Effects of climate change on biomass carbon sequestration in old-growth forest ecosystems on Changbai Mountain in Northeast China


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1. Introduction

Global warming is caused by increased concentrations of greenhouse gases in the atmosphere, especially that of carbon dioxide. Reduction of carbon emissions and increase of carbon absorption are effective approaches to alleviating the rate of rise in temperature. An old-growth forest ecosystem is a huge carbon pool, and recent research has found that such a forest can continue to accumulate atmospheric carbon dioxide, suggesting that old-growth forests can serve as a global carbon sink (Zhou et al., 2006, 2011; Luyssaert et al., 2008; Tan et al., 2011). However, the impacts of climate change on the capacity of carbon sequestration in old-growth forest ecosystems remains uncertain.

By definition, old-growth forest biomass is that remaining at the point when gains from tree growth and recruitment are balanced by losses due to the deaths of trees and parts of trees. Previous studies on carbon sequestration in old-growth forest ecosystems have found that biomass sequestration has decreased (Taylor and MacLean, 2005; Helama et al., 2011) because mortality is roughly equal to or higher than the production of surviving trees, and thus stand biomass sequestration is close to zero or negative (Xu et al., 2011). In some cases the carbon sink is supplied mainly from soil (Zhou et al., 2006) and woody debris (Zhou et al., 2011). However, some researchers have found that old-growth forests may also display an increase in biomass generated by living tree growth (Luyssaert et al., 2008), especially for very large trees (DBH > 60 cm) (Tan et al., 2011). This may indicate that the carbon sequestration pattern in old-growth forest ecosystems may vary.

In light of the above, increases of biomass carbon in old-growth forests may likely be attributed to the following factors: (a)
age-related: the forest has not reached a fully mature or over-mature state and thus growth has continued (Wang et al., 2011) and (b) climate-induced: changes in climatic factors have altered the balance of photosynthesis and respiration (Boisvenue and Running, 2006). To date, most results regarding carbon sequestration have been derived from long term site-specific monitoring (e.g., Zhou et al., 2006, 2011). By comparing monitoring data from different observational periods, variations in tree DBH, height, and density can be analyzed to estimate forest ecosystem biomass carbon. However, this approach cannot uncover the underlying dynamic of annual carbon accumulation nor explain the reasons for carbon pool variation.

Changbai Mountain Natural Reserve (CMNR) in Northeast China, most of which is covered by primary forest ecosystems, has not been subject to human disturbance and provides a living laboratory for studying forest carbon sequestration under natural environmental conditions. In order to explore the long term dynamics of stand structure and community composition, three permanent sample plots, representing the three major forest ecosystems types in the reserve, were established on the north slope of the CMNR in 1981. Plot altitudes ranged from 750 m to about 1950 m asl. Studies utilizing data from the permanent sample plots during the past 30 years have reported that all of the three forest ecosystems are carbon sinks (Zhou et al., 2011). However, in two of the three forest types – Korean pine (Pinus koraiensis Sieb. et Zucc) and broad-leaved mixed forest and Erman’s birch (Betula ermanii Cham.) forest – carbon sequestration has occurred primarily in living trees, the carbon density of which increased by 48.5 and 47.0 t C ha$^{-1}$, respectively. In the third type – spruce-fir forest (Picea jezoensis Carr. var. komarovi (V.Vassil.) Cheng et L.K. Fu)-(Abies nephrolepis (Trautv.) Maxim.) – carbon sequestration has occurred mainly in woody debris and soil. Living tree biomass carbon decreased by 23.8 t C ha$^{-1}$, while carbon in woody debris and soil increased by 28.4 and 24.0 t C ha$^{-1}$, respectively. The actual factors affecting the carbon sink capacity and its variation in old-growth forest ecosystems on Changbai Mountain is still unknown.

To date, researchers in Northeast China have designed models to simulate the dynamics of forest composition and structure and the potential distribution of major forest types under different climate change scenarios (e.g., Zhao et al., 1998; Shao, 1996; Shao et al., 2003; He et al., 2005). These studies have suggested that distributions of the dominant conifer tree species in the region under climate warming will be manifest via northward geographic and upward altitudinal shifts. However, few studies have focused on the biomass sequestration or net primary productivity (NPP) under climate warming. Recently, tree ring research has revealed that spruce growth will decrease with increasing temperature in the CMNR (Yu et al., 2011; Li et al., 2011), while the other dominant tree species will benefit from climate warming (Zhang et al., 2007; Yu et al., 2011). While these results may help us better understand how the forest structure will shift under climate warming, the effects of warming climate on biomass sequestration for whole forest ecosystems remain unclear.

Combining tree ring analysis with vegetation monitoring via permanent plots, this study analyzed forest biomass sequestration characteristics and radial growth for every tree species on the north slope of the CMNR in the context of their responses to climate change. The goal of the study was to explore: (1) trends in temperature and precipitation change in the CMNR during the past 30 years; (2) dominant tree radial growth trends in each forest ecosystem and their relationship to climatic factors; and (3) carbon stocks of each forest ecosystem and of all tree species therein during the past 30 years; in order to assess whether carbon sequestration is related to climate change and to identify which climatic factors influenced carbon sequestration in the three old-growth forest ecosystems.

