Landscape Ecol
DOI 10.1007/s10980-014-0051-x

RESEARCH ARTICLE

Spatial simulation of the effect of fire and harvest on aboveground tree biomass in boreal forests of Northeast China

Xu Luo · Hong S. He · Yu Liang · Wen J. Wang · Zhiwei Wu · Jacob S. Fraser

Received: 23 December 2013 / Accepted: 9 June 2014

Abstract Fire and timber harvest are two major forest disturbances in boreal forests. Predicting the dynamics of boreal forest biomass requires accounting for both of those effects. Related stochasticity and other uncertainties can produce great variation in predicted responses of forests to fire and timber harvest. In this study, we investigated the effects of fire and timber harvest on landscape-level predictions of the tree component of stand biomass in a boreal forest landscape in Northeast China. We used a forest landscape model (LANDIS PRO) to predict the tree biomass over three time intervals (0–50, 50–150, and 150–300 years). We then compared the simulated results of fire and timber harvest and their interactions with observed biomass and its spatial distribution over short-, mid-, and long-term intervals. For additional prediction comparisons, we observed uncut, unburned stands (i.e., the succession-only scenario). Compared to the succession-only scenario, we found that predicted biomass was reduced by 3.8 ± 2.1, 9.1 ± 3.6, and 11.2 ± 5.1 tons/ha in fire-only, harvest-only, and combined fire and harvest scenarios, respectively. Our results indicated that the effect of harvest on biomass exceeded that of fire, and that the interaction of fire and harvest was more effective in reducing biomass than the effects of fire or harvest separately. Biomass predictions that did not consider effects of fire and timber harvest tended to inflate biomass estimates. The spatial distribution of tree biomass moreover changed with simulation period. These results have important implications in designing prescriptions for improving forest sustainability.

Keywords Fire · Harvest · LANDIS · Model verification · The Great Xing'an Mountains

Introduction

Boreal forests retain larger carbon reserves than other biomes (Melillo et al. 1993) and play important roles in global carbon balance. As an important source of forest products, aboveground biomass of forest trees (hereafter referred to as biomass) comprises a large proportion of total carbon storage in boreal forests (Goodale et al. 2002; Houghton 2005). Although tree biomass is the most dynamic part of forest carbon

X. Luo · Y. Liang (✉) · Z. Wu
State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences,
Shenyang 110016, China
e-mail: liangysts@gmail.com

H. S. He · W. J. Wang · J. S. Fraser
School of Natural Resources, University of Missouri,
Columbia, MO, USA

storage (Houghton et al. 2009), forests are also very susceptible to fire, timber harvest, and wind (Brown 2002; Pregitzer and Euskirchen 2004; Mkhabela et al. 2009; Hagemann et al. 2010). Thus, quantitative information and mapping of biomass is essential to predicting carbon stocks and ecosystem productivity responses to fire and harvest.

For boreal forests around the world, fire and timber harvest are two major forest disturbances. The effects of fire and harvest on biomass dynamics have been found to be more important than climatic change (Gustafson et al. 2010; Li et al. 2013), and fire and harvest significantly influence boreal forest biomass predictions (Conard et al. 2002; Lee et al. 2002; Cavard et al. 2010; Holtsmark 2012). However, some of these biomass studies were plot-based estimations rather than predictions. Although some studies focused on biomass prediction, they did not incorporate fire and timber harvest and thereby could not be further verified. Because previous studies have inadequately considered effects of harvest and fire on biomass predictions in boreal forests, such predictions may possess low predictive accuracy.

Studies on biomass (carbon) prediction based on biogeochemical/ecophysiological process models have limitations in incorporating the effects of fire and harvest on biomass (Running 1994; Hurtt et al. 2002; Sitch et al. 2008). For example, Bond-Lamberty et al. (2006) predicted stem and leaf biomass of trees using the Biome-BGC model. Medvigy and Moorcroft (2012) predicted the biomass of forests using the ED2 model. However, in those process-based models, only empirical ecological process relations were considered. Thus they may not have adequately considered fire and harvest to obtain landscape-scale results (such as species composition and distribution), which are critical to landscape scale biomass prediction.

