

Modelling the influence of harvesting on Chinese boreal forest carbon dynamics

Hong Jiang^{a,b,*}, Michael J. Apps^{a,b,c}, Changhui Peng^{c,d,1},
Yanli Zhang^{a,2}, Jinxun Liu^{c,3}

^aDepartment of Renewable Resource, University of Alberta, Edmonton, Alta., Canada AB T6G 2H1

^bNatural Resources Canada, Canadian Forest Service, 5320-122 Street, Edmonton, Alta., Canada AB T6H 3S5

^cFaculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, Ont., Canada ON P7B 5E1

^dMinistry of Natural Resources, Ontario Forest Research Institute, 1235 Queen Street East, Sault Ste. Marie, Ont., Canada ON P6A 2E5

Abstract

Chinese boreal forests, geographically distributed in the Daxinganling Mountains of northeastern China, are the most southern part of the global boreal forest biome. The dominant species is larch (*Larix gmelinii*) with other major species including birch (*Betula platyphylla*), pine (*Pinus sylvestris* var. *mongolica*) and oak (*Quercus mongolica*). In this study, the terrestrial ecosystem process model CENTURY 4.0 was used to investigate the influence of different harvest disturbance regimes on the carbon stocks and fluxes of Chinese boreal forest ecosystem relative to a natural disturbance regime. Managed disturbance regime scenarios examined include harvesting intensity (no biomass removal (NBR), conventional harvesting (CH) and whole tree harvesting (WTH)) and rotation length (from 30 to 400 years). Field data were assembled from three forest regions (Xinlin, Tahe and Mohe), representing the northern, middle and southern parts of the Chinese boreal forest, respectively. The results presented in this study indicate that biomass, litter and soil carbon stocks (averaged over a rotation period) can be elevated significantly by suppression of all disturbances (NBR scenario) but are lowest under the most intense harvest scenarios (WTH). Harvest rotation length had a significant influence on carbon stocks (biomass, litter and soil carbon); the lowest simulated carbon stocks were found with the shortest rotations, and relatively higher stocks under longer rotations. Net primary production (NPP) decreased with increasing harvest intensity or decreasing rotation length. Net ecosystem production (NEP) decreased with decreasing harvest intensity or decreasing rotation length. NPP and NEP reach maximum values at rotation lengths of about 200 and 100 years, respectively. Observations and simulated data for ecosystem carbon stocks (biomass, litter and soil carbon) and carbon fluxes (NPP and NEP) in the southern region were slightly higher than those in the mid- and northern regions. The high productivity and biomass of the Chinese boreal forests relative to those of Canada, USA and Russia, are likely due to their southerly location: warm temperature and adequate precipitation create good conditions for forest development and growth. Nevertheless, the long history of forest use by human has resulted in much of the boreal forest in China landscape being in less than a primary state. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Boreal forest; China; Harvesting disturbance; Biomass; Litter; Soil carbon; NPP; NEP; Ecosystem modelling; CENTURY model

* Corresponding author. Present address: Conservation Biology Institute, 260 SW Madison Avenue, Suite 106, Corvallis, OR 97333, USA. Tel.: +1-541-757-0687; fax: +1-541-752-0518.

E-mail address: hongjiang@consbio.org (H. Jiang).

¹ Present address: Institute of Atmospheric Sciences, College of Earth Systems, South Dakota School of Mines and Technology, Rapid City, SD 57701-3995, USA.

² Present address: Department of Entomology, Oregon State University, Corvallis, OR 97333, USA.

³ Present address: Department of Geography, University of Toronto, Toronto, Ont., Canada.

1. Introduction

The boreal forest, covering more than $12 \times 10^6 \text{ km}^2$ (Baumgartner, 1979), is one of the world's largest forest biomes and contains more than 700 Pg of carbon in forest vegetation, soils and forested wetlands (Bolin and Sukumar, 2000; Dixon et al., 1994; Apps et al., 1993). Chinese boreal forests comprise the most southern components of the global boreal biome (Shugart et al., 1992). In China, the boreal forest ecosystems are important for forest timber production (Cheng, 1990). Despite this importance as a national forest resource, however, human activities over a long period of use have produced vast areas of degraded forests in the boreal regions of China (Zhou, 1985; Cheng, 1990).

Intensive timber harvesting has been identified as a potentially major component of disturbance and degradation of forests in general (Kimmins, 1977; Jurgensen et al., 1997). Intensive timber harvesting, consisting of short rotations and high levels of biomass utilization, has the potential to reduce forest site productivity through alteration of the dynamics of soil organic matter and nitrogen availability (Boyle et al., 1973; Keenan and Kimmins, 1993; Jurgensen et al., 1997). Harvesting is recognized as the primary disturbance factor in the boreal biome of China (Wu, 1995). Since the 1950s, the landscape pattern of boreal forests, both planned and unplanned, has been changing rapidly as a result of large-scale timber cutting, resulting in a conversion of many old-age forests to young, secondary forests (Tian et al., 1995). Net primary productivity (NPP) and biomass in the Chinese boreal forests have been estimated using measurement data, remote sensing and empirical vegetation-NPP models (Jiang et al., 1999; Liu, 1994). These studies, however, focused on the patterns of NPP and biomass stocks, and did not examine the influence of different harvest regimes on ecosystem carbon stocks and fluxes. Moreover, NPP is an inadequate indicator of the contribution of terrestrial ecosystems to the global carbon cycle because it only incorporates one component (vegetative uptake) of the net carbon exchange with the atmosphere (IGBP Terrestrial Carbon Working Group, 1998). Unfortunately, few studies have been reported that investigate carbon stock and net total carbon flux dynamics in boreal

China. Although there is a growing awareness of the need for such information to support the sustainable management of Chinese forests (Peng and Apps, 1997), the effect of different harvesting regimes on the carbon budgets of the boreal forests of China is still poorly understood.

Over the past decade, there has been rapid development of quantitative techniques for measuring and simulating fluxes and stocks components of the carbon cycle. In particular, the terrestrial ecosystem process model, CENTURY 4.0, has previously been used to simulate the carbon stock and fluxes of boreal forests in central Canada (Peng et al., 1998; Peng and Apps, 1999; Jiang et al., 2001). In the present paper, the CENTURY model was used: (1) to examine the dynamics of carbon stock and fluxes of Chinese boreal forests; (2) to examine the likely impacts of harvesting disturbance regime on these carbon stock and fluxes; and (3) to compare the estimates obtained for carbon stock and fluxes in Chinese boreal forests with other those from other boreal regions.

2. Methods

2.1. Study sites

Three study sites were selected in each of the boreal forest regions in China (Fig. 1). The Mohe forests represent the northern extent of China's boreal forest, Tahe is located in the mid-boreal region, and Xinlin lies in southern boreal region. The characteristics of the three boreal forest sites, listed in Table 1, reasonably represent the range of environment condition of China's boreal forest, given its relatively small geographical extent.

Dahurian larch (*Larix gmelinii*) covers more than 70% of the boreal forest ecosystems in northeast of China (Xu, 1998; Wang et al., 2001). *L. gmelinii*–*Ldum palustre*, *L. gmelinii*–grass and *L. gmelinii* *Rhododendron dahurica* are the three major tree species in the *L. gmelinii* dominated boreal forests of this region. Other overstorey tree species found in this region include Korean spruce (*Picea koriensis* Nakai), white birch (*Betula platyphylla* Suk.), Scots pine (*Pinus sylvestris* L. var. *mongolica* Litv.) and aspen (*Populus davidiana* Dole).

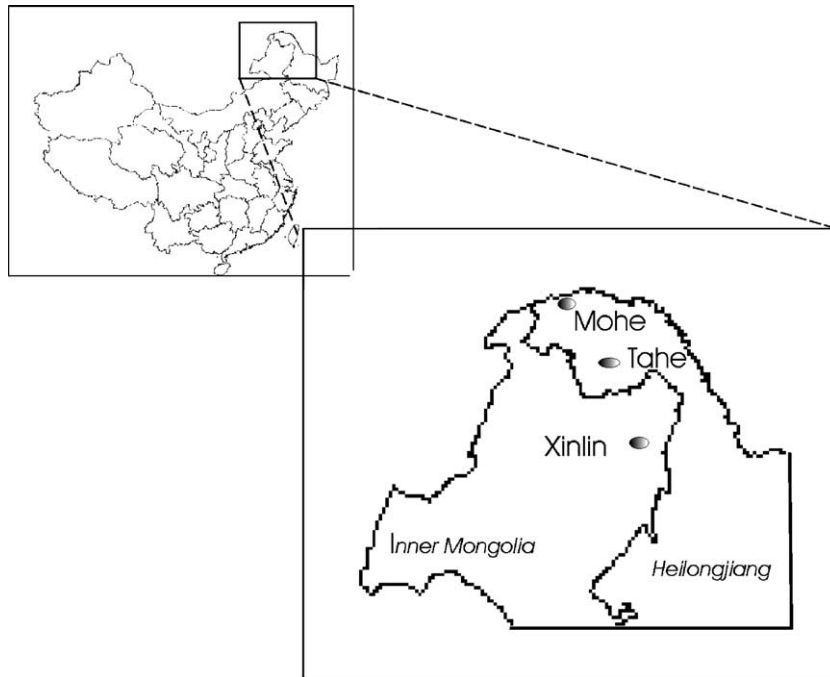


Fig. 1. The location of study sites in Chinese boreal forests.

