamics are fundamental to design effective sampling strategies in future study.

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1. Introduction

Forest ecosystems play a major role in the global carbon budget since they harbor important above- and below ground biomass stocks and have a strong carbon sequestration potential (Dixon et al., 1994; Pan et al., 2011; Fang et al., 2014). Whether or not forests will be able to continue to sequester additional carbon is a key concern in an era of global change (McMahon et al., 2010; Dai

et al., 2013; Anderson-Teixeira et al., 2015). Recent studies have shown growth enhancement over the past several decades across many forest types due to environmental changes, such as elevated CO₂ and nitrogen deposition (Silk et al., 2013; McMahon et al., 2010; Hember et al., 2012; Fang et al., 2014; Wu et al., 2014). For example, Fang et al. (2014) demonstrated that about 8.4–21.6% of biomass carbon sink in Japan's forests was induced by climatic changes from 1980 to 2005, and simultaneously reported that the growth enhancement differs among forest types, age classes, and regions.

Yet, despite significant effect of environmental changes on forest growth at the regional and global scale (Phillips et al., 1998; Malhi et al., 2006; Chave et al., 2008; Toledo et al., 2011), soil nutrients

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and water availability may be the stronger driver of spatial variation in biomass increment at local scales (Oren et al., 2001; DeWalt and Chave, 2004; Paoli et al., 2008). From an ecological perspective, nutrient rich soil will support a greater growth than poor soils in accordance with the idea that soil nutrient supply was the main limiting factor for primary production (Chase and Leibold, 2003). But, higher soil nutrients could lead to lower biomass with faster rates of turnover on rich sites because mortality rates could increase faster than growth rates on rich soils (Russo et al., 2005; Paoli et al., 2008). Because stand biomass accumulation is the sum of gain and loss, the relative importance of two processes will have contrasting implications for the magnitude and trend of forest biomass storage changes (Chao et al., 2009; Holzwarth et al., 2013). For example, long-term studies in several old growth forests have indicated that biomass accumulation is close to zero or negative as a result of biomass loss due to mortality is roughly equal to or higher than production of surviving trees (DeBell and Franklin, 1987; Chave et al., 2003; Taylor and MacLean, 2005; Feeley et al., 2007; Xu et al., 2012). Alternatively, Eisen and Barker Plotkin (2015) showed that biomass increase in northeastern U.S. forests was due to the increase in size and low disturbance of large dominant trees. Despite these efforts, more empirical studies are needed to examine whether forests exhibit dramatic difference in growth and/or mortality rates across local habitats, and these eventually lead to differences in forest directional change trend at local scale (Chave et al., 2003; McMahon et al., 2010; Wang et al., 2011; Xu et al., 2012).

Moreover, it is generally accepted that the ability of forests to sequester carbon decreases with size (or age), and that old-growth forests become carbon neutral (Carey et al., 2012). However, empirical studies have proved that large, “old” trees do not act simply as senescent carbon reservoirs but actively fix larger fraction of carbon compared to smaller trees (Zhou et al., 2006; Luysaert et al., 2008; Silk et al., 2013; Stephenson et al., 2014). For instance, a literature review by Luysaert et al. (2008) reported that forests older than 200 years sequestered on average $2.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in AGB though about 20% variation existed. Large trees have recently started to attract the attention of ecologists not simply because they are becoming increasing rare (Lindenmayer et al., 2012), but because they contribute to forest carbon storage and the accumulation rates increases continuously with tree size (Zhou et al., 2006; Luysaert et al., 2008; Silk et al., 2013; Stephenson et al., 2014). In a recent study, Slik et al. (2013) showed that large trees were responsible for the great amount of biomass variation across the tropics. Chave et al. (2003) suggested that stems commonly defined as large, that is above 70 cm in diameter (Clark and Clark, 1996), only accounted for 0.22% of overall and contributed over 13% of the AGB increment on Barro Colorado Island (BCI) plot. In particular, small trees (e.g. $\text{DBH} < 10 \text{ cm}$) are generally excluded from some studies, or a few small stems are directly measured in very small proportion of larger plots (Zhou et al., 2011; Vincent et al., 2015). Thus, it remains unclear the relative importance of tree size class in shaping forest carbon accumulation over time, which is critical for predicting future carbon sequestration in a given forest ecosystem (Silk et al., 2013).

Much of our knowledge about forest structure, dynamics and demography has come from observations of permanent plots (Gilbert et al., 2010; McMahon et al., 2010; Wagner et al., 2010; Anderson-Teixeira et al., 2015). These plots are the empirical basis for the current debate on forest dynamics that has been focused on the detection of recent changes in AGB fluxes and stocks (Lewis et al., 2014; Malhi et al., 2006; Chave et al., 2008). Unlike standing stock, it will need considerably more sampling effort to obtain a reliable estimate of AGB dynamics (e.g. tree growth, mortality and

recruitment) as it represents the intersection and difference of two measurements (Chave et al., 2003; Wagner et al., 2010). Subtle changes (e.g. growth, recruitment and mortality) may be missed by insufficient sample size resulting from ignoring great local spatial variation (Fox, 2001; Valencia et al., 2009). Thus, large-scale permanent plots may be required to decipher unambiguous trends in natural forest dynamics.