2. Material and methodology

2.1. Climate and vegetation of the study area

The study site is located on the northern slope of the Changbai Mountain Natural Reserve (CMNR) in Northeast China (41°43′–42°26′ N,127°42′–128°17′E) (Fig. 1). The reserve is about 200,000 ha in size, with an elevation ranging from 740 to 2691 m. It was established in 1960 and added to the World Biosphere Reserve Network in 1980 as part of the Man and the Biosphere Program. There has been little human disturbance in the

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**Fig. 1.** Location of the Changbai Mountain Natural Reserve in Northeast China.
core zone, since Changbai Mountain was protected as the legendary birthplace of the imperial family during the Qing Dynasty (AD 1644–1911) and as a national natural reserve at the beginning of the 1960s.

The climate of the study area is characterized by cold, windy winters and wet summers. According to data for 1958–2011 obtained from the Erdao meteorological station, which is nearest to the reserve (Fig. 1), average annual precipitation is 815 mm and about 80% of the total annual precipitation occurs between June and September. Average annual temperature is 3.7°C, with monthly mean temperatures remaining below 0°C from May to October. July is the warmest month, with a mean temperature of 20.1°C. The mean storm (wind > 17 m/s) frequency increases with altitude, from 30 days/year at 774 m asl to 267 days/year above 2623 m asl (Liu, 1997).

Influenced by the climatic gradient, clear altitudinal vegetation zones occur from the base to the top of the CMNR. These include: (1) Korean pine and broad-leaved mixed forest [KBF] (740–1100 m), dominated by Korean pine, Amur linden ([Tilia amurensis Rupr.]), Manchurian ash ([Fraxinus mandshurica Rupr.]), and other broad-leaved species; (2) spruce-fir forest [SFF] (1100–1700 m), dominated by spruce fir and Erman's birch (3) Erman's birch forest [EBF] (1700–2000 m), comprised solely of this species; and (4) tundra.

### 2.2. Sample plots

In 1981, four permanent plots – three of size 1 ha (plots 1–3), and one 0.06 ha (20 m × 30 m) in size (plot 4) – were established in the lower three forested vegetation zones on the north slope of the CMNR. However, some of the original data for plot 2 (situated in the lower distribution of SFF at 1268 m asl) is no longer accessible. Therefore, the other three plots were selected for this study – plots 1, 3 and 4 are representative of KBF, SFF, and EBF forests, respectively (Fig. 1, Table 1). Every tree ≥ 6 cm in DBH within the plots was identified, numbered, and DBH and height were recorded. Original measurements in 1981 and their derivatives for plot 1 at 740 m (KBF), plot 3 at 1680 m (SFF), and plot 4 at 1920 m (EBF) were used in this article for computing carbon density in 1981. In 2010, the three permanent plots were re-measured following the same procedure used in 1981.

In order to detect year-to-year variation in tree growth, in 2011 three 600 m² (20 m × 30 m) sample plots in KBF, two 400 m² square sample plots in SFF, and two 100 m² square sample plots in EBF were established close to the permanent plots. In 2010, Korean pine, Amur linden, and Manchurian ash accounted for 76.6% of total stand basal area in KBF permanent plot; in SFF permanent plot, spruce and fir accounted for 79.7% of total stand basal area; while the EBF permanent plot was comprised exclusively of Erman's birch (Table 1). Thus these six tree species were selected for sampling. At each of the seven sample plots, living trees from among the above six species with DBH ≥ 6 cm were selected and paired increment cores were taken at breast height (~1.3 m) in two radial opposite directions. For Manchurian ash, when the number of stems available for dendrochronological analysis was less than 20, trees on the edge of the plots were sampled. In some instances (N = 29) where a tree was partially rotten, only one core was taken. Additionally, the ring series lengths for 10 trees less than 20 years of age were discarded. On an overall basis, a total of 212 trees and 424 cores were used in this study (Table 2).

### 2.3. Forest biomass carbon estimation

#### 2.3.1. Stand biomass carbon storage (TBC)

Species-specific allometric equations based on tree diameter at breast height (DBH) or height (H) were applied to estimate the forest living tree biomass in 1981 and 2010, including stem, branch, leaf and root. Equations for Korean pine, [Picea jezoensis] and [Betula platyphylla], spruce and fir used in this study were developed by Zhu et al. (2010) for Changbai Mountain; while equations for other species were developed by Wang (2006) for Xiaoxinganling Mountain in Northeast China. Since no equation was available for Erman’s birch, this study used the equation for [B. platyphylla] as a substitute. In order to eliminate measurement error, tree height was estimated via a conversion factor from DBH (Zhu et al., 2010). Carbon storage was estimated utilizing a biomass transformation coefficient of 0.5. The net increase of stand biomass carbon in a permanent plot (ATBC) is equal to TBC in 2010 minus TBC in 1981.