2.2. Simulation model: CENTURY 4.0

CENTURY 4.0 is a process-based, terrestrial ecosystem model that simulates long-term (100–10,000 years) dynamics of carbon (C), nitrogen (N), phos-

phorus (P) and sulphur (S) in different plant-soil systems (Parton et al., 1987, 1993). It incorporates representations of key process relating to carbon assimilation, turnover and decomposition, using a set of internal modules. The forest production module

Table 1
Site parameters for boreal forest in Northeast China^a

	Mohe	Tahe	Xinlin
Latitude (°N)	53.28	52.19	51.42
Longitude (°E)	122.22	124.43	124.29
Altitude (m)	296	357	450
July, mean temperature (°C)	28.27	27.65	27.10
January, mean temperature (°C)	−34.36	−33.24	−32.70
Annual precipitation (mm)	500.92	558.41	523.11
Dominant species	<i>L. gmelinii</i>	<i>L. gmelinii</i>	<i>L. gmelinii</i>
Soil type	Brown forest soil ^b		
Soil texture (%)			
Clay	32	30	38
Silt	30	30	40
Sand	38	40	22

^a In Chinese boreal forests, the range of percentage of *L. gmelinii* among other species is 80–100%, the site class is from class I to III, the tree volume is from 50 to 400 m³ ha^{−1}, the mean annual increment is from 0.59 to 4.00 m³ ha^{−1} per year (Chinese Academy of Forest Survey, 1981; Zhang, 1986; Wu, 1995).

^b Zhang (1986).

partitions tree biomass into foliage, fine and coarse roots, fine branches, and large wood compartments. Carbon (C) and nitrogen (N) are allocated to the different plant parts using a fixed allocation scheme. The soil module simulates eight organic matter pools: four of which represent surface and root litter and the remaining four represent soil organic matter (SOM). The SOM pools include: two “active” fractions having rapid turnover times (1–5 years) that represents microbial biomass and metabolites divided into a surface and a soil pool; a “slow” fraction with an intermediate turnover time (20–40 years) that represents stabilized decomposition products; and a “passive” fraction with a slow turnover time (200–15,00 years) that represents highly stabilized organic matter. CENTURY 4.0 also includes a water balance submodel which calculates monthly evaporation, transpiration, water content of soil layers, snow water content, and saturated flow of water between soil layers. The model also permits simulation of many management measures, including grazing, cropping, fertilization, irrigation, and control of wildfire. For detailed discussion of the model structure and logic of CENTURY 4.0, the reader is referred to the original manuscripts (Parton et al., 1987, 1993), the user manual (Metherell et al., 1993), and applications such as Peng et al. (1998) and Peng and Apps (1999).

For the present study, site-specific parameters and initial conditions, such as soil texture (clay, silt and sand content), bulk density, soil pH, soil C content for the 0–20 cm layer, and drainage characteristics of soil were obtained from published reference data (Zhang, 1986). Mean maximum and minimum monthly temperature and monthly precipitation data were calculated by CENTURY 4.0 using meteorological data, including temperature and precipitation for the period of 1951–1980 compiled from the meteorological field stations in this region (Beijing Meteorological Center, 1984). The site parameters for climate, soil type, soil texture and vegetation data used in the simulations are listed in Table 1. Some site-specific parameters for boreal forest ecosystems were unavailable, requiring modification of default values for temperate coniferous forests (the parameterization procedure for boreal forests is discussed in greater detail in Peng et al., 1998). These parameters include maximum gross and net forest production, optimum and maximum temperature for production and a scaling factor for

potential evapotranspiration (PET). CENTURY 4.0 also requires estimations of N fluxes to the ecosystem. Atmospheric N fixation and deposition variables that were not available from published literature were estimated using a simple linear function of precipitation based on observed data (Metherell et al., 1993).

2.3. Algorithms for productivity indicators and carbon fluxes

Forest productivity as well as carbon fluxes to and from the atmosphere is usually described by two key indicators: NPP and net ecosystem productivity (NEP) defined by Eqs. (1) and (2), respectively.

$$\text{NPP} = \text{GPP} - R_a \quad (1)$$

$$\text{NEP} = \text{NPP} - R_h \quad (2)$$

where GPP is the gross primary production, R_a the autotrophic respiration, and R_h the heterotrophic respiration. Annual changes in GPP are calculated as a function of time using a biome-specific maximum gross productivity parameter that is modified by simulated changes in soil moisture, temperature and live leaf area index. Changes in autotrophic respiration R_a are calculated as a function of simulated changes in wood N content and air temperature using a relationship developed by Ryan (1991). Heterotrophic respiration (R_h) is estimated within CENTURY as the annual CO_2 respiration from decomposition, which is the sum of all respiration fluxes of dead organic matter—functionally equivalent to the net decomposition releases of the losses from the litter and soil pools.

In this paper, the annual changes in these productivity indicators and carbon stock variables are presented both as time series data and as averaged values (where the average is taken over a complete rotation).

2.4. Model validation

Two methods have been used to validate the CENTURY 4.0 model (Bolker et al., 1998; Parton et al., 1993; Peng et al., 1998). The first method used a linear regression of the observed data against simulation model results; the second checked the model estimates against predictions from other well-established models such as empirical regression models. Previous works on the validation and application of the CENTURY 4.0 model for the boreal forests in central Canada found that

simulated average values for above ground biomass, net N mineralization, and soil carbon were consistent with observed data or regional scale empirical regression modelling data (Peng et al., 1998; Jiang et al., 2001). In this study, no attempt was made to further validate the model, but the simulated average values for biomass C and NPP have been compared previously with observed data ranges for Chinese boreal forests (Jiang et al., 1999; Chinese Academy of Forestry Sciences, 1996).

2.5. Simulation strategy and harvesting scenarios

For each site, starting from arbitrary initial conditions, CENTURY 4.0 simulations were run for sufficient time (2000 years) to establish steady state (no evident residual trends) under natural conditions using repeated mean monthly temperature and CENTURY's stochastic precipitation generator. Natural fire return intervals in boreal forests range from 28 to 500 years, with a modal value of around 100 years (Zheng et al., 1986; Payette, 1992; Larsen, 1997). Hence for the run-up period (referred to as the initialization phase), a random fire disturbance regime (with an average interval of 100 years over the 2000-year run-up) was used to represent the natural disturbance regime.

Four additional random sequences (with the same average interval) were used for the initialization simulations to provide an estimate of the variability in carbon indicators during this natural regime.

Following the initialization phase, each of the scenarios discussed below were then run for a further 5000 years (referred to as an equilibration phase), and the analyses performed on simulation results of the last 400 years (analysis phase, simulation years 6600–7000). It was found that this long period (5000 years) of equilibration was required to ensure that artifacts associated with the initial conditions (end of the 2000-year run-up) did not influence the comparison of results in the analysis phase.

Following the approach of Bengtsson and Wistrom (1993), dynamic changes in carbon stocks and fluxes were simulated and compared under three harvesting intensities:

- No biomass removal (NBR): no disturbances (including harvesting) and no stem, branches, needles (leaves) or roots killed or removed from site other than through natural mortality and litterfall.

- Conventional harvesting (CH): 100% removal of stem from site but branches, needles (leaves), and roots left on site.
- Whole tree harvesting (WTH): 100% removal of stem from site, 90% removal of branches and needles (leaves), the remaining branches and needles (leaves) and all roots remain on site.

Although in reality, site treatments such as burning or scarification may have been undertaken following harvesting, for simplicity these have been ignored in the simulations. All residual dead organic matter associated with harvest slash was assumed to be additional litter input to the decomposing forest floor.

For these comparisons, a uniform rotation length of 100 years was used in order to compare the effect of harvesting intensity on the carbon dynamics. The NBR simulations represent a situation in which all stand-replacing disturbances (such as harvest or wild-fire) are fully suppressed: the only mortality occurs through random death of individual trees within the CENTURY model.

The model parameters that specify the fractions of live leaves, live fine branches, live large wood, and fine and coarse roots removed from pools under the different harvesting scenarios are shown in Table 2.

Table 2

Parameters for three harvesting intensities used in CENTURY 4.0 simulations

Specific parameters	NBR	CH	WTH
Percentage of tree biomass removed from pools			
Live leaves	0	0	90
Live fine branches	0	0	90
Live large wood	0	100	100
Percentage of live root components that die			
Fine root	0	90	90
Coarse root	0	70	70
Percentage of carbon in killed material that is returned to the ecosystem			
Live leaves	100	100	10
Fine branches	100	100	10
Large wood	100	0	0
Percentage of nitrogen in killed material that is returned to the ecosystem			
Live leaves	100	100	10
Fine branches	100	100	10
Large wood	100	0	0

Table 2 also lists the fraction of nutrients returned to the soil in organic matter from each biomass component that is affected by the harvesting event (Metherell et al., 1993; Parton et al., 1993).

A second set of simulations was performed to study the effect of harvesting at different rotation lengths on carbon dynamics. These simulations, with a series of rotation-length scenarios (30, 50, 100, 200, and 400 years), were performed using the WTH harvesting intensity. Note that the NBR simulation described in the first set of scenarios is functionally equivalent to a rotation of infinite duration.