In the present study, we used a 25 ha fully mapped forest plot where all trees with a $\text{DBH} \geq 1 \text{ cm}$ have been tagged, identified, measured in 2004 and re-surveyed in 2014. We investigate the spatial variation and short-term dynamics (2004–2014) of AGB in 25 ha old-growth temperate forest plot in northeastern China. Specifically, we aim to answer the following questions: (1) Do the forest in different habitats have similar directional change (growth, recruitment and mortality) in this old growth forest? We expected significant differences in AGB change because trees growing in nutrient rich habitat area expected to have better performance. (2) Do large trees contribute more carbon sequestration than medium or smaller trees? We expected the AGB gaining mainly come from the big trees due to its great AGB stock. (3) Are more sampling efforts needed to estimate the forest AGB dynamics than stock? In other words, whether the inherent spatial variations of forest AGB dynamics larger than stock?

2. Materials and methods

2.1. Study site

The Changbai Mountain Nature Reserve (CMNR) in northeastern China is the largest protected temperate forest in the world (Hao et al., 2007; Yang et al., 1985, Fig. 1). Our study site is located in a core zone of broad-leaved Korean pine mixed forest ($42^{\circ}23'N$ and $128^{\circ}05'E$), with mean canopy tree age of 280 years (Yuan et al., 2012; Hao et al., 2007). This area has a temperate continental climate with long, cold winters and warm summers. Rainfall averages 700 mm yr^{-1} , most of which occurs from June to September ($480\text{--}500 \text{ mm}$). Mean annual temperature is 2.8°C , with a January mean of -13.7°C , and a July mean of 19.6°C (Liu, 1997; Yang et al., 1985).

This area was rarely disturbed by fire due to the humid climate environment and steady protection policy by local government. The natural disturbance comes from the strong wind in spring and winter season (Zhou et al., 2011).

2.2. Plot survey and biomass calculation

The broad-leaved Korean pine (*Pinus koraiensis*) mixed forest is the dominant vegetation type in northeastern China, which is well-known for high species richness and a unique species composition for temperate forests (Stone, 2006). In the summer of 2004, a 25-ha ($500 \times 500 \text{ m}$) plot was established, henceforth referred to as the CBS (Changbaishan) plot, representative of forests in the area, in the core zone of the CMNR to avoid the influence of human activities. All free-standing woody stems $\geq 1 \text{ cm}$ in trunk diameter were mapped, measured and identified to species. The first plot census started in July 2004 and ended in September 2004, and the second census was carried out in July and August of 2014. The first census found 36,907 individuals (not including branches) belonging to 52 species to 32 genera and 18 families while 30,543 individuals belonging to 51 species were surveyed in 2014. This work was conducted based on Forestry Standards “Observation Methodology for Long-term Forest Ecosystem Research” of People’s Republic of China (LY/T 1952–2011). Our previous studies have shown that the forest species composition and structure of CBS plot is similar with results from other forests in this area (Song et al., 2014; Zhao et al.,