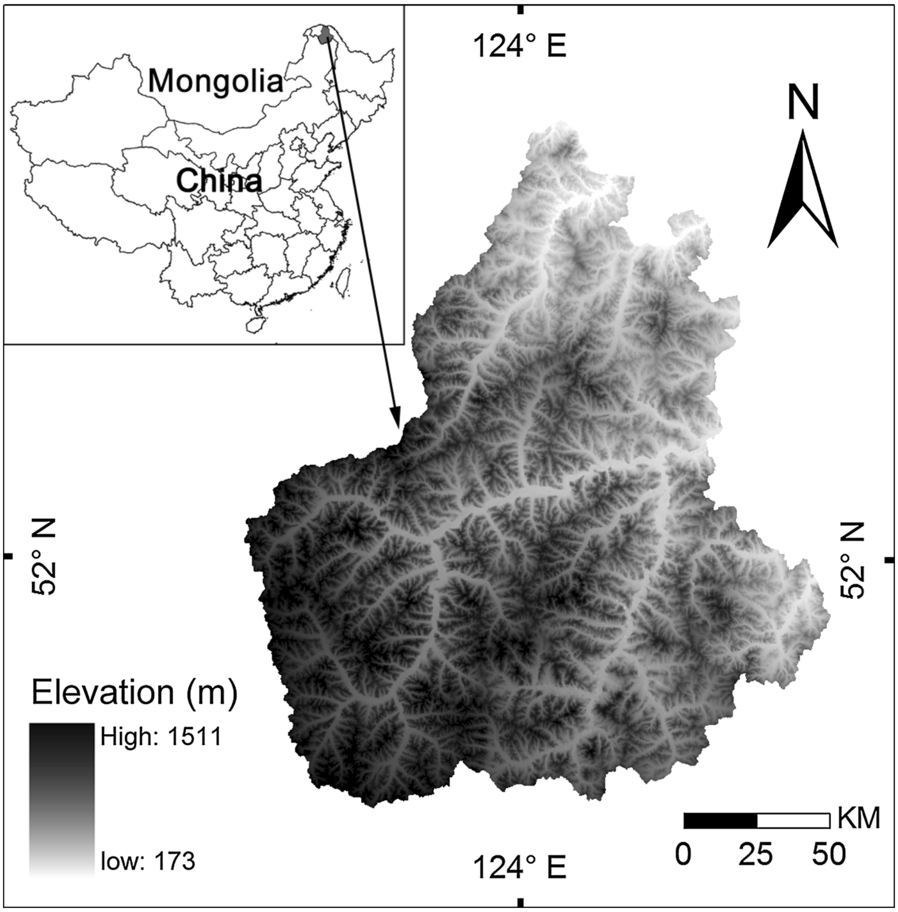
Fire and tree harvest occur at large spatial and long temporal scales, making it difficult to incorporate their effects on biomass using traditional plot-scale studies (He et al. 2002). Because of the stochastic nature of fire and tree harvest and the complex interactions between them and forest succession, reliable predictions of biomass in the boreal forest are challenging (He et al. 2002; Liu et al. 2011). The spatially explicit forest landscape models (FLMs) are effective tools for exploring these broad-scale issues (Scheller and Mladenoff 2007; Xu et al. 2004, 2010). With FLMs, landscape scale studies can include vital module parameters, which can be changed to more flexibly evaluate the complex interactions occurring in landscape biomass processes (He and Mladenoff 1999; Schumacher et al. 2004; Shifley et al. 2008).

For many years, models have been used to investigate effects of fire and timber harvest in boreal forests in the US (Gustafson et al. 2004; Scheller et al. 2011a, Canada (Groot et al. 2003; Bernier et al. 2010), and Europe (Pennanen and Kuuluvainen 2002). Although those models provide information on aboveground biomass and its distribution by species and age structure, they have not produced stand information (e.g., tree density and basal area) that can be compared directly to the forest inventory data. Such models thus have not been rigorously verified largely because the experimental data for doing so rarely has been available (Taylor et al. 2008; Shifley et al. 2009; Gustafson et al. 2010). Verification of the effects of fire and harvest on simulations can determine the acceptability of simulation results, and thereby reduce prediction uncertainties. Previous verification of FLMs has usually been based on comparing simulated results with other model simulations or field data (Bugmann 2001; Scheller and Mladenoff 2004; He et al. 2005). But few studies have actually verified simulation results of fire and harvest effects.

In China, about 30 % of forests are boreal forests, which comprise about 40 % of the country's forest biomass (Fang et al. 2001; Wang 2006). Biomass studies of Chinese boreal forests thus are important to understanding carbon cycles. It has been reported that fire and timber harvest strongly affect forest composition, structure, spatial distribution, and thus forest biomass in those forests (Li et al. 2004; Zhao and Zhou 2005). Quantification of fire and timber harvest on biomass prediction thus is needed in this region.

The objective of this study therefore was to investigate effects of fire and timber harvest on predicting tree biomass in a boreal forest landscape in Northeast China. To do this, we used a forest landscape model (LANDIS PRO) to predict tree biomass over long time periods (up to 300 years). Specifically, we: (a) verified simulated fire and timber harvest against observed field data; (b) quantified the separate effects of fire and harvest; and (c) quantified their combined (interactive) effects on predicting total biomass and its spatial distribution over short- (0–50 year), mid- (50–150 year), and long-term (150–300 year) intervals.