### Table 1

Characteristics of permanent plots in 2010.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Elevation (m asl)</th>
<th>Area (ha)</th>
<th>Forest type</th>
<th>Dominant tree species</th>
<th>Basal area proportion (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>748</td>
<td>1</td>
<td>Korean pine and broad-leaved mixed forest</td>
<td>Pinus koraiensis</td>
<td>27.49</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tilia amurensis</td>
<td>22.74</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Fraxinus mandshurica</td>
<td>26.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Quercus mongolica</td>
<td>7.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Acer spp.</td>
<td>10.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Others</td>
<td>5.37</td>
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<td></td>
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<td>Total</td>
<td>100</td>
</tr>
<tr>
<td>3</td>
<td>1680</td>
<td>1</td>
<td>Spruce-fir mixed forest</td>
<td>Abies nephrolepis</td>
<td>16.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Picea jezoensis var. komarovi</td>
<td>63.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Betula ermanii</td>
<td>13.93</td>
</tr>
<tr>
<td></td>
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<td>Others</td>
<td>6.36</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>100</td>
</tr>
<tr>
<td>4</td>
<td>1920</td>
<td>0.06</td>
<td>Erman’s birch forest</td>
<td>Betula ermanii</td>
<td>100</td>
</tr>
</tbody>
</table>

### Figure 2

Monthly total precipitation, mean temperature, and mean maximum and minimum temperatures for the Changbai Mountain Nature Reserve from 1959–2010 recorded at the Erdao meteorological station.
2.3.2. Species-specific biomass carbon sequestration (BCS)

Since many of the tree number tags originally attached to individual trees were missing, the annual DBH of an individual tree in the period of 1981–2010 was calculated via the following:

\[
DBH_{1981} = DBH_{1980} - 2 \times \sum_{i=1}^{N_{s_j}} RW_i
\]  

(1)

\[
DBH_{1980+t} = DBH_{1980} + 2 \times \sum_{i=1}^{N_{s_j}} RW_i \quad (t = 1, 2, 3, \ldots, 30)
\]  

(2)

where DBH_{1980} indicates DBH of the tree in 1980 and RW_i is ring width in year i (i = 1981, 1982, ..., 2010).

Utilizing species-specific allometric equations, biomass carbon sequestration (BCS) of each individual tree in a given year (i) was calculated via:

\[
BCS_i = f(DBH_i, H_i)
\]  

(3)

where DBH_i and H_i is DBH and height of the tree in year i; and the annual BCS for an individual tree in a given year (i) was calculated by:

\[
\Delta BCS_i = BCS_i - BCS_{i-1}
\]  

(4)

Species-specific current annual BCS was obtained via:

\[
\Delta BCS_{ij} = \sum_{k=1}^{N_{j}} \Delta BCS_{ik}
\]  

(5)

where \( \Delta BCS_{ij} \) is the annual BCS of the tree species j in year i; k is the number of tree species j in the sample plots (k = 1, 2, 3, ..., N_{s_j}).

The total species-specific current annual BCS in permanent plots (\( \Delta TBCS_i \)) was obtained according to the species-specific annual BCS in sample plots and tree numbers (N_{p}) in permanent plots in 2010. For tree species for which cores were not taken, the current annual biomass carbon sequestration was calculated based on the difference in biomass over the entire period (1981–2010) utilizing the equation:

\[
\Delta TBCS_i = \sum_{j=1}^{S} \Delta BCS_{ij}/N_{s_j} \times N_{pj} + (BCS_{p2010} - BCS_{p1981})/30
\]  

(6)

where \( N_{s_j} \) is the number of tree species j in the sample plot; \( N_{pj} \) is the number of tree species j in the permanent plot; and \( S \) is number of tree species for which cores were taken in sample plots; Thus, for example, \( BCS_{p2010} \) means that the tree species \( nj \) were found in a permanent plot but cores were not taken.

According to the biomass carbon sequestration for living trees (\( \Delta TBCS \)) and the net increase of stand biomass carbon in a permanent plot (\( \Delta TBC \)), the loss of stand biomass carbon (\( \Delta TBCL \))—which is the difference between the biomass decrease induced by tree death and the biomass increase induced by the tree with DBH < 6 cm in 1981 and DBH ≥ 6 cm in 2010—was calculated via the following:

\[
\Delta TBCL = \Delta TBCS - \Delta TBC
\]  

(7)

2.4. Growth-climate relationship

All cores were mounted, sanded, and visually cross-dated. The ring widths were measured to the nearest 0.001 mm. Visual cross-dating was subsequently verified using the COFECHA program (Holmes, 1983), which helps to identify segments of a core or group of cores where dating or measurement errors might occur. All tree cores for which ring identification and/or cross-dating was difficult were eliminated from the site chronology. The final sample size for each plot can be found in Table 2.

Tree-ring standardization—the removal of biologically induced age-trends—was performed using the program ARSTAN (Cook, 1985). Each ring-width series was detrended by individually fitting a cubic smoothing spline with a 50% frequency cut-off equal to 67% of the series length to retain high frequency (Cook, 1985; Holmes, 1992). Fitting these curves reflects the underlying assumption that each individual growth trend is driven primarily by biological growth (Cook et al., 1990). The ring-width of each core was divided by the fitted line value to produce a standardized tree-ring series. These individual dimensionless index series were then averaged using a bi-weight robust mean to develop standardized chronologies (STD) (Cook et al., 1990; Wu, 1990). The expressed population signal (EPS), which quantifies the degree to which a particular sample chronology portrays a hypothetically perfect chronology, was determined by calculating each chronology signal as a fraction of the total chronology variance.

Climate data—temperature and precipitation, 1957–2010—were obtained from the Erdao meteorological observation station (42°53′N, 128°25′E). The Palmer Drought Severity Index (PDSI) can be used to determine the beginning, end, and severity of a drought period (Dai et al., 2004). In this study, PDSI data for 1957–2003 were obtained from the 2.5° × 2.5° grid box closest to the CMNR at 127.5°–130° N, 40°–42.5° E by the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl).