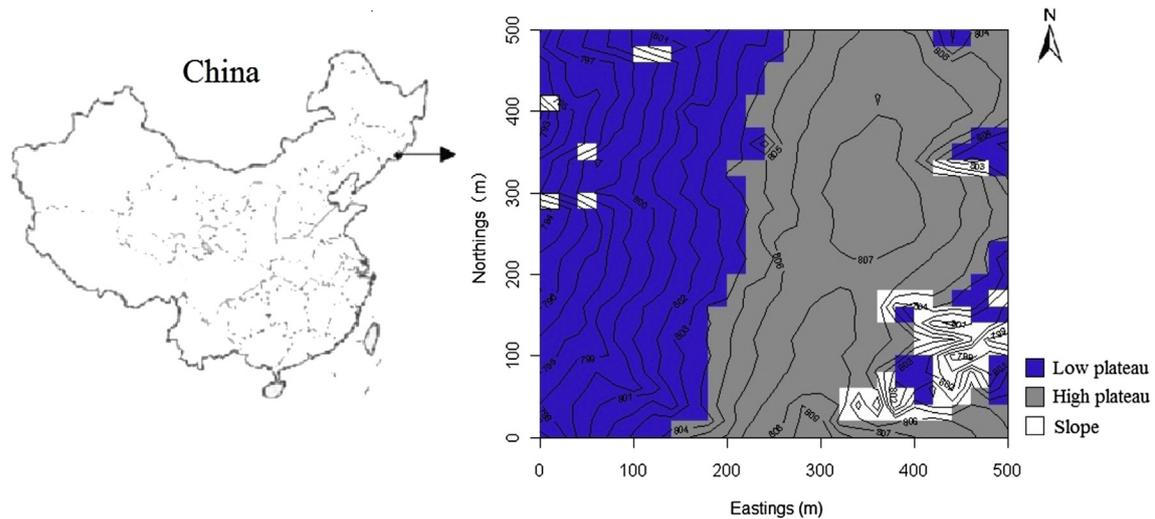


Fig. 1. The location and habitat classifications of the 25 ha (500 × 500 m) Changbai forest plot.

2014; Wu et al., 2016).

The AGB of each stem was estimated from diameter at breast height (1.3 m) using allometric regression equations. For eight of the dominant species (*Pinus koraiensis*, *Tilia amurensis*, *Quercus mongolica*, *Fraxinus mandshurica*, *Acer mono*, *Phellodendron amurense*, *Betula platyphylla*, *Populus davidiana*), recently developed species-specific equations were used to estimate AGB (Wang, 2006). The AGB of shrub species was estimated according to Li et al. (2010) (see Appendix S1).

2.3. Habitat categorization

The entire plot was subdivided in subplots of 20 × 20 m to model topography. A total station was used to survey the plot and determine the elevations of corners of all 20 × 20 m quadrats (Condit, 1998). The elevation ranges from 791.8 to 809.5 m, with a mean elevation of 801.5 m above sea level (Hao et al., 2007). Three topographic attributes –elevation, slope, and convexity –were calculated for each 20 × 20 m quadrat (Harms et al., 2001). Based on these attributes, three habitats were classified as follows: low plateau (slope < 7°, elevation < 804.0 m), high plateau (slope < 7°, elevation ≥ 804.0 m) and slope (slope ≥ 7°). This classification accounted for most of the variation in elevation (Ye et al., 2011). There existed a topographic gradient that caused the surface

transport of water creating a gradient of soil moisture conditions though the relatively gentle terrain of CBS plot (Table 1), leading to significant high soil moisture in low plateau sites (see Appendix S3).

2.4. Data analysis

For each census year, AGB (aboveground biomass) was calculated by summing all the stems with DBH ≥ 1 cm. In addition, we classified the AGB as due to growth, recruitment, and mortality between the two census intervals. Growth (G) was defined as the AGB growth of trees that were alive in two successive censuses (i.e. ten years), recruitment (R) as the AGB increment attributable to recruitment into the minimum diameter class between the two censuses, and mortality (D) as the loss of AGB due to the mortality of trees between the two censuses (Chave et al., 2003; Valencia et al., 2009). Coarse woody productivity (CWP) as G + R and relative net change as $100 \times (\log(AGB_2)/\log(AGB_1))/5$; where AGB1 and AGB2 correspond to the AGB in census 2004 and 2014, respectively. Averages of these metrics were calculated for the plot as a whole and for each habitat type. Bootstrap re-sampling with 999 replicates was used to determine 95% confidence limits for all variables across 20 × 20 quadrats. For each of the 999 randomizations, the intersection and difference of the stem codes of the selected

Table 1

Distribution of aboveground biomass (AGB) among size classes divided in tree size classes. For each tree size class (in increments of 10 cm), the number of stems and mean diameter in each census (2004 and 2014) and the mean AGB, biomass (% over the total) and cumulative biomass over the two censuses is shown.

Diameter class (cm)	Abundance		Mean diameter (cm)		AGB stock (Mg ha ⁻¹)	Biomass (% total)	Cumulative biomass (%)
	2004	2014	2004	2014			
1–10	48,161	48,092	2.54	2.70	1.59	0.6	0.6
10–20	3925	3709	14.46	14.33	7.17	2.7	3.3
20–30	2110	1922	24.76	24.78	17.39	6.5	9.7
30–40	1572	1455	35.05	35.04	29.23	10.9	20.6
40–50	1348	1308	44.89	45.01	49.25	18.3	38.9
50–60	968	990	54.61	54.78	63.20	23.5	62.3
60–70	437	507	64.55	64.53	49.51	18.4	80.7
70–80	174	219	74.36	74.19	28.16	10.5	91.2
80–90	49	64	84.81	84.36	11.34	4.2	95.4
90–100	18	21	94.13	94.49	4.07	1.5	96.9
100–120	14	11	109.96	110.43	3.65	1.4	98.3
>120	12	14	136.28	139.11	4.69	1.7	100.0
Total	58,788	58,312	740.4	743.75	269.3	100%	

quadrat recorded in the census of 2014 and 2004 were obtained, and then AGB variables (G, R and D) were calculated following the above mentioned method. Repeated measures ANOVAs followed by a Tukey's HSD post-hoc test were performed to determine the minimum significant difference ($P < 0.05$) between different habitat types.