The results of each simulation, when plotted against simulation year, represent the changes in pool or productivity indicators over time for a typical site. For the purposes of comparing the effects of different harvest intensities and rotation period at the whole forest scale, it was assumed that the forest would be managed for a normal age-class distribution in each scenario. Thus for the 100-year rotation, 1% of the forest would be harvested each year, with subsequent harvests taking place at culmination of the rotation on each site. Under these conditions, the age-class distribution is rectangular in shape, with equal area in each age class up to the rotation age. With this age-class distribution, it can be shown that for each pool, or productivity indicator, the average over the forest is identical to the average of that pool or productivity indicator over a rotation provided there is no systematic change in environmental conditions.

3. Results

3.1. Equilibration and long-term dynamics of carbon stocks and fluxes

Fig. 2 shows the CENTURY simulations of ecosystem carbon pools (biomass plus litter plus soil), NPP and NEP during the initialization phase (years 1–2000), the equilibration phase (2000–6600) and the analysis phase (6600–7000). Similar time-sequence data was obtained with all scenarios.

During the initialization phase under a random fire regime (in all scenarios), the mean values of ecosystem carbon, NPP, and NEP (averaged over simulation years 726–2000) were 226 Mg C ha⁻¹, 4400 and 1390 kg C ha⁻¹ per year, respectively.

These mean values of ecosystem carbon varied between different random disturbance sequences by 2–11%. For a typical sequence (Fig. 2) representing a typical site, the peak-to-peak excursions occurred at the times of the disturbance events and averaged 231.2 Mg C ha⁻¹ (ecosystem carbon), 3817 kg C ha⁻¹ per year (NPP) and 950 kg C ha⁻¹ per year (NEP) during the initialization interval.

When disturbances were suppressed (NBR equilibration phase, Fig. 2A–C), the ecosystem carbon levels increased towards a significantly higher value of 460 Mg C ha⁻¹, a 104% increase while NPP and NEP values relaxed towards lower values of 3660 and 0 kg C ha⁻¹ per year, respectively. When WTH harvesting on a 100-year rotation replaced the random fire disturbance, the (average) ecosystem carbon, NPP and NEP all dropped slightly by 42, 32 and 26%, respectively (all averaged over a rotation during the last 400 years of the simulation) (Fig. 2D–F). Mean biomass and litter carbon pools relaxed most quickly (within 3–4 rotations) to their equilibrium values, while soil pools took much longer (>20 rotations). With shorter harvest rotations following the random fire initialization, the decreases in ecosystem carbon, NPP and NEP were more pronounced (75, 58 and 54%, respectively) and equilibration achieved more quickly in all pools. With longer rotations (e.g., 400 years), the declines in NPP and NEP were 15 and 57%, respectively, while ecosystem carbon pools increased by 45% (to 328 Mg C ha⁻¹) mainly due to significantly increased biomass stocks (246% relative to the 100-year rotation) (Figs. 3–8).

3.2. Carbon stocks and fluxes of Chinese boreal forests

Reported biomass carbon stocks in Chinese boreal forest stands are 114.3 ± 8.0 Mg C ha⁻¹ (mean value ± standard deviation) at Mohe, 120.5 ± 34.4 Mg C ha⁻¹ at Tahe and 123.8 ± 49.1 Mg C ha⁻¹ at Xinlin (Table 3). Estimates of NPP (*op cit*) are 3800 ± 700 kg C ha⁻¹ per year at Mohe, 3910 ± 725 kg C ha⁻¹ per year at Tahe, and 3980 ± 820 Kg C ha⁻¹ per year at Xinlin (Table 3). As expected the southern site (Xinlin) has a higher carbon stock and carbon flux than that at the northern site (Mohe). Simulation results at the forest scale (averaged over a rotation) from CENTURY 4.0 (Table 3) under the different harvesting scenarios are consistent with these observations, but the undisturbed

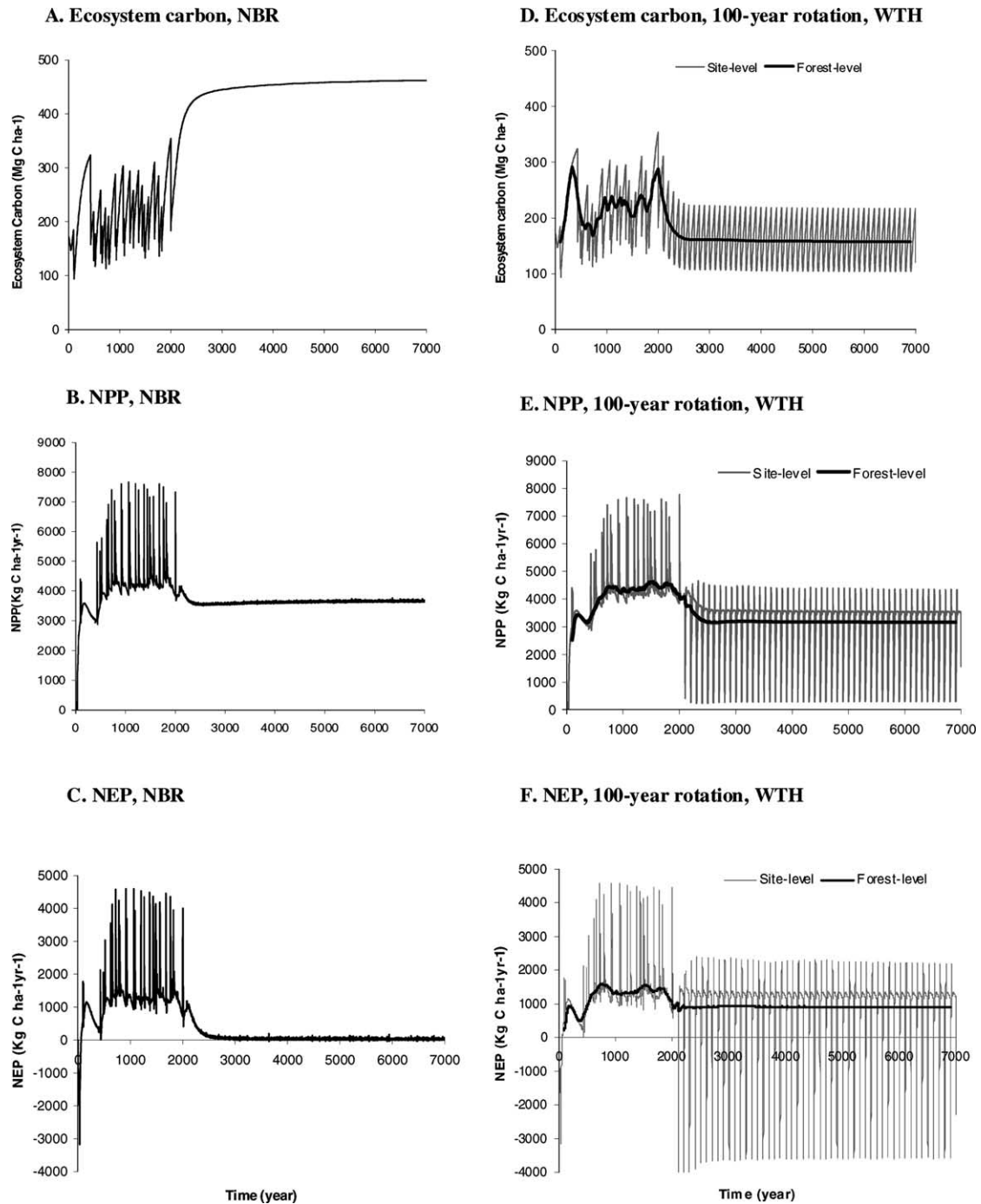


Fig. 2. Simulated changes in ecosystem carbon pool (panel A and D), NPP (B and E) and NEP (C and F) during initialization (years 1–2000) and equilibration sequence (years 2001–7000) at the mid-boreal Tahe site. The same initialization phase (random fire with a 100-year mean interval) was used for all scenarios. Panels (A)–(C) show equilibration under a no disturbance (NBR) scenario; panels (D)–(F) illustrate a harvesting scenario (WTH, 100-year rotation); the light line shows typical site-level dynamics, the darker line (averaged over a rotation; 200-year running average for the random initialization phase) shows the forest-scale dynamics.