Correlations between tree ring chronologies and the climatic variables—i.e., monthly mean minimum temperature, total monthly precipitation (1958–2010), and PDSI (1958–2003)—extending over a 14-month window from September (the last month of mean temperature over 5°C of the previous year (t – 1) to October (the last month of mean temperature over 0°C of the current year (t) (Fig. 2) were examined using Pearson correlation.

2.5. The effect of climate variation on biomass carbon sequestration

Given that the effects of climate on tree growth were likely intensifying as temperature increased from 1981 to 2010, the slope of the fitting line for raw ring width series in this period may indicate the extent of climate effects on tree growth. Under the assumption that tree growth changed at the same rate in each year, this study took the intercepts of the fitting line for raw ring width
series in this period as the hypothetical value for annual carbon sequestration over the 30-year period under conditions of no climate warming. This provided a baseline for comparison with carbon sequestration under conditions of no climate warming in the period of 1981–2010.

The equation of the six tree species in the three plots were:

Plot 1: \( Y_{\text{Pinus koraiensis}} = -0.0232X + 1.6863 \quad (r^2 = 0.39, p < 0.01) \);
\( Y_{\text{Fraxinus mandshurica}} = 0.0131X + 0.9012 \quad (r^2 = 0.50, p < 0.01) \);
\( Y_{\text{Tilia amurensis}} = -0.0002X + 1.013 \quad (r^2 = 0.01, p > 0.05) \);
Plot 2: \( Y_{\text{Picea jezoensis}} = -0.0072X + 1.5338 \quad (r^2 = 0.155, p < 0.01) \);
\( Y_{\text{Abies nephrolepis}} = -0.0028X + 1.3206 \quad (r^2 = 0.097, p < 0.05) \);
\( Y_{\text{Betula ermanii}} = 0.0023 + 0.5686 \quad (r^2 = 0.0186, p > 0.05) \)

where \( Y \) is the ring width (mm), \( X \) is the years from 1980 (\( X = 1, 2, \ldots, 30 \)).

3. Results

3.1. Climate variation trends

According to observation data from the Erdao surface meteorological station dating from 1958, the annual mean temperature has increased significantly \( (R^2 = 0.54, p < 0.01) \), especially the mean minimum temperature \( (R^2 = 0.73, p < 0.01) \) (Fig. 3a). The annual mean temperature has increased by about 2 °C, while the annual mean minimum temperature has increased by 3.4 °C from 1958 to 2010 (Fig. 3a). At the same time, total precipitation displayed a slight decrease \( (R^2 = 0.0014, p > 0.1) \) [Fig. 3b]. Thus climate became somewhat more dry in the area. Evidence for this is also provided by the decrease of PDSI from 1958 to 2010 \( (R^2 = 0.22, p < 0.01) \) [Fig. 3c].

Fig. 3. Dynamics of annual mean temperature (a) and mean minimum temperature (b) obtained from the Erdao meteorological station from 1959–2010, and PDSI (c) from 1959–2003 derived from grid data.

3.2. Tree ring width chronologies and radial growth patterns

Although this study did not attempt to focus on larger size trees, the mean age of Korean pine in plot 1 was still less than would have been expected in this old-growth forest. The maximum age just reached 157 years (Fig. 4a), while for the dominant broadleaf tree species – Manchurian ash and Amur linden – the oldest trees can be traced back to the 1770s (Fig. 4b and c). In plots 3 and 4, the maximum age of spruce reached 200 years (Fig. 4d), while both that of fir and Erman’s birch displayed smaller mean ages than expected (Fig. 4e and f).

The mean DBH and SD of trees selected for core sampling were close to those obtained for the permanent plots (Table 2), suggesting that the selected trees effectively represent actual tree growth in the entire plots. Korean pine displayed the largest mean ring width (1.53 mm), and Erman’s birch in plot 4 had the smallest width (0.87 mm) [Table 2].

High rbar values (0.33–0.62), with SFF displaying the highest values, confirmed common variance and suggested the operation of a strong common climatic force (Table 2). EPS values (0.89–0.93) were high for all tree species, indicating that the theoretical
population for each species is well represented. Mean sensitivity (MS) and standard deviation (SD) ranged from 0.15 to 0.22 and from 0.141 to 0.291, respectively. The high variance in the first principal component (PC1) ranged from 35.7% to 47.1%, suggesting that all tree chronologies contain a large amount of climatic information (Table 2).

Trees growth in the CMNR displayed different patterns during the past 30 years (Fig. 4). All of the conifer tree species have decreased in radial growth in the period of 1981–2010, while growth for all of the broadleaved tree species has increased, with the exception of a slight decrease for Amur linden (Fig. 4a–f). However, only the radial growth of Korean pine displayed a significant decrease in this period ($R^2 = 0.26, p < 0.01$) [Fig. 4a]; no significant trends were found for the other tree species.