To evaluate the effect of tree size on the forest AGB stock and dynamics estimation, biomass patterns were also examined for diameter classes divided at 1, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 120, and >120 cm. For each size class AGB, CWP, AGB growth (including recruitment in the case of the smallest size class), AGB loss from mortality, and net AGB change was calculated. Individual tree growth and mortality are attributed to the diameter class of the initial census regardless of any shift to a larger DBH category during the 10 y census interval (Valencia et al., 2009).

To examine the inherent variations of forest AGB stock and dynamics, we explicitly formulated how the range of expected variability for AGB stock, CWP and loss (mortality rate) changes through continuous subplot areas. First, we defined grain sizes ranging from 10×10 m (0.01 ha) to 150×150 m (2.25 ha) with fixed distance of length 5 m. Second, we randomly selected square subplots at each spatial grain scale with 999 repetitions in the 25 ha plot. To eliminate boundary effect, only those individuals with a distance greater than or equal to subplots edge length from the forest plot edges were included at each selection. Third, for each selection at each spatial grain the mean AGB between two censuses, CWP and mortality rate were calculated. Finally, we derived the coefficient of variation (CV) of AGB, CWP and mortality at a given grain scale (i.e. 999 bootstrapped values) as a normalized measure of dispersion of forest AGB variables (Pearson, 1894). The use of the CV enabled comparison of the different forest biomass variables on a similar scale.

The basic statistical theory is that the CV scales inversely with the square root of sample size. So we chose inverse power-law functions to fit the relationship between CV and subplot area (ha). To this end, we applied a generalized least squares method based on the following formula (Wagner et al., 2010):

$$CV = \frac{\alpha}{S^\beta} \times \varepsilon \quad (1)$$

Where CV is the coefficient of variation of a given grain scale, S is the subplot area (ha), α , β are the parameter for the model and ε is the fitted model residuals.

For the computation, the Equation (1) was log transformed to obtain linearity (2).

$$\log(CV) = \log(\alpha) - \beta \times \log(S) + \log(\varepsilon) \quad (2)$$

We then compute the minimal number of plots required (N) to ensure there was 95% probability for the predicted values of AGB, CWP and mortality to within 20% ($\pm 10\%$) of the observed values using the Formula (3):

$$N = \frac{t_{(0.95, n-1)}^2 \times s^2}{d^2} \quad (3)$$

Where t is the student's t-statistic value with 95% confidence interval (here is set to 1.96), s^2 is the unbiased sampling variance estimate, and d is the observed mean value $\times 10\%$.

The boots-trapping was performed using the package "boot". All calculations were carried out in R version 3.1.2 (R Development Core Team, 2014).

3. Results

The mean aboveground biomass (AGB) stock of CBS forest across the two censuses was 269.3 Mg ha^{-1} (Table 1). Between 2004 and 2014, stem density of overall forest decreased by 0.34% per year, while AGB increased 0.51% per year (Table 2). The impact of recruitment on biomass dynamics was negligible ($0.035 \text{ Mg ha}^{-1} \text{ y}^{-1}$): nearly all the change was due to growth ($2.70 \text{ Mg ha}^{-1} \text{ y}^{-1}$) and mortality ($1.38 \text{ Mg ha}^{-1} \text{ y}^{-1}$).

Forests on high plateau (295 Mg ha^{-1}) had a significantly higher AGB than the average, but average tree density, suggesting this habitat holds more big trees than the rest of the forest (Table 2). All habitats showed a trend towards increasing biomass during 2004–14. Tree growth had best performance in slope habitat, which holds poorest soil nutrient condition. Mortality in high plateau habitat was $1.67 \text{ Mg ha}^{-1} \text{ y}^{-1}$ loss, nearly twice as much as in the slope habitat ($0.87 \text{ Mg ha}^{-1} \text{ y}^{-1}$). Low plateau and high plateau habitat had similar changes in CWP, in spite of great differences in soil nutrients content.

Less than 1% of the total AGB was stored in stems <10 cm in DBH, and about 17% in trees with stems ≥ 70 cm with 267 individuals in 2004 (Table 1). The mean annual AGB gaining rate is 2.73 Mg ha^{-1} from 2004 to 2014, over 70% of which was attributed to an increase in mean diameter of trees in the 30–70 cm size classes (Fig 2). Mortality induced by AGB loss was more evenly distributed, with a median in 50–60 cm trees. AGB change positive in 1–70 cm and 100–120 cm diameter class, but negative in the 80–100 cm class (Fig 2).