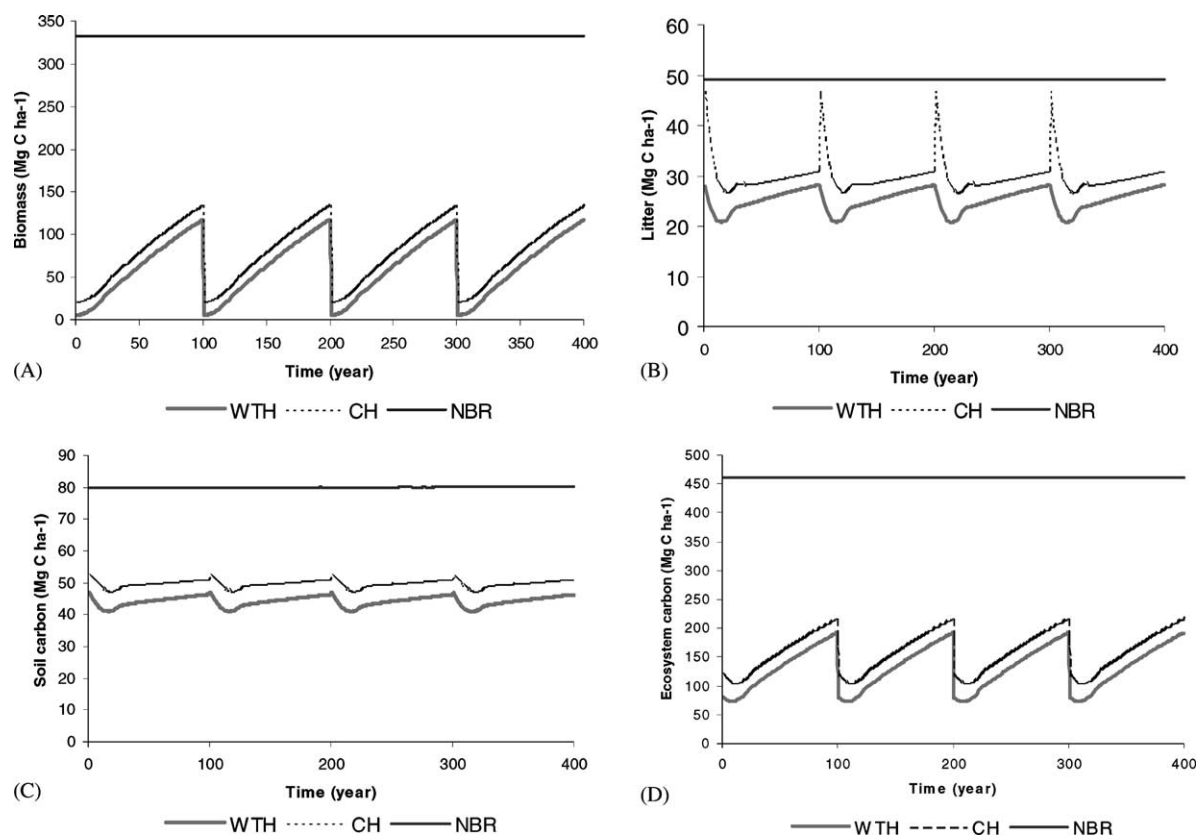


Fig. 3. The dynamics of carbon stocks (biomass, litter and soil carbon) under different harvesting intensity with 100-year rotation length in Tahe site. (A) Biomass; (B) litter; (C) soil carbon; (D) ecosystem carbon.

Table 3

Comparison of biomass and NPP simulated by CENTURY 4.0 with observed data^a

Site	Biomass (Mg C ha ⁻¹)					NPP (kg C ha ⁻¹ per year)				
	Observation ^a	Simulation ^b				Observation ^a	Simulation ^b			
		NBR	Natural	Harvest			NBR	Natural	Harvest	
				CH	WTH				CH	WTH
Mohe	114.3 ± 38.0	320	139 ± 8	75	18.1–144	3800 ± 700	3600	3780 ± 35	3086	1812–3763
Tahe	120.5 ± 34.4	330	143 ± 8	78	18.3–152	3910 ± 725	3660	3820 ± 40	3166	1836–3826
Xinlin	123.8 ± 49.1	335	149 ± 9	80	18.6–155	3980 ± 820	3690	3880 ± 50	3225	1850–3867

^a Data are from Jiang et al. (1999) and Chinese Academy of Forestry Sciences (1996). Altitudes of observation sites in the Mohe, Tahe and Xinlin forests range from 400 to 850, 510 to 1000 and 450 to 1100 m, respectively.

^b Simulation results are averaged over a rotation. The harvest simulations are CH (the rotation lengths is 100 years) and WTH (the ranges are for increasing rotation lengths from 30 to 200 years). The values in the column “Natural” are the mean ± standard deviation for years 726–2000 during the random fire initialization phase.

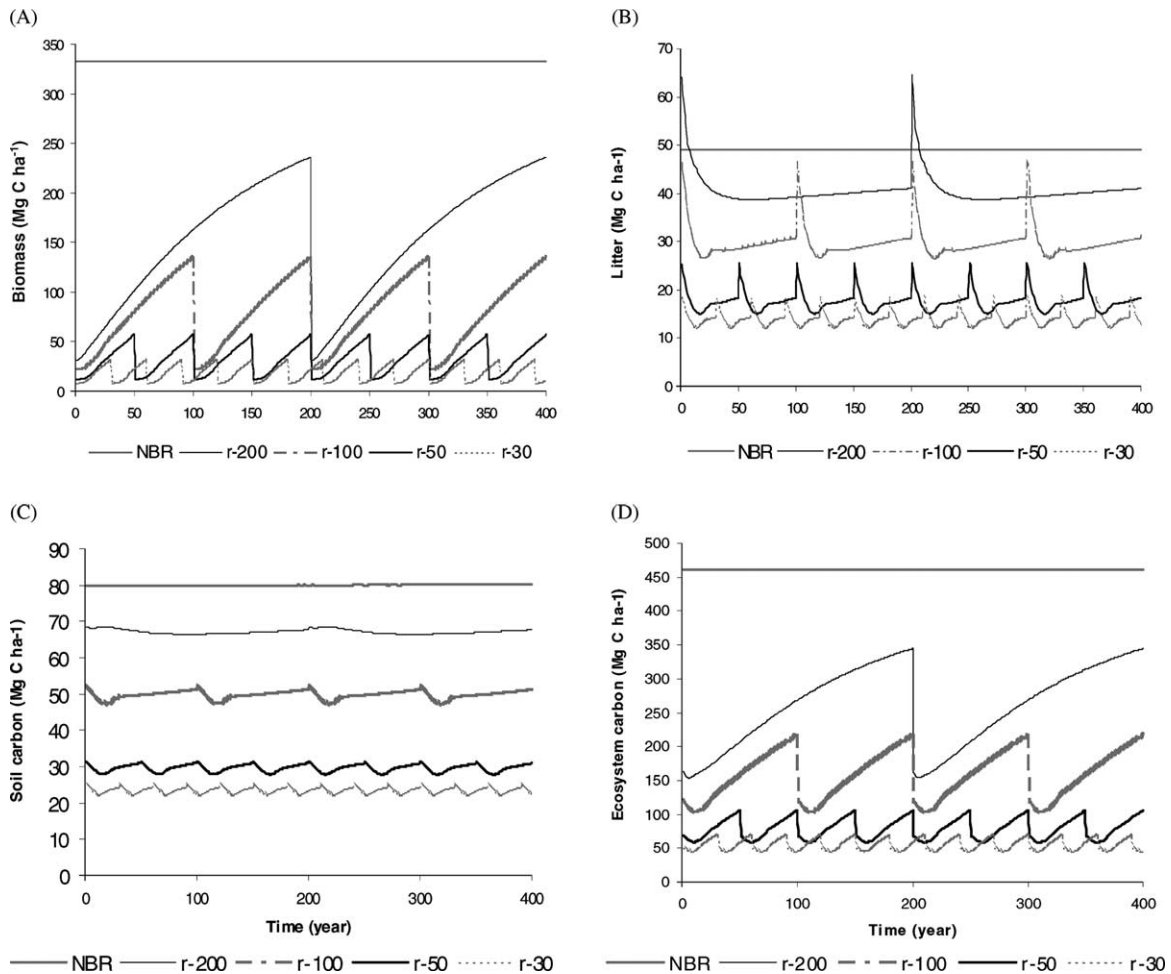


Fig. 4. The dynamics of carbon stocks (biomass, litter and soil carbon) under WTH at different rotation lengths at the Tahe site. (A) Biomass; (B) litter; (C) soil carbon; (D) ecosystem carbon.

values (NBR) are quite different. Observed biomass carbon values, e.g., are considerably lower than the NBR simulations, but comparable with the harvest scenario results.

3.3. Carbon stocks of Chinese boreal forests under different harvesting regimes

Simulated site-level changes over time in biomass, litter, soil carbon and ecosystem carbon pools under different harvest intensities and rotations are shown in Figs. 3 and 4 using the Tahe site as an example (similar dynamics are seen at the other sites). At a typical site, biomass declines abruptly at the time of harvesting, then

increases slowly with re-growth of the trees. Litter pools increase abruptly with slash inputs associated with harvesting, then rapidly decline with subsequent decomposition of this slash. The litter pools reach a minimum, typically 10–20 years after the harvest, and then rebuild as litter inputs again increase gradually with re-establishment of forest cover. Soil carbon decreases for some years after harvesting and then recovers with the re-accumulation of inputs from litter decomposition. The changes in these individual components add up to the changes in total ecosystem carbon pools shown in Fig. 2.