### 3.3. Climate–growth relationship

Complex relationships were found between monthly climate variables and STD chronologies (Fig. 5). Monthly minimum temperature was negatively correlated with Korean pine radial growth, with significant correlations occurring with September and October of the previous year ($t-1$) and January, February, April, June, August and October of the current year ($t$). Precipitation in September ($t-1$) and September ($t$) were positively correlated with Korean pine growth. In addition, positive correlations of Korean pine radial growth were also found with all monthly PDSI measures except that for September ($t-1$) [Fig. 5a]. Similar effects of climate variables on growth were found for spruce, and correlations with almost all monthly PDSI measures were significant, with the exception of the three-month period from April ($t$)–June ($t$) [Fig. 5d]. The general positive effects of PDSI indicate that water stress is an important factor limiting radial growth of these two species. In contrast, temperature was positively correlated with the radial growth of Manchurian ash (Fig. 5b), with significant effects evident in September ($t-1$), October ($t-1$), November ($t-1$), August ($t$) and October ($t$). No significant correlations were found for temperature with growth of Amur linden or Erman’s birch, but precipitation was significant for both in July ($t$) [Fig. 5c and f]. Growth of fir was significantly correlated with temperature and precipitation in September ($t-1$) and September ($t$) [Fig. 5e].

### 3.4. Total biomass carbon stock

Forest biomass carbon stock of living trees (TBC) clearly increased in plot 1 over the past three decades from 147.47 to 201.22 t, with an annual increment ($\Delta$BC) of 1.79 t, and in plot 4, from 52.79 to 89.49 t, with an annual increment of 1.22 t. In plot 3, however, the carbon stock clearly declined, dropping from 123.1 to 106.5 t with an annual decrease of 0.55 t (Tables 3 and 4).

### 3.5. Species-specific biomass carbon stock

Carbon stock and mean DBH for all tree species increased over the 30-year period, with the exception of *P. davidiana* in permanent plot 1 (Table 3). In contrast to Amur linden, the number of Korean pine and Manchurian ash decreased in plot 1, but the carbon stock of all three dominant tree species increased by a total of 41.77 t, accounting for 77.7% of the carbon stock increase during the past 30 years. Mean DBH for all tree species in plot 3 increased, while the total number for all tree species clearly declined (Table 3 and 4). The total number of fir, spruce and Erman’s birch decreased by 118, 88, and 35 individuals, respectively. However, only carbon stock of spruce and Erman’s birch decreased, while that of fir increased slightly (0.69 t) [Table 3]. When the carbon stock of trees accounting for the above losses is estimated in relation to the carbon stock per tree in 1981, the decrease in carbon stock of spruce and birch in plot 3 is 19.97 t and 1.07 t, respectively. Thus spruce accounted for 95% of the total decrease for these two species. This results in a total reduction in carbon storage for the three dominant tree species of 20.35 t, which was equivalent to 17.1% of total biomass carbon stock for living trees in 1981. In plot 4, while the number of Erman’s birch decreased, both DBH and carbon stock increased by 3.2 cm and 36.7 t, respectively. These results indicate that the number of young/small size trees decreased for fir, Korean pine and Erman’s birch, while the number of old/large size trees increased (Tables 3 and 4).
### Table 3

<table>
<thead>
<tr>
<th>Tree species</th>
<th>DBH(SD)(cm)</th>
<th>Density</th>
<th>Carbon stock (t ha(^{-1}))</th>
<th>Carbon stock per tree (t per tree)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot 1</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Pinus koraiensis</td>
<td>27.1(10.8)</td>
<td>33.8(12)</td>
<td>150</td>
<td>127</td>
</tr>
<tr>
<td>Tilia amurensis</td>
<td>27.9(15.3)</td>
<td>31.4(17.0)</td>
<td>79</td>
<td>106</td>
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<tr>
<td>Fraxinus mandshurica</td>
<td>46.3(16.1)</td>
<td>51.5(21.9)</td>
<td>58</td>
<td>50</td>
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<tr>
<td>Betula platyphylla</td>
<td>13.0</td>
<td>14.1</td>
<td>1</td>
<td>1</td>
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<td>Syringa amurensis</td>
<td>8.8</td>
<td>8.7(0.2)</td>
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<td>Ulmus japonica</td>
<td>25.3(16.6)</td>
<td>26.6(18.4)</td>
<td>15</td>
<td>21</td>
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<tr>
<td>Phelelodonemorounse</td>
<td>18.4(6.6)</td>
<td>29.7(7.8)</td>
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<td>7</td>
</tr>
<tr>
<td>Quercus mongolica</td>
<td>38.1(14.5)</td>
<td>48.9(16.7)</td>
<td>18</td>
<td>17</td>
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<tr>
<td>Acer spp.</td>
<td>13.6(3.8)</td>
<td>13.1(4.4)</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>Acer mono</td>
<td>20.4(9.9)</td>
<td>21.0(10.4)</td>
<td>105</td>
<td>88</td>
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<tr>
<td>Maiorica amurensis</td>
<td>10.3</td>
<td>14.4(4.0)</td>
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<td>23</td>
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<tr>
<td>Populus davidiana</td>
<td>15</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>28.2(15.0)</td>
<td>28.4(17.6)</td>
<td>443</td>
<td>535</td>
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<td>Plots 2 and 4</td>
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<tr>
<td>Larix olgensis</td>
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<td>61.7(6.1)</td>
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<td>4</td>
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<tr>
<td>Sorbus pohusahansensis</td>
<td>12.8(4.2)</td>
<td>14.7(3.9)</td>
<td>16</td>
<td>46</td>
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<tr>
<td>Acer ukurudense</td>
<td>11.4(2.7)</td>
<td>12.2(4.0)</td>
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<tr>
<td>Total</td>
<td>19.9(12.8)</td>
<td>21.3(12.6)</td>
<td>953</td>
<td>745</td>
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<tr>
<td>TBCL</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Betula ermanii</td>
<td>11.9(4.2)</td>
<td>15.1(5.1)</td>
<td>1833</td>
<td>1750</td>
</tr>
</tbody>
</table>

* Converted from 0.06 ha.