Biomass variables (AGB and CWP) in 10×10 m subplots were not normally distributed and had larger variation than in 50×50 m subplots (Fig 3). Among 0.04 ha (20×20 m) plots, the mean standard deviation was 93.1 Mg ha^{-1} , and the 95% confidence interval on the mean AGB was around 14.5 Mg ha^{-1} . More than 90 percent of the inherent variability of these variations in AGB, CWP and mortality were explained by plot size (Table 3). The accuracy of AGB stock and CWP calculation increased with subplot area with the CV estimates of AGB stock had a smooth slope due to the low value of both the parameter α (10.3) and β (0.37) (Table 3 and Fig. 4). The value of the latter suggested a strong negative autocorrelation. The CVs of AGB mortality were high and depended on plot area. The number of subplots needed to estimate the mean AGB stock and dynamics within a 20 percent error of the mean with 95% confidence interval were dramatically different from AGB loss (Table 4).

4. Discussion

The present study provides two important advances in our understanding of AGB stock and dynamics in temperate old-growth forest. First, a directional tree growth trend independent of habitat nutrients heterogeneity was found in this old growth forest. The observed increases in AGB stock are mainly attributed to the growth of intermediate size trees (30–70 cm DBH), indicating that this forest is still reaching its mature stage (Wirth and Lichstein, 2009; Stephenson et al., 2014). Second, we indicate that biomass loss due to mortality reduces living biomass may be the primary factor to affect forest biomass dynamics in this area. More sampling efforts are required to obtain a reliable AGB dynamic than stock due to independence of mortality events.

4.1. Tree growth independent of soil nutrient

As indicated in Table 2, a higher forest recruitment rate (stems <1 cm in this study) were found in nutrient rich habitat (low-plateau) in line with the hypotheses of soil nutrient supply being the main limiting factor for recruitment and performance of small

Table 2

Variation in forest structure and dynamics among habitats. The number of individuals per hectare in each census, the change in the number of individuals between censuses, as well as the aboveground biomass (AGB) in each census and between census is shown for the entire forest and in each habitat type (low-plateau, high-plateau and slope). In addition, AGB is divided into that attributed to growth, recruitment and mortality. The 95% confidence intervals estimated for each value (according to 999 restricted permutations) is shown between parentheses.

	Forest-wide 25 ha (100%)	Low-plateau 11.24 ha (44.9%)	High-plateau 11.92 ha (47.7%)	Slope 1.84ha (7.4%)
Individuals in census 1 (ha ⁻¹)	2504 (2461, 2546)	2474c* (2432, 2515)	2614b (2571, 2656)	2681a (2631, 2733)
Individuals in census 2 (ha ⁻¹)	2418 (2375, 2460)	2518a (2479, 2562)	2450a (2408, 2494)	2404a (2361, 2447)
Change in stem density (ha ⁻¹ yr ⁻¹)	-8.5 (-12, -5)	4.5a (0.74, 8.3)	-16b (-20, -13)	-28c (-31, -25)
AGB census 1 (Mg ha ⁻¹)	265.4 (260.2, 271.1)	243.6c (238.3, 249.2)	290.0a (285, 295)	257.4b (250.1, 264.4)
AGB census 2 (Mg ha ⁻¹)	269.7 (261.9, 277.4)	257.7c (252.1, 263.4)	299.5a (293.8, 305.2)	278.1b (270.4, 285.5)
AGB change (Mg ha ⁻¹ yr ⁻¹)	1.36 (1.17, 1.55)	1.41b (1.24, 1.58)	0.93c (1.24, 2.10)	2.07a (1.88, 2.26)
Growth rate (Mg ha ⁻¹ yr ⁻¹)	2.70 (2.61, 2.79)	2.64b (2.55, 2.73)	2.58b (2.49, 2.66)	2.91a (2.79, 3.04)
Mortality rate (Mg ha ⁻¹ yr ⁻¹)	1.38 (1.21, 1.55)	1.27b (1.13, 1.40)	1.67a (1.46, 1.88)	0.87c (0.72, 1.01)
Recruitment rate (Mg ha ⁻¹ yr ⁻¹)	0.035 (0.022, 0.048)	0.036a (0.023, 0.049)	0.024b (0.015, 0.033)	0.024b (0.019, 0.029)
CWP (Mg ha ⁻¹ yr ⁻¹)	2.74 (2.65, 2.83)	2.68b (2.58, 2.77)	2.60b (2.52, 2.69)	2.94a (2.81, 3.06)
Relative net change (% yr ⁻¹)	0.46 (0.38, 0.55)	0.51a (0.44, 0.59)	0.30b (0.22, 0.38)	0.69a (0.62, 0.75)

*Different letters indicate significant differences (ANOVA, $P < 0.05$, Tukey's post-hoc analysis) among habitats.