Similar responses to the different harvest regimes are seen at all three sites, although the magnitude of the

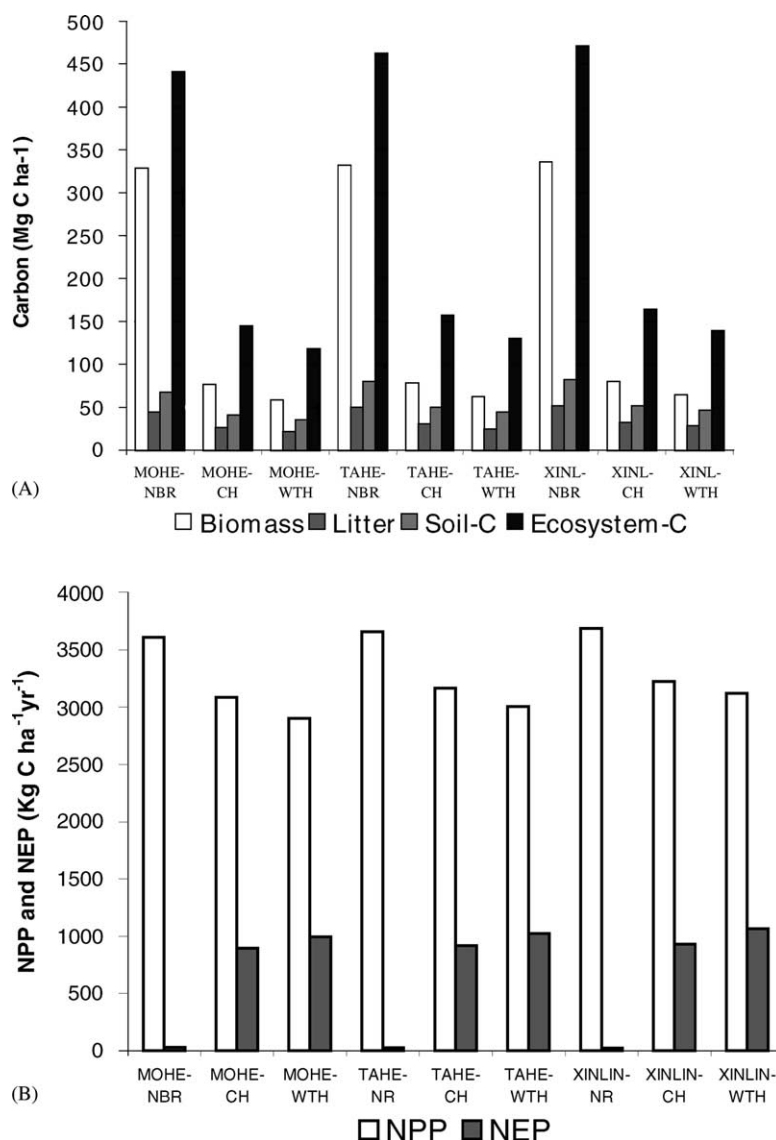


Fig. 5. Influence of harvest intensity on carbon stocks (biomass, litter and soil carbon) and fluxes (NPP and NEP) of Chinese boreal forests (rotation length 100 years). (A) Carbon stocks; (B) carbon fluxes. NBR: no biomass removal; CH: conventional harvesting; WTH: whole tree harvesting.

stocks and changes differ (Figs. 5A and 6A). Biomass, litter and soil carbon stocks (averaged over a rotation) are all highest under NBR and lowest under WTH, with CH for the same rotation length (100 years) lying between these two values (Fig. 5A). The total ecosystem carbon stock at equilibrium is $461.7 \text{ Mg C ha}^{-1}$ for NBR, markedly higher than for CH and WTH at the Tahe site (158 and 131 Mg C ha^{-1} , respectively). The variation in ecosystem carbon stocks over a

rotation at a typical site are significantly smaller for the WTH harvesting (131 Mg C ha^{-1}) than for CH (158 Mg C ha^{-1}), because the peak biomass stocks are lower. In contrast, the no-harvest scenario (NBR) at the same typical site shows only small variations (3 Mg C ha^{-1}) arising from inter-annual weather changes (based on 30-year normal climate). Similar but more complex variations were observed in simulated litter and soils (Fig. 3).

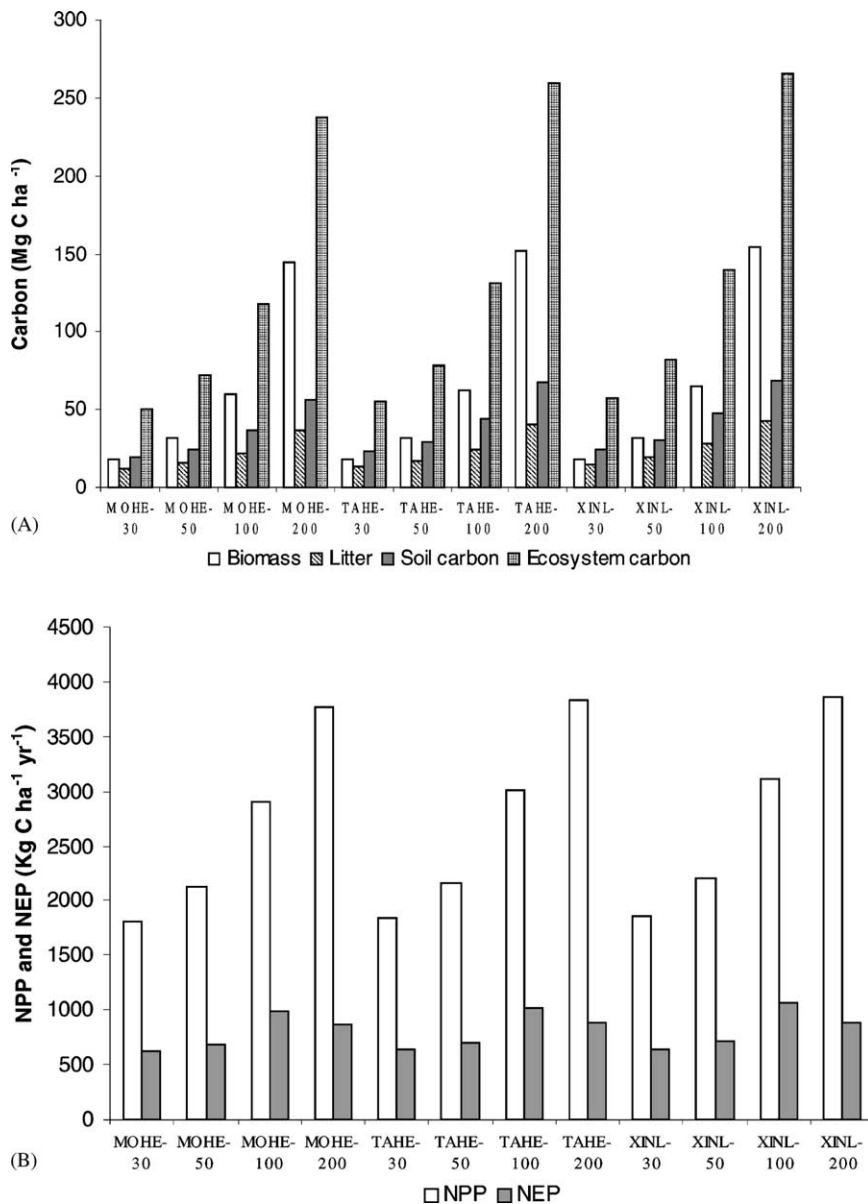


Fig. 6. Influence of harvest rotation length on carbon stocks (biomass, litter and soil carbon) and carbon fluxes (NPP and NEP) of Chinese boreal forests (harvesting intensity WTH). r-30, r-50, r-100, r-200 are harvest rotation lengths of 30, 50, 100 and 200 years, respectively.

Rotation length had a significant influence on carbon stocks. Lower simulated carbon stocks were found with shorter rotations, and relatively higher stocks under longer rotations. Using the Tahe forests as an example, the average biomass (forest scale, averaged over a rotation) under the 30-year rotation was only 12% of the 200-year rotation (Figs. 4A and 6A).

Large reductions in soil (35%) and litter stocks (34%) are also evident in Figs. 4B, C and 6A. The total ecosystem carbon stocks, averaged over a rotation, have simulated values of 56, 79, 131 and 260 Mg C ha⁻¹ for rotation lengths of 30, 50, 100 and 200 years, respectively (Fig. 4D). In the absence of any harvesting or other disturbance, the total simulated ecosystem

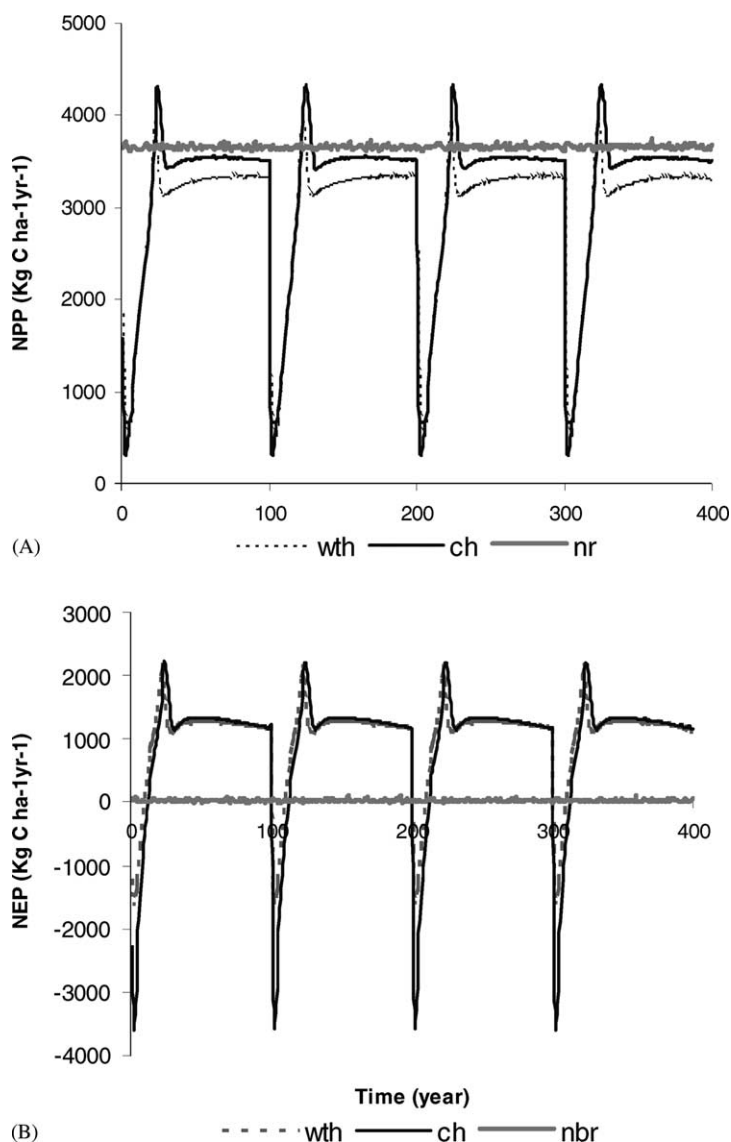


Fig. 7. Dynamics of carbon fluxes (NPP and NEP) under different harvesting intensities with 100-year rotation length in Tahe forests. (A) NPP; (B) NEP.

stock (Figs. 3D and 4D, NBR simulation) was 462 Mg C ha^{-1} .