### Table 4

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<tr>
<th>TBC</th>
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</table>

DT: Dominant tree species in the plot; PK: Pinus koraiensis; FM: Fraxinus mandshurica; TA: Tilia amurensis; PJ: Picea jezoensis var. komarovi; AN: Abies nephrolepis; BE: Betula ermanii.

### 3.6. Stand biomass carbon sequestration

Despite the decreasing trend for radial growth in Korean pine, spruce, and fir, annual biomass carbon sequestration in living trees (ATBCS) of whole stands all increased from 1981–2010. Increases of 59.87 t, 58.45 t, and 33.80 t occurred in plots 1, 3, and 4, respectively. Average annual sequestration was 2.00 t in plot 1, 1.95 t in plot 3, and 1.13 t in plot 4 (Table 4). The following levels of carbon sequestration occurred in individual species: Korean pine – 17.52 t; Manchurian ash – 16.52 t; Amur linden – 13.84 t; spruce – 42.13 t; and fir – 13.67 t (Table 4). The patterns of annual carbon sequestration for plots 1 and 3 were highly correlated (r = 0.96, p < 0.01). The correlation coefficient of annual carbon sequestration between plots 3 and 4 is 0.28 (p = 0.13), and between plots 1 and 4 is 0.023 (p = 0.96) (Fig. 6). This suggests that there exists a different pattern of carbon sequestration in birch forests from that in the other forest types.

According to ATBCS and the net increase of biomass carbon (ATBC) for the three plots, the losses of the biomass carbon storage (ATBCL) are 6.12 t in plot 1, 75.09 t in plot 3, and –2.90 t in plot 4. With respect to the dominant tree species in the plots, these losses in plot 1 were: Korean pine – 6.39 t; Manchurian ash – 4.86 t; Amur linden – 5.14 t; and in plot 2 were: spruce – 62.10 t; and fir – 12.98 t (Table 4).

### 3.7. Effects of climate warming on stand biomass carbon sequestration

As evident in Fig. 5, climate warming and corresponding drought has a significant impact on tree growth, with concurrent effects on carbon sequestration. Under such conditions...
climate-induced biomass carbon storage of dominant tree species (ΔTCGL) decreased by 0.96 t and 7.30 t in plots 1 and 3, respectively (Table 4). Plot 4 displayed a slight increase in carbon storage of 0.18 t from 1981 to 2010. Comparing this to the condition under which climate warming has no effect on tree growth, in plot1 climate-induced carbon sequestration decreased by 4.42 t (20.1%) in Korean pine and 0.68 t (4.9%) in Amur, while for ash it increased by 4.14 t (33.4%) [Fig. 7]. In plot 3, climatic-induced carbon sequestration decreased by 6.93 t (14.1%) in spruce and 0.37 t (2.6%) in fir. In plot 4, climate-induced carbon sequestration in birch increased by 0.18 t (0.45%) [Table 4, Fig. 7].

4. Discussion

4.1. Forest biomass carbon storage

Our estimated value for biomass carbon stock of living trees in the KFB was slightly less than that of Li et al. (1981), but slightly larger than estimates of Zhu et al. (2010) and Zhou et al. (2011). With respect to SFF and EBF, our results were less than levels reported by Li et al. (1981), Zhu et al. (2010) and Zhou et al. (2011). For the SFF in particular, the carbon storage estimate in this study was 65% lower than that reported by Zhu et al. (2010). Differences may be due to the sample plots or to estimation methods. For instance, the mean DBH of the birch forest in the sample plots selected in the study by Li et al. (1981) was 20 cm, while the permanent plot in the EBF utilized in this study displayed a mean DBH of only 11.9 cm in 1981. Additionally, the parameters for estimation equations are different from those in this study. Spline function fitting method was applied in Li et al. (1981), while in this study the power function fitting method was utilized.

Despite differences in the estimated value of carbon stock in this study from that of Zhou et al. (2011), the carbon stock in the two studies displayed a similar trend over the three-decade study period – biomass carbon stock for KFB and EBF increased, while that for SFF declined. However, when compared to the forest biomass carbon storage in 1981 calculated by Li et al. (1981) with that in 2010 estimated by Zhu et al. (2010), the carbon storage in 2010 remained larger than that in 1981. This may suggest that not all of the SFF in the CMNR has experienced the same decrease in biomass carbon stock as that in the immediate area of the permanent and sample plots in this study.

4.2. Effects of climate warming on tree radial growth

Korean pine and spruce are water-loving tree species (Wei et al., 1995); thus climate warming and induced occurrence of drought may negatively affect the radial growth of these species. Previous studies have reported a negative correlation of temperature with radial growth of spruce growing at its upper altitudinal limit in the CMNR (Li et al., 2011), as well as a positive correlation with PDSI (Yu et al., 2011). Similar results were found in this study. Almost all monthly PDSI measures were positively correlated with radial growth of spruce and Korean pine (Fig. 5a and d), suggesting that radial growth of these species is vulnerable to water stress. More specifically, we found that Korean pine radial growth was negatively correlated with all monthly mean temperatures, while for spruce this occurred only with respect to May (t) mean temperature. These results indicate that Korean pine growing at low elevations in the CMNR suffered greater stress from the rise in temperature, while spruce in SFF suffered more from water imbalance.