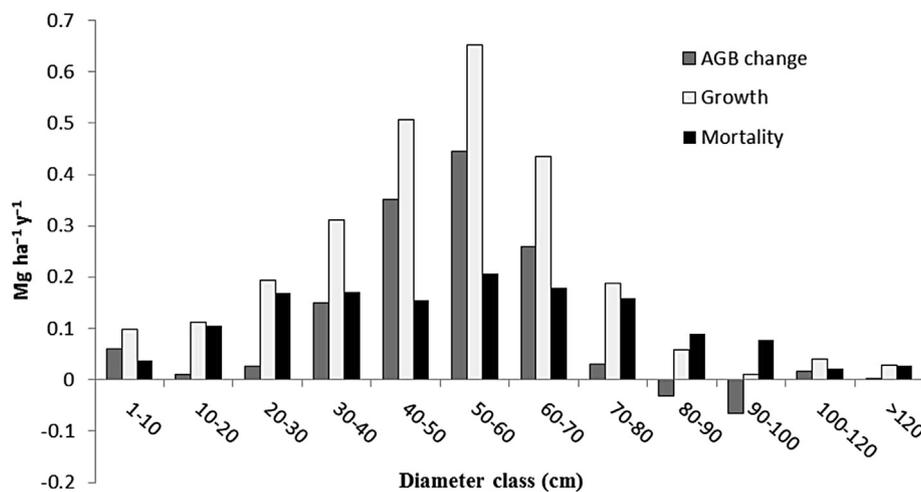


Fig. 2. AGB fluxes by tree size class in the CBS plot. Individual growth and mortality are attributed to the size class of the initial census regardless of any shift to a larger class during the 10 y census interval. AGB change in the smallest size class also includes in growth (net recruitment) of newly measured saplings. The net change reflects the difference between growth and mortality, as well as fluxes in and out of the size class.

trees (Chase and Leibold, 2003). Previous experiments in temperate forests have shown that the effect of nutrient addition is positive (de Vries et al., 2009), and limited element additions often resulted in doubled stem growth rates in small trees but had no effect on larger trees (Clare et al., 2013). By contrast, trees in most area of this 25 ha plot have similar growth rate and stems in nutrient rich habitat did not show a better performance than other sites, implying the local soil condition did not enhance larger plant growth. Coexistences of tree species in temperate forests was driven primarily by competition for light because of vertical stand structure resulting in larger heterogeneity in tree height and leaf display (Morin et al., 2011; Jucker et al., 2014). Thus, trees in slope habitats will intercept more light and grow faster due to complex

topographic differentiation will meet different light requirements of vertically structured canopies (Morin et al., 2011).

Carbon accumulation are almost entirely the result of increases in biomass of stems with 30–70 cm DBH, a size class that accounts for over 70% of coarse woody productivity, which suggest that mixed broad leaf-conifer forest in northeastern China is still moving toward greater maturity and has great carbon sequestration potential (Wirth and Lichstein, 2009). Our results also have shown that smaller trees (<10 cm diameter) hold less than 1% of the AGB stock, which implies that studies only including stems ≥ 10 cm will leads to acceptable AGB stock estimation in this temperate forest (Zhou et al., 2011). However, without considering small trees it will be impossible to account for the proportion of biomass