Fig. 1 Geographic location of the study area



Methods

Study area

Our study was located in the central Great Xing'an Mountains of northeastern China, which encompasses 2.7 million ha (Fig. 1). Mean annual precipitation is 428 mm, which mainly occurs during the summer. The average elevation is 849 m and ranges from 167 to 1,523 m. Mean annual temperature is −2.8 °C with a January mean of −27.8 °C and a July mean of 18 °C. Vegetation in the area is cool-temperate, with mixed deciduous and coniferous species dominated by larch (*Larix gmelinii*), white birch (*Betula platyphylla*), aspen (*Populus davidiana*), Mongolian Scots pine (*Pinus sylvestris var. mongolica*), and Korean spruce (*Picea koraiensis*).

Fire and timber harvest are two major forest disturbances in the Great Xing'an Mountains; strong winds occur rarely in the study area and their overall effects are minimal compared to fire and harvest. Fire has been routinely suppressed, and the average fire return interval has increased from 30 years in the past to 270 years under fire suppression (Xu 1998). Consequently, over time fires have changed from frequent to infrequent and low-intensity burns, but at times to catastrophic burns (Chang et al. 2008).

Timber harvest is another important anthropogenic disturbance. Its intensity and frequency have directly influenced stand age structure and species composition (Gustafson et al. 2000). The study area has been a major timber supply source in China since 1964. In 2000, the government of China implemented a natural forest conservation project in the region. Before then, the total annual harvest in the study area was approximately to 2.1×10^6 m^3. After year 2000, the annual harvest was about 4.5×10^5 m^3, which represents a large harvest reduction (Hu and Liu 2006).

Decades of fire suppression and timber harvest have extensively altered forest structure, age, and species composition. As a result, these forests have become more fragmented, and now comprise a more simplified forest structure and composition (Xu 1998; Chang et al. 2007).

The LANDIS PRO model

We used a spatially explicit landscape model, LANDIS PRO (v. 7.0, website: http://landis.missouri.edu), to simulate forest change resulting from forest growth, succession, fire, and timber harvest (Wang et al. 2013). The model uses forest inventory data for model parameterization, calibration, and validation. LANDIS PRO directly estimates biomass and carbon from tree DBH and stand density by species using allometric equations (Wang 2006).

The LANDIS PRO succession and dispersal module tracks species' age cohorts, numbers of trees, and DBH by species' age cohort for each observed raster cell. This module also provides an approach to landscape modeling well suited to our purpose of quantifying stand-scale resource competition expressed as growing space occupied (GSO) by trees. GSO provides a relative measure of stand density designed to broaden the application of Reineke's widely used stand density index (SDI) (Reineke 1933; Wang et al. 2013). But unlike SDI, GSO is applicable to both mixed species stands with multiple age classes (such as ours) and to even-aged monocultures. GSO moreover considers stages of stand development (Oliver and Larson 1996) along with tree competition, both essential to our modeling needs. It thus provides a flexible expression of the percentage of a cell (raster) area occupied by trees in relation to their minimum growing space requirements and to stand development stage. Those factors in turn regulate seedling establishment and self-thinning (Reineke 1933; Wang et al. 2013).

The fire module simulates multiple fire regimes across heterogeneous landscapes. It includes three fire simulators: (1) fire occurrence, (2) fire spread, and (3) fire effects. Fire occurrence simulates how many fires occur and when and where each occurs (Yang et al. 2004). Fire spread simulates how fires spread across the landscape from their ignition point (Yang et al. 2008). Fire effects simulate which species' age-cohorts are killed on each burned cell (He and Mladenoff 1999). Those effects then are quantified as fire intensity class, which are passed on to the fuel module to determine amount of fuel consumed (He et al. 2004).

Timber harvesting was simulated using management area maps and stand maps (Fraser et al. 2013). To do this, the study area was divided into different management areas, which defined the boundaries around specific timber harvest events. The stand map thus provided a basic-unit map for harvesting operations. Stands comprised the smaller contiguous units within a management area.