At any specific site, the carbon stocks undergo large swings associated with each disturbance event (fire in the run-up phase and harvest in the various scenarios). The size of these variations depends on the history of disturbances for the site, and especially on the time since the last disturbance (Fig. 2). Thus the largest variations were found for intermediate rotation lengths,

with much smaller changes in the short rotations (where the stocks are smallest) and at the longer 200-year rotation. With very long rotations (e.g., in the absence of harvesting or other disturbances), the stock changes were much smaller. The magnitudes of site-level changes in the total ecosystem carbon are 25, 50, and 120 Mg C ha^{-1} for the 30, 50, and 100-year rotations, respectively. This variation drops to 90 Mg C ha^{-1} for the 200-year rotation, to 40 Mg C ha^{-1} for the 400-year

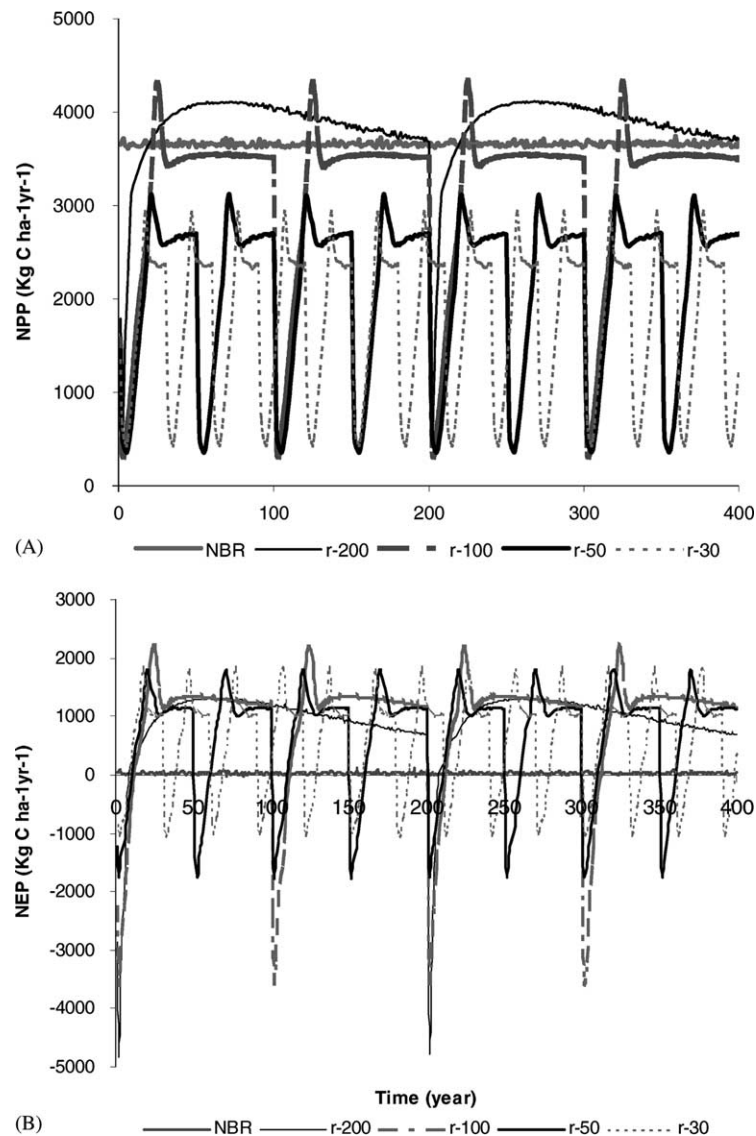


Fig. 8. Dynamics of carbon fluxes (NPP and NEP) under different harvest rotation lengths (WTH) in Tahe forests. (A) NPP; (B) NEP.

rotation and to near zero for the no-harvest scenario (in the NBR simulation a small variability of 3 Mg C ha⁻¹ arises from weather variability).

3.4. Changes in productivity between sites and under different harvesting regimes

Figs. 5B and 6B show the effect of harvesting intensity and rotation length on simulated ecosystem carbon fluxes in terms of NPP and NEP.

Averaged over a rotation, simulated NPP (Fig. 5A) had the highest (3613–3686 kg C ha⁻¹ per year), median (3086–3225 kg C ha⁻¹ per year) and lowest (2905–3121 kg C ha⁻¹ per year) values for NBR, CH and WTH, respectively. (The ranges of values shown are for the Mohe and Xinlin forests, respectively.) In the absence of harvesting (NBR), simulated NPP was 3613, 3657, and 3686 kg C ha⁻¹ per year for Mohe, Tahe and Xinlin forests, respectively. With harvesting (Fig. 6B), NPP (averaged over a rotation) was lowest under

30-year rotations (1814–1846 kg C ha⁻¹ per year) and highest under the 200-year rotation (3762–3827 kg C ha⁻¹ per year) with intermediate values (2131–2203 and 2905 to 3121 kg C ha⁻¹ per year) for the 50- and 100-year rotations.

NEP shows the same weak decreasing trend as NPP across the north–south gradient, but with a much stronger variation with harvesting regime than does NPP (Fig. 5A). For example, NPP with no harvesting (NBR) differs by only ~2% between the Mohe and Xinlin forests, while the variation in NEP is ~20% (similar observations can be made from inspection of Fig. 5B for the other sites and harvest regimes). The simulated NEP (averaged over a rotation) was the highest (994–1052 kg C ha⁻¹ per year), median (905–930 kg C ha⁻¹ per year) and lowest (22.9–29.5 kg C ha⁻¹ per year) values in the WTH, CH and NBR scenarios, respectively (Fig. 5B). (The ranges of values cited are for the Xinlin and Mohe forests, respectively.) Simulated NEP was lowest (630–643 kg C ha⁻¹ per year) with the 30-year rotation period, and highest (994–1052 kg C ha⁻¹ per year) with a 100-year rotation; intermediate values (691–713 and 871–894 kg C ha⁻¹ per year) were found for the 50- and 200-year rotations (Fig. 6B).

Figs. 7 and 8 show the variation of the simulated productivity indicators at a typical site over time. In response to harvesting, simulated NPP drops abruptly, then recovers over the next 20–40 years with an “overshoot” whose magnitude depends on the harvest intensity (Fig. 7A) and weakly on the rotation length (Fig. 8A), but is typically of the order of 10–20%. After the short-lived overshoot (lasting typically 15 years), NPP then exhibits a longer-term oscillation, tending towards the no disturbance result (NBR), if it were not interrupted by a subsequent harvest.

Site-scale NEP dynamics show similar temporal patterns to NPP following harvest (Figs. 7B and 8B). Unlike NPP, however, simulated NEP goes sharply negative (–1000 to –5000 Kg C ha⁻¹ per year) at the time of harvest, and remains negative for 5–10 years (Figs. 7B and 8B, WTH). These negative values are larger than the positive values (1500–2000 kg C ha⁻¹ per year) observed during the overshoot recovery 5–10 years after disturbance. After this positive overshoot, NEP relaxes towards the no-disturbance value of zero (as can be seen most clearly with the 200-year rotation in Fig. 8B).

Table 4

Comparison of estimates of biomass and NPP of boreal forests

Country	Biomass (Mg C ha ⁻¹)	NPP (kg C ha ⁻¹ per year)
Alaska, USA	42.5–180.8 ^a	250–1660 ^a
Canada	26.0–213.8 ^{a,b,c}	1170–3800 ^b
Russia, European	22.9–166.1 ^a	1270–3140 ^a
Russia, Siberia	55.6–237.4 ^{a,d}	310–6750 ^{a,d}
China	55.6–318 ^{a,e,f}	1810–7800 ^{a,e,f}
This study	18.1–335	1810–3930
Gower ^a	318	3230
Jiang ^e	69–267	2570–7220
CAFS ^f	55.6–253	2530–7800

^a Gower et al. (2001), Table 4.

^b Gower et al. (1997).

^c Halliwell et al. (1996).

^d Shvidenko and Nilsson (1994, in press).

^e Jiang et al. (1999).

^f Chinese Academy of Forestry Sciences (1996).