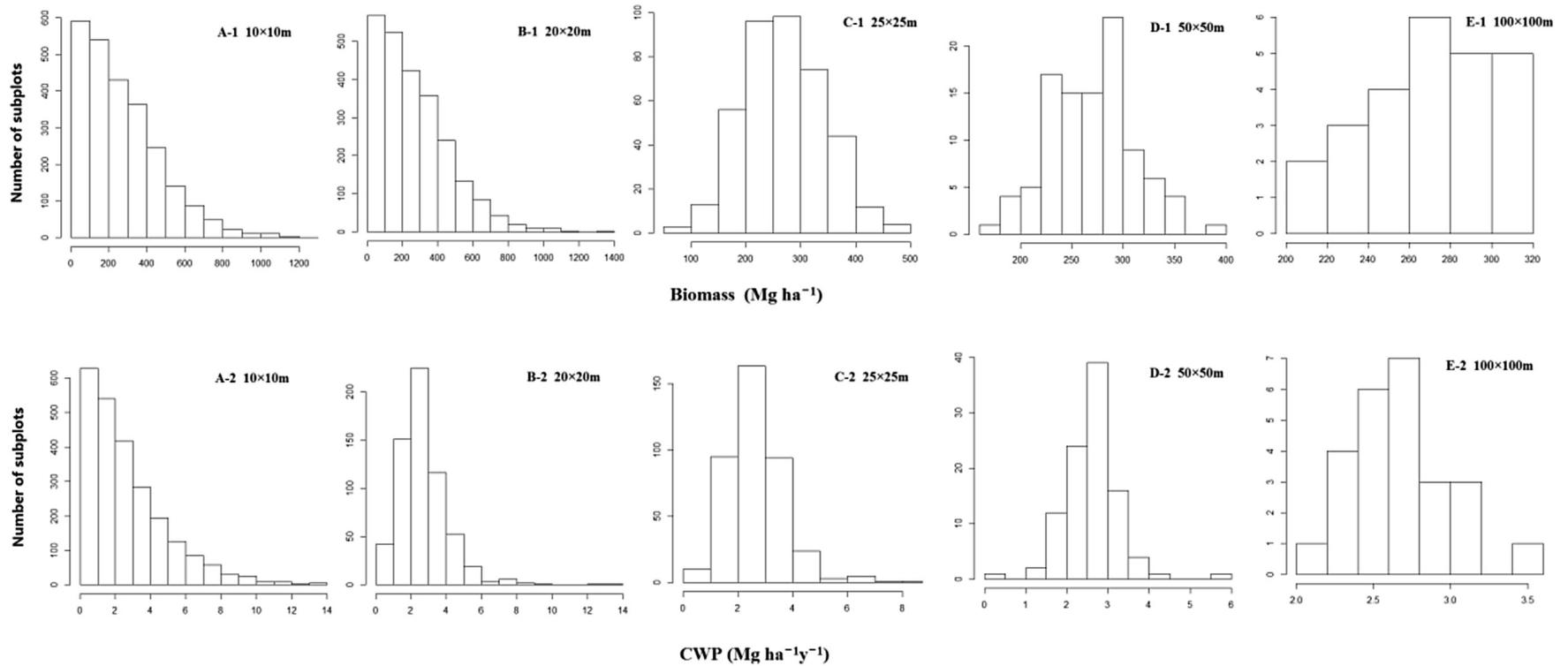


Fig. 3. Aboveground biomass (AGB) and coarse woody productivity (CWP) in subplots of the CBS plot. (A) Numbers of 0.01 ha (10×10 m) subplots per AGB (high) and CWP (below) class in the 25-ha plot. (B) 20×20 m subplots, (C) 25×25 m subplots, (D) 50×50 m subplots, and (E) 100×100 m.

Table 3

Predicting coefficient of variation (CV) of the descriptors of forest above-ground biomass stock and change. Shown are mean \pm SD of the estimated parameters and the quality of the fit of the model.

Variables	Parameter estimates \pm SD		R2
	α	β	
AGB (Mg ha^{-1})	10.3 ± 1.02	0.37 ± 0.02	0.95
CWP ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)	20.5 ± 1.01	0.38 ± 0.01	0.98
Mortality ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)	52.9 ± 1.03	0.50 ± 0.01	0.99

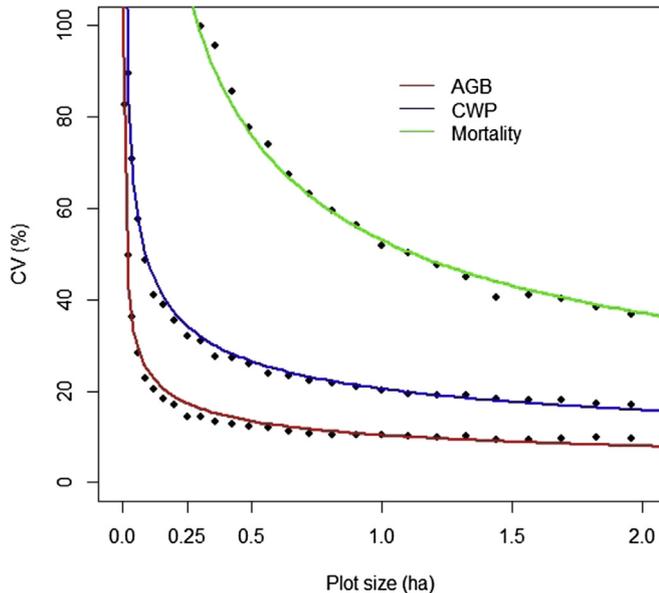


Fig. 4. The coefficient of variations (CV) of forest AGB, CWP and mortality rate changes with plot area in the CBS plot. CVs of forest AGB, CWP and mortality as a function of plot size. $\log(\text{CV}) = \log(\alpha) - \beta \log(S) + \log(\epsilon)$, with S the plot area, α , β the fitted model parameters and ϵ the model residuals.

accumulation due to recruitment (Valencia et al., 2009; Vincent et al., 2015).