In contrast, all measures of monthly temperature were positively correlated with Manchurian ash growth (Fig. 5b), which is consistent with an earlier study by Zhang et al. (2007), and suggests that growth of ash in KFB will benefit from climate warming. Comparing Amur linden and Erman's birch, measures of growth displayed similar correlations with climate variables (Fig. 5c and f). Three monthly temperatures – October (t – 1), February (t) and August (t) – negatively influenced radial growth of Amur linden, while only one [October (t – 1)] did so for Erman's birch. This suggests that Amur linden in KFB suffered somewhat more stress from climate warming than did Erman's birch in EBF. Previous research at the tree line in the CMNR has found that radial growth of Erman's birch was positively correlated with temperature and precipitation (Yu et al., 2007). However, this was not found in this study. The sample plots of birch in our study were located at the middle distribution of EBF (1, 920 m asl), so the effects of climate variables on growth may have been diminished from those operating at the tree line. The correlation coefficients of monthly temperature with the growth of fir were relatively smaller than temperature correlations with other tree species. This may be because the height of fir is less than that of spruce in SFF, given that fir generally grows under a spruce canopy, perhaps sheltering it somewhat from the more severe effects of variations in climate.

Although variations in all ring width indices in STD chronologies did not exactly match those with the variation of temperature in this region in the period of 1981–2010 (Fig. 3 and 4), significant correlations of annual mean minimum temperature [from October (t – 1) to September (t)] we were found with radial growth of Korean pine (r = –0.51, p < 0.001), Manchurian ash (r = 0.44, p < 0.01), and spruce (r = 0.46, p < 0.01). The three species were those whose radial growths have been most affected by climate in CMNR (Table 4). The results were in agreement with the previous studies in the region (Zhang et al., 2007; Yu et al., 2011; Li et al., 2011). In
this sense, employing the slopes of the fitting line for the raw tree ring widths as an indication of climate effects on tree growth is reasonable.

4.3. Amount and influencing factors of stand carbon sequestration for living trees

In line with the definition of an old-growth forest, the net increase of stand biomass carbon in a permanent plot (ΔTBC) should be equal or close to zero, and the biomass carbon sequestration for living trees (ΔTBCs) should be equal to the loss of stand biomass carbon (ΔTBCL) (Helama et al., 2011). Although estimates of species-specific net carbon sequestration obtained from tree ring analysis in the sample plots could not exactly match those derived from permanent plot measurements, the large ΔTBC may suggest that the old-growth forests in the CMNR has not as yet reached a state of equilibrium between the gain from tree growth and recruitment and the loss due to the death of trees or parts thereof.

4.3.1. Korean pine and broad-leaved mixed forest (KBF)

Tree radial growth provided an insight into levels of carbon sequestration in different forest types at varying altitudes. Climate warming was significantly and negatively correlated with Korean pine growth (Fig. 5a), but positively correlated with radial growth of Manchurian ash (Fig. 5a). However, the number of trees for each of these species declined from 1981 to 2010, while the number of Amur linden, as well as that for plot 1 as a whole, greatly increased. Further analysis of DBH distribution of Korean pine and ash over the observation period showed that the number of Korean pine with DBH > 40 cm increased by 16 and that of Manchurian ash with DBH > 60 cm increased by 12; while the number of Amur linden increased in all DBH classes (Dai et al., 2011). The carbon storage per tree in plot 1 also increased from 1981 to 2010 (Table 3). Given the slow growth in an old-growth forest in a situation approaching a balance between the capture and release of carbon, the climate-induced sharp decrease in growth would seem likely to increase the mortality of old trees. However, in plot 1 the mortality rate of living trees was far lower (6.12 t ha⁻¹) than the net biomass carbon sequestration (59.87 t ha⁻¹), and the number of old trees increased in the period of 1981–2010. These seemingly contrary results in the KBF may indicate that this forest was still maturing and did not reach a state of balance between carbon capture and release in the period of 1981–2010.

Previous studies have reported that the maximum and average life spans of Korean pine are 550 and 480 years, respectively; while those for Manchurian ash and Amur linden are 300 and 270 years, and 370 and 330 years, respectively (Miles et al., 1983). Although some core samples could not reach the center of Korean pine, the maximum age of 157 years in this study is much lower than the average life span for this species. With respect to Manchurian ash and Amur linden, for which cores are easily obtainable, the maximum age for both was only about 240 years. Therefore, despite a decrease in growth of Korean pine under climate warming (0.96 t ha⁻¹), because the mean mortality in this permanent plot was lower than levels typical of a fully mature or over-mature forest, the annual level of net carbon sequestered increased in the focal period. Compared to carbon capture storage under the condition of no climate warming, climate warming has led to a decrease of carbon capture of Korean pine by 20.1%, while contributing to an increase of that by ash of 33.4% and having only a small effect on carbon capture by Amur linden (Fig. 7). As the forest continues toward full maturity, the mortality rate of older Korean pine will increase, in the process reducing the proportion of Korean pine as a component of KBF, which is in agreement with results from earlier models (e.g., Yan et al., 2000; Shao et al., 2003).