3.5. Comparison with other boreal forest regions

Table 4 shows the ranges of biomass carbon stocks and NPP estimated in this study and others for China with those reported for boreal forests in Alaska, Canada, and Russia (Russian values are presented separately for the European and Siberian regions). Although the ranges are broad, these data indicate that the boreal forests of China have somewhat higher biomass and NPP than most other boreal forests in the world, with the exception of Siberia, which has comparable ranges.

4. Discussion

4.1. Influence of harvesting on carbon stocks

There have been numerous studies of the effects of harvesting on timber stocks and forest productivity, but relatively few have looked at the impacts on total ecosystem carbon stocks, and none that deal specifically with Chinese boreal forests. In one of the few reported observation-based studies, Morrison et al. (1993) demonstrate that CH results in a 20–30% carbon loss and as much as 35–44% for more intensive harvesting regimes in Canadian southern boreal forests. These Canadian observations are in rough agreement, although somewhat lower than the simulated impacts reported here for China.

The results presented here not surprisingly confirm that biomass and litter are more sensitive to harvesting impacts than soil carbon over short time scales (Figs. 3, 4, 5A and 6A). Fluctuations of soil carbon is heavily damped relative to those in litter and biomass but shows similar trends over time (Figs. 3C and 4C). This is consistent with the relationship proposed by Bhatti et al. (2000) relating changes over time in soil to biomass dynamics using an exponential damping factor. The results are also consistent with those previously reported in northern hardwood forests (Aber et al., 1978), northern mixed forest (Hendrickson et al., 1989), and Scots pine and Norway spruce forests (Olsson et al., 1996).

Studies of the influence of harvesting on the soil component have generally concentrated upon nutrient losses and gains, with much less attention being paid to soil organic matter until recently (e.g., Marion, 1979; Johnson et al., 1982, 1988). Those assessments that do appear in the literature—primarily modelling studies—suggest similar trends and magnitudes to those found in the present study, with distinct losses in ecosystem carbon with increased harvesting intensity or frequency. Delcourt and Harris (1980), e.g., assumed that clearing and cultivation caused 40% reduction in soil carbon in southeastern US. In their global carbon model, Houton et al. (1983) assume 30, 50, and 15% losses of litter and soil carbon after forest clearing in tropical, temperate and boreal forests, respectively, and a further delayed loss to 50% of original carbon content with cultivation. In the absence of hard information on change in soil carbon following harvesting in the US Pacific Northwest, Harmon et al. (1990) apparently took a conservative approach by assuming no change; they indicate, however, that this assumption is like false and that soil organic matter will most likely decrease under intensive management.

Observational data for managed pine stands in southern US reported by Gholz and Fisher (1982) show similar biomass, litter and soil dynamics following harvest to those simulated here. For example, they found that forest floor and soil carbon declined (by about 25%) after harvest, reaching a minimum approximately 20 years later before recovering to pre-harvest levels later in the rotation.

The simulated post-harvest dynamics of soil carbon pools in the present study (Figs. 3C and 4C) agree with the result of Covington (1981) and Federer (1984) for

the northern hardwood stands of New Hampshire. In their study, a series of stands of different ages was used to describe the pattern of forest floor mass and soil organic matter content during succession following logging. Covington (1981), studying the dynamics of soil organic carbon estimated a loss of 50% of forest floor organic matter in the first 20 years after the disturbance. Federer tested Covington's results by adding 13 more stands in the same region and found the same decline in soil organic matter dynamics after logging. Covington and Federer found the forest floors of the oldest stands had the most organic matter and those between 10 and 30 years old had the least, a result attributed to rapid loss of organic matter from increased decomposition and reduced litter inputs in young stands. Similar trends are simulated in the present study (Figs. 3C and 4C). After harvesting, soil carbon declines to a minimum value at 10–20 years, and subsequently increases slowly back to the pre-harvest level as litter production is re-established.

4.2. The effects of harvesting on the carbon fluxes

Harvesting impacts on forest productivity have been largely limited to impacts on timber yield, although some studies examine broader scale changes in NPP. Unfortunately, as with biomass impacts, none of the published studies are specific to Chinese or boreal forests. Nevertheless, most published studies conducted at the site-scale are broadly consistent with the present study. For example, Gholz and Fisher (1982) observed a peak in measured NPP approximately 25 years after commercial harvesting of a pine stand in the southern US. This peak occurs somewhat earlier than that found in the present simulations (~40 years) for boreal China, likely because of the warmer conditions and shorter natural rotation lengths of pine in the southern US. The simulated decreases in NPP with increasing intensity of harvesting and shortening of rotation length are also consistent with the findings of Bengtsson and Wistrom (1993) who report decreased productivity in spruce forest stands with increased harvesting intensity.

The dynamics of carbon fluxes (NPP and NEP) is related to the slope (first derivative) of ecosystem carbon stocks over time. At a typical site, both NPP and NEP decrease sharply at the time of disturbance (with NEP going negative), and then recovering towards the pre-harvest levels as vegetation is

re-established, litter re-accumulates and soil organic inputs again match decomposition losses (Fig. 8A and B). The dynamics of NPP post-harvesting disturbance is a strong function of stand age, reaching a maximum value relatively soon in stand development. The subsequent substantial decline is a widely observed feature of forest development (Gower et al., 1996; Ryan et al., 1997; Smith and Resh, 1999). The present simulations suggest that this post-harvest peak and subsequent decline are associated with complex interactions between nutrient cycling times in litter (and other detritus) and in regrowing vegetation. Thus the simulated NPP shows a different shape for short rotations (exhibiting overshoots and underdamped oscillatory behaviour) than for long rotations (with an overshoot, but a smooth damped recovery)—these responses are attributed to the differing turnover times (and hence nutrient cycling times) of the slash and detritus associated with young and older vegetation.

NPP at the forest scale (i.e., averaged over a rotation) is slightly influenced by the harvesting intensity with CH, yielding values approximately 6% higher than WTH, but strongly by the rotation length. NPP increases strongly with increasing rotation length, reaching a peak at a rotation length of about 200 years (Fig. 6B).

As described in Eq. (2), NEP is the difference between NPP and R_h . Thus the simulation results for NEP, when averaged over a rotation (i.e., at the forest scale) show a similar behaviour to NPP (Fig. 6B). Because it is a direct function of detrital production, R_h shows a similar dependence on rotation length as NPP and tends towards that curve at longer rotation lengths. As a consequence, the peak value of NEP is achieved at substantially shorter rotations than that for NPP and the subsequent decline is towards zero NEP (the NBR result) as shown in Fig. 5B. The dependence of NEP on harvesting intensity is similar to that of NPP, but in the opposite direction, with WTH yielding about 6% higher average NEP than CH (Fig. 5B). (This increase in NEP is associated with the export of more decomposable harvest material from the site in the WTH scenario and hence a change in heterotrophic respiration.)

The simulated results produced by CENTURY 4.0 indicated insignificant difference for both biomass and NPP along S–N gradient in Chinese boreal forests (Table 3). This may be attributed to the narrow latitude variation (only 4° of latitude) from southern to northern

boundary. The variation in altitude is significant, however, ranging from 200 to 1400 m in Chinese boreal forests (Wu, 1995; Zhang, 1986) and this variation shows up in the wide range of observational data in Table 3. Indeed, the variation in productivity across the altitudinal gradient of Chinese boreal forests is greater than the variation with latitude. For example, the mean value and standard division of observed biomass and NPP are $123.8 \pm 49.1 \text{ Mg C ha}^{-1}$ and $3980 \pm 820 \text{ kg C ha}^{-1}$ per year at Xinlin site (Table 3), but the range of biomass and NPP are from 74.1 to 267.4 Mg C ha^{-1} , and from 3760 to 7220 kg C ha^{-1} per year, respectively (Jiang et al., 1999; Chinese Academy of Forestry Sciences, 1996; Zhou, 1985; Zhang, 1986). Unfortunately, the absence of elevation and field weather station data at Mohe, Tahe and Xinlin restricted our efforts to investigate the effects of vertical altitude on carbon stocks and fluxes in this study.

5. Conclusions

Harvesting disturbance has become a major disturbance agent and plays a central role in boreal forests in Northeast China. The relatively high productivity and biomass of the Chinese boreal forests, compared to other circumpolar boreal biomes, is likely due to their southerly location: warm temperature and adequate precipitation create good conditions for forest development and growth. Nevertheless, the long history of forest use by humans has resulted in much of the boreal forest in China landscape being in less than a primary state. The impacts of harvesting simulated in this study suggest that the long-term decreases in carbon stocks (biomass, litter and soil carbon) are significant, resulting in a reduction of 81% in biomass and of 49% in litter under WTH with a 100-year rotation, relative to a no-harvest (NBR) reference. With a short rotations (30 years), the decrease in simulated biomass and litter were more pronounced (88 and 66%, respectively) relative to a 200-year rotation. Soil carbon shows the same decreasing trend as biomass with increasing harvest intensity and decreasing rotation length. NPP decreased significantly, but NEP increased following an increase of harvesting intensity. A shorter rotation length may result in a lower NPP and NEP. The simulation results presented here indicate that the disturbance regime (random fire and different levels of

harvesting) have significant influences on ecosystem carbon pool and the carbon fluxes (NPP and NEP) of the Chinese boreal forests. Compared with a random fire regime (assumed to be similar to the natural regime), suppression of all disturbances (NBR) results in increased ecosystem carbon stocks and NPP, but lower NEP. Intensive harvesting (WTH) on a short rotation (30–100 years) results in decreased ecosystem carbon stocks, NPP and NEP. Intensive harvesting (WTH) on a longer rotation (greater than about 200 years), resulted in increased ecosystem carbon, but decreased NPP and NEP. The simulated ecosystem carbon stocks under moderate harvest scenarios are consistent with the observed stocks, which are considerably lower than the no-disturbance scenario (NBR) and the random fire scenario. These simulations suggest that reducing harvesting intensity and extending harvesting rotation length may be a good strategy for maintaining the sustainability of production and carbon sequestration in Chinese boreal forests.