4.2. Mortality shapes the AGB change

Our analysis underline that biomass loss due to mortality may be the primary factor affecting forest biomass accumulation in this area. Though at local scale, the high plateau and slope habitat are remarkably different in AGB loss, with the high plateau having nearly twice times higher mortality. This pattern seems to be caused by the small scale disturbances associated with tree death (Clark, 2007; Feeley et al., 2007). As forests age, the major driver of tree death will shift from competition for resources to survival and exposure to disturbances (Taylor and MacLean, 2005). Although a variety of natural disturbances exists in forests, such as wind, ice storms, droughts, fires, insects and disease outbreaks, wind is the

most pervasive forces regulating forest composition and structure in this area (Liu, 1997). According to our previous study and Table 2, more large trees occur on high elevations are more likely to fall due to wind throw because the plateau may has higher wind speed than low sites and therefore lead to higher mortality. Previous study in this area also showed that stems living a higher elevation sites suffered much wind damage than other two lower-elevation forests in (Zhou et al., 2011). As the calculation of AGB change equals growth plus recruitment minus loss, the death of large trees is the primary process driving change of forest biomass in the middle and high latitudes of the northern hemisphere where steady tree growth is enhanced by climatic change (Taylor and MacLean, 2005; Xu et al., 2012; Holzwarth et al., 2013). For example, Xu et al. (2012) suggested shifts in mortality from the loss of small trees to the loss of large trees, rather than changes in biomass production, driver stand AGB accumulation in a *Quercus*-dominated forest.

Tree death can be induced by a multitude of processes simultaneously with highly stochastic and the assessment of mortality was considered to be one of the greatest challenges in quantifying forest dynamics (Chao et al., 2009; Holzwarth et al., 2013). As shown by our model, the inherent variations of forest AGB stock and mortality are quite different, and more sampling efforts are required to obtain a reliable AGB dynamic than standing stock. Similar results were found by Jansen et al. (2008), who indicated that at least 9-ha area would be needed to estimate AGB increment but at least 40 ha to reliable estimate AGB loss. Compared with mortality of seedling and small trees, disturbance-driven deaths of dominant, big trees that have greater impact on stand biomass accumulation are rare and intermittent (Berger et al., 2004). Importantly, the variation of tree mortality simply cannot incorporated into chronosequence researches and require more sampling effort to obtain a reliable estimate of AGB change (Wagner et al., 2010; Holzwarth et al., 2013). It is worthy to note that ten years intervals metrics in forest may be inherently very noisy (Chave et al., 2008). For example, the AGB of Barro Colorado Island increased in 1985–90, decreased in 1990–1995, and increased again in 1995–2000. These studies warn that long-term monitoring is necessary to accurately reflect long-term trends in forest biomass change under a changing environment.

5. Conclusions

Based on ten years forest monitoring data from a 25 ha temperate forest plot, the analysis of the role of habitat and tree size on pattern and dynamics of biomass stock leads to three major conclusions.

First, we provided empirical evidence that a steady tree growth trend independent of habitat nutrients heterogeneity was found from 2004 to 2014. However, biomass loss due to mortality reduces living biomass in high plateau habitat was significantly higher than other habitat. Thus, tree death rates may be the primary factor to affect the local variability of forest biomass dynamics in this area.

Second, the observed increases in AGB stock were mainly attributed to the growth of intermediate size trees (30–70 cm

Table 4

Estimates of the number of randomly distributed subplots needed to obtain the mean of above ground biomass and coarse woody productivity within a 20 percent error (± 10) of the mean with 95% confidence interval for various subplot sizes.

Plot area (ha)	Estimated number of subplots				
	0.04 (20 × 20 m)	0.09 (30 × 30 m)	0.25 (50 × 50 m)	1.00 (100 × 100 m)	2.25 (150 × 150 m)
Above ground biomass (AGB)	13	6	3	1	1
coarse woody productivity (CWP)	50	21	13	4	3
Mortality rates	778	339	117	26	12

DBH), indicating that this forest is still reaching its mature stage. Our results also demonstrated that without considering small trees (DBH < 10 cm) had negligible effect on AGB stock estimation but will significant influence the proportion of biomass accumulation due to recruitment.

Third, the inherent spatial variations of forest AGB dynamics (increment, mortality) were larger than standing stock. More sampling efforts were required to obtain a reliable AGB dynamic than stock due to great variation independence of mortality event.

Author contributions statement

F.L. and Z.H. designed the experiments, Z.Y, F.L, X.W, J.Y, Y.W, Y.S and JS conducted the experiments, and Z.Y and A.G analyzed the data and wrote the manuscript. All authors contributed to the discussion of the results.

Acknowledgments

We gratefully thank Dr. Helene C. Muller-Landau and Ryan Chisholm for their valuable suggestions to improve the manuscript. This study was sponsored by the external cooperation program of BIC, Chinese Academy of Sciences (151221KYSB20130003), National Natural Science Foundation of China (41301057, 41101188 and 31370444). This paper was also supported by CFERN & GENE Award Funds on Ecological Paper.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2016.06.007>.

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