4.3.2. Spruce-fir forest (SFF)

In the spruce-fir forest, high mortality of older trees was the cause of biomass stock decrease from 1981 to 2010. The stand density decreased by 209 individuals over the three-decade study period, with numbers of spruce and fir decreasing by 88 and 118, respectively. Large fir with DBH > 20 cm increased by 17; while spruce with DBH greater than 20 cm and 40 cm decreased by 33 and 14 trees, respectively. On an overall basis, carbon stock of fir has increased in SFF, while that of spruce has decreased, suggesting a high mortality rate for old/large spruce.

The age structure in SFF is such that the maximum measured age of spruce reached as high as 200 years. Considering that most of the old/large trees are heart-rotten, the maximum age of spruce may actually have attained 250 years. (The mean missing length in DBH was about 10 cm, which is equivalent to 50 years growth according to the mean raw ring width of 1.01 mm.) Taking this into consideration, the SFF is over-mature. If the high mortality of spruce is size- or age-related, the decrease in growth of old/large trees should be more apparent than that of young trees. However, although annual radial growth in older trees (DBH > 50 cm; mean 0.87 mm since 1920) was less than that in younger trees (DBH < 30 cm; mean 1.24 mm since 1920), the trend in variation of radial growth in younger and older trees was significantly correlated (r = 0.80, p < 0.001) (Fig. 8). This may indicate that the high mortality in spruce was neither size- nor age-related.

Ecologists and foresters have long noted that as the growth rate of trees declines, the probability of mortality increases (Monserrud, 1976), and the individual tree is at risk when the rate drops below 10% of the “optimal growth rate” for the species (Hawkes, 2000; Wyckoff and Clark, 2002). However, recent climate-induced radial growth of spruce declined only slightly. The average ring width for the last 5 years of the observation period (1981–2010) was 87.9% of that of the first 5 years in this period, which is much higher than the threshold of tree mortality. These results suggest that the high mortality for spruce was not climate-induced. Considering the frequency of strong winds at higher elevations on Changbai Mountain (Dai et al., 2011), the decrease in the number of spruce may possibly have been influenced most strongly by wind. This could also be demonstrated by the large number of fallen trees (as opposed to standing dead trees) in the SFF. Compared with spruce in SFF, the height and DBH of canopy fir is lower than that of canopy spruce; therefore, its growth suffered from only small effects of wind and climate warming, and both the net increase of biomass carbon and the climate-induced variation of biomass carbon were close to zero (0.69 and 0.37 respectively). Overall, the decrease in biomass carbon stock possibly attributable to wind was 75.9 t, about
3.3. Erman's birch forest (EBF)

Previous studies have shown that the composition and distribution of vegetation in the CMNR are closely linked to the history of volcanic eruptions (Machida et al., 1987). The last eruptions occurred in 1702 (Machida et al., 1987). Although studies have pointed out that these eruptions were rather small in scale (Liu and Wang, 1992), it is likely they most strongly affected the forest near the volcanic center. Thus the EBF growing at higher elevations in that area would have been completely or at least partly destroyed. This could explain why the maximum age of birch in plot 4 was only 140 years in 2010 (Fig. 4) and the mean stand DBH only reached 15.1 cm (Table 3). Furthermore, the fact that there was a net gain of biomass carbon in EBF indicates that the carbon sequestration from living trees was greater than the stand net increase biomass carbon storage in the period of 1981–2010. These results suggest that the EBF is continuing to mature.

Most research has found that trees growing at high elevations display increased annual radial growth under climate warming, especially the increase of minimum temperature (Yu et al., 2007, 2011). This study also found that the substantial increase in temperature has led to increased radial growth of birch at elevations above 1800 m (Fig. 4f). However, the climate-induced stand carbon sequestration had a small increase in the period of 1981–2010 (0.18 t ha⁻¹), suggesting that in this case climate warming had no obvious effect on birch radial growth.

5. Conclusion

In 2010 the biomass carbon density of living trees in the Korean pine and broadleaf mixed forest (KBF) on Changbai Mountain, as measured by permanent and sample plots and data derived therefrom for the period of 1981–2010, was 201.22 t ha⁻¹, while for spruce-fir (SFF) and Erman’s birch forest (EBF) it was 106.46 t ha⁻¹ and 89.49 t ha⁻¹, respectively. During the past 30 years net biomass carbon density has increased in the KBF and EBF, with annual net increases of 1.79 t ha⁻¹ and 1.22 t ha⁻¹, respectively; while net carbon density has decreased in the SFF, with an annual net decrease of 0.55 t ha⁻¹. The increased net carbon density in KBF and EBF was primarily age- or size-related, since these stands are still maturing. On the other hand, the decrease in net carbon density in the SFF may be caused by a climate-induced decline in radial growth of dominant trees and increased mortality related to frequent strong winds. Climate warming has reduced carbon sequestration of Korean pine by 4.42 t ha⁻¹, that of Amur linden by 0.8 t ha⁻¹, that of Erman’s birch by 0.18 t ha⁻¹. As a result, stand carbon sequestration has decreased in KBF by 0.96 t ha⁻¹ and in SFF by 7.3 t ha⁻¹, but in EBF that has increased by 0.18 t ha⁻¹. At the same time, tree mortality in SFF, possibly due to the frequency of strong winds, has led to a decrease in stand carbon stock by 75.09 t ha⁻¹, about 10.3 times that attributed to climate warming. This study also suggests that the dominance of Korean pine in KBF will decrease and that of Manchurian ash will increase under climate warming, which is in agreement with the results from previous forest models.

Acknowledgments

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References


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