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References

- Aber, J.D., Botkin, D.B., Melillo, J.M., 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* 9, 10–14.
- Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G., Vinson, T.S., 1993. Boreal forests and tundra. *Water Air Soil Pollut.* 70, 39–53.
- Baumgartner, A., 1979. Climatic variability and forestry. In: *Proceedings of the World Climate Conference on World Meteorological Organization*, Geneva, WMO-No. 537, pp. 581–607.
- Beijing Meteorological Center, 1984. *Ground Climate Data of China (1951–1980)*. Data Department of Beijing Meteorological Center. Meteorological Press, Beijing, China, p. 452.
- Bengtsson, J., Wistrom, F., 1993. Effects of whole-tree harvesting on the amount of soil carbon: model results. *NZ J. For. Sci.* 23, 380–389.
- Bhatti, J.S., Apps, M.J., Jiang, H., 2000. Examining the carbon stocks of boreal forest ecosystems at stand and regional scales. In: Lal, R., Kimble, J.M., Follet, R.F., Stewart, B.A. (Eds.), *Assessment Methods for Soil Carbon*. Advances in Soil Science. CRC Press, Boca Raton, FL, pp. 513–531.
- Bolin, B., Sukumar, R., 2000. Global perspective. In: Watson, R., Noble, I.R., Bolin, B., Ravindranath, N.H., Verardo, D.J., Dokken, D.J. (Eds.), *Landuse, Land-use Change, and Forestry*. A Special Report of the IPCC. Cambridge University Press, Cambridge, pp. 23–51.
- Bolker, B.M., Pacala, S.W., Parton, W.J., 1998. Linear analysis of soil decomposition: insights from century model. *Ecol. Appl.* 8, 425–439.
- Boyle, J.R., Philips, J.J., Ek, A.R., 1973. Whole-tree harvesting: nutrient budget evaluation. *J. For.* 71, 760–762.
- Cheng, H. (Ed.), 1990. *The Handbook of Natural Resources in China*. Science Press, Beijing, China, p. 902.
- Chinese Academy of Forest Survey, 1981. *The Mountain Forests of China*. Agriculture press, Beijing, China, p. 340.
- Chinese Academy of Forestry Sciences, 1996. *Forest Production Database of China*. CAFS Research Reports.
- Covington, W.W., 1981. Changes in the forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* 62, 41–48.
- Delcourt, H.R., Harris, W.F., 1980. Carbon budget of the south-eastern US biota: analysis of historical change in tend from source to sink. *Science* 210, 321–323.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–189.
- Federer, C.A., 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* 14, 763–767.
- Gholz, H.L., Fisher, R.F., 1982. Organic matter production and distribution in slash pine (*Pinus elliotii*) plantations. *Ecology* 63, 1827–1839.
- Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. *Tree* 11, 378–382.
- Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., Stow, T.K., 1997. Carbon distribution and aboveground net primary production in Aspen, Jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J. Geophys. Res.* 102 (D24:29), 29–41.
- Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., Wang, C., 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* 11, 1395–1411.
- Halliwell, D.H., Apps, M.J., Price, D.T., 1996. A survey of the forest site characteristics in a transect through the central Canadian boreal forest. *Water Air Soil Pollut.* 82, 257–270.
- Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects of carbon storage of conversion of old-growth forests to young forests. *Science* 247, 699–702.

- Hendrickson, O.Q., Chatarpaul, L., Burgess, D., 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. *Can. J. For. Res.* 19, 725–735.
- Houton, R.A., Hobbie, J.E., Melillo, J.M., Moore, B., Peterson, B.J., Shaver, G.R., Woodwell, G.M., 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980. Net release CO₂ to atmosphere. *Ecol. Monogr.* 53, 235–262.
- IGBP terrestrial carbon working group, 1998. The terrestrial carbon cycle: implications for the Kyoto protocol. *Science* 280, 1393–1394.
- Jiang, H., Apps, M.J., Zhang, Y.L., Peng, C.H., Woodard, P.M., 1999. Modelling the spatial pattern of net primary productivity in Chinese forests. *Ecol. Model.* 122, 275–288.
- Jiang, H., Apps, M.J., Peng, C., Zhang, Y., 2001. Modeling the effects of fire disturbances on the carbon dynamics of boreal forests in central Canada. *Global Change Biology*, submitted for publication.
- Johnson, D.W., West, D.C., Todd, D.E., Mann, L.K., 1982. Effects of sawlog vs. whole-tree harvesting on the nitrogen, phosphorus, potassium, and calcium budgets of an upland mixed oak forest. *Soil Sci. Soc. Am. J.* 46, 1304–1309.
- Johnson, D.W., Henderson, G.S., Todd, T.E., 1988. Changes in nutrient distribution in forests and soils of Walker Branch Watershed, Tennessee, over an eleven-year period. *Biogeochemistry* 5, 275–293.
- Jurgensen, M.F., Harvey, A.E., Graham, R.T., Page-Dumroese, D.S., Tonn, J.R., Larsen, M.J., Jain, T.B., 1997. Impact of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland northwest forests. *For. Sci.* 43, 234–251.
- Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clear-cutting. *Environ. Rev.* 1, 121–144.
- Kimmins, J.P., 1977. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole tree harvesting. *For. Ecol. Manage.* 1, 169–183.
- Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *J. Biogeogr.* 24, 663–673.
- Liu, S., 1994. Climate change with forest of China. *Res. Chinese For.* 7, 425–430.
- Marion, G.K., 1979. Biomass and nutrient removal in long-rotation stands. In: Leaf, A.L. (Ed.), *Impact of Intensive Harvesting on Forest Nutrient Cycling*. State University of New York, Syracuse, pp. 98–110.
- Metherell, A.K., Harding, L.A., Cole, C.V., Parton, W.J., 1993. CENTURY Soil Organic Matter Model Environment, Technical Documentation, Agroecosystem. Version 4.0. Great Plains System Research Unit, Technical Report No. 4. USDA-ARS, Fort Collins, CO, 250 pp.
- Morrison, I.K., Foster, N.W., Hazlett, P.W., 1993. Carbon reserves, carbon cycling, and harvesting effects in three mature forests types in Canada. *NZ J. For. Sci.* 23, 403–412.
- Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., Rosen, K., 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. *For. Ecol. Manage.* 82, 19–32.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Am. J.* 51, 1173–1179.
- Parton, W.J., Scurlock, M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.C., Seastedt, T., Moya, E.G., Kamnalrut, A., Kinyamario, J.I., 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem. Cycles* 7, 785–809.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, B. (Eds.), *A System Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge, 1992, pp. 144–169.
- Peng, C.H., Apps, M.J., 1997. Contribution of China to the global carbon cycle since Last Glacial Maximum: reconstruction from palaeovegetation maps and an empirical biosphere model. *Tellus B* 49, 393–408.
- Peng, C.H., Apps, M.J., 1999. Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecol. Model.* 122, 174–193.
- Peng, C.H., Apps, M.J., Price, D., Nalder, I.A., Halliwell, D.H., 1998. Simulating carbon dynamics along the boreal forest transect case study (BFTCS) in central Canada. 1. Model testing. *Global Biogeochem. Cycles* 12, 381–392.
- Ryan, M.G., 1991. Effects of climate change on plant respiration. *Ecol. Appl.* 1, 157–167.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27, 214–262.
- Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), 1992. *A System Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge, pp. 1–10.
- Shvidenko, A., Nilsson, S., 1994. What do we know about the Siberian forests. *Ambio* 23, 396–404.
- Shvidenko, A., Nilsson, S., in press. Photomass, increment, mortality and carbon budget of Russian forests. *Climatic Change*.
- Smith, F.W., Resh, S.C., 1999. Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. *For. Sci.* 45, 333–341.
- Tian, H., Xu, H., Hall, A.S., 1995. Pattern and change of a boreal forest landscape in northeastern China. *Water Air Soil Pollut.* 82, 465–476.
- Wang, C., Gower, S.T., Wang, Y., Zhao, H., Yan, P., Bond-Lamberty, B.P., 2001. The influence of fire on carbon distribution and net primary production of boreal *Larix gmelinii* forests in north-eastern China. *Global Change Biol.* 7, 719–730.
- Wu, Z. (Ed.), 1995. *Chinese Vegetation*. Science Press, Beijing, China, 1382 pp.
- Xu, H., 1998. *Forests in Daxinganling Mountains China*. Science Press, Beijing, China, pp. 22–53.
- Zhang, W. (Ed.), 1986. *Chinese Forest Soils*. Science Press, Beijing, China, p. 1012.
- Zheng, H., Jia, S., Hu, H., 1986. Forest fire and restoration in Daxinganling. *J. Northeast For. Univ.* 10, 40–47.
- Zhou, Y., 1985. *The Vegetation of Daxinganling*. Science and Technology. House of Heilongjiang, Harbin, p. 310.