Model initialization and calibration

Five tree species were included in our study. They accounted for more than 95 % of aboveground forest biomass in the region (Xu 1998) (Table 1). The forest composition map consisted of density (numbers of trees) and their size, and species' age-class information for each cell. We constructed the initial forest composition map based on the stand map and China National Forest Inventory Second and Third Tier data

Table 1 Species life history attributes for the study area

Species name	Larch	Pine	Spruce	Birch	Aspen
Longevity (years)	300	250	300	150	120
Maturity age (years)	20	25	30	15	10
Shade tolerance (class)[a]	2	2	4	1	1
Fire Tolerance (class)[b]	4	3	1	3	2
Maximum seeding distance (m)	150	200	150	2,000	2,000
Minimum sprouting age (years)	0	0	0	15	10
Maximum sprouting age (years)	0	0	0	150	120
Maximum DBH (cm)	55	60	60	30	50
Maximum SDI (trees/ha)	600	560	520	690	680
Number of potential germination seeds[c]	10	20	10	30	30

[a, b] Shade/fire tolerance classes 1–5: 1 = least tolerant, 5 = most tolerant

[c] Mean number of potential germinating seeds produced/tree/year

(http://www.cfsdc.org). The stand map was a GIS layer comprised of 113,778 survey units (polygons each 23 ha) that included boundaries of survey units and forest composition information within each. The Second and Third Tier data (2,172 plots), obtained from the local forest bureau, contained numbers of trees by age class and DBH by species and plot; plots were evenly distributed across the study area. Both datasets were obtained from field plots measured during or close to year 2000. We integrated the stand map (polygon) and the Second and Third Tier (point) data to derive numbers of trees by age class for each species in the initial forest composition map (raster). To balance the realistic representation of the simulated landscape and computational load, the forest composition map was rasterized at a 90 × 90 m cell size resolution, which yielded 2,217 columns × 2,609 rows.

In LANDIS, the landtype map delineates heterogeneous landscapes into relatively homogeneous landtype units based on climate, terrain, and soil. Thus, each landtype is assumed to be homogeneous in terms of resource availability represented by the maximum growing space that can be occupied (MGSO) by trees, and species' assemblages as represented by species establishment probability (SEP). SEPs are derived for each landtype based on the responses of each species to soil moisture, soil N, soil C, and local climate. LANDIS uses SEPs as inputs and indirectly captures the spatial variability of climate. Species with high SEPs have higher probabilities of establishment than those with lower values. SEPs for our study area were derived from previous LANDIS modeling studies (Liu et al. 2012; Li et al. 2013). We characterized the spatial variation in climate, soil, and terrain by delineating heterogeneous landscapes into multiple, relatively homogenous landtypes.

The model stratifies heterogeneous disturbance regimes using the landtype map. Each landtype was assumed to be a unique fire regime since most fire regimes follow the environmental controls encapsulated by landtype. Fire regimes are characterized by ignition frequency and mean fire return interval, which were calculated from historical fire records from 1967 to 2005 (Table 2). We assumed that fire parameters remained unchanged throughout the simulation period.

The timber harvest region was divided into three management areas where harvesting was permitted, restricted, and banned, respectively. Each management area then was subdivided into stands that averaged 23 ha. In this study, we assumed that management area and timber harvest prescriptions remained unchanged (Table 3). Thinning comprised the primary harvest events. In the past 30 years, pine and spruce were heavily cut because of their high economic value. The reduction of stocks of those species has resulted in their protection by local forestry bureaus. In accordance with current management policy, the harvested species are now limited to larch, birch and aspen.

Based on a data-splitting approach (Araújo et al. 2005), we used 70 % of the inventory plots (1,520 plots) to initialize the forest composition map. In the initialization process, we iteratively adjusted species growth rates until the initialized forest composition matched the 70 % of inventory plots of year 2000. We then used the remaining 30 % (652 plots) to verifying the initialized forest landscape. We also used the data-splitting approach to calibrate the number of potentially germinating seeds for each species from year 2000 to 2010 until the simulated forest composition for 2010 matched the undisturbed inventory data for 2010. Because of the lack of adequate time-series data,

Table 2 Parameters for the fire scenario

Land type	Mean fire return interval (years)	Fire ignition density[a]	Mean fire size (ha)	Standard deviation (ha)	Time since last fire (years)
Non forest	1,500	0.002	0	0	375
Terrace	500	0.00175	90	100	100
South-facing slope	150	0.00329	200	475	50
North-facing slope	160	0.00292	210	346	60
Ridge top	140	0.0081	238	500	30
Water body	0	0	0	0	0

[a] Number of fires/decade/hectare

Table 3 Harvest criteria parameters

Manageme-nt area	Area occupied (ha)	Harvest type	Removal order	Harvest interval (years)[a]	Area treated (proportion)	Target BA (m^2/ha)
Harvest banned	931,238	–	–	–	–	–
Harvest restricted	1,117,263	BA limit	Largest first	5	0.13	17.2
Harvest permitted	684,148	BA limit	Largest first	5	0.15	14.9

Natural regeneration was used throughout the study area

[a] Interval between successive harvests

only 2000 and 2010 forest inventories were available. Because the inventory data of 2010 covered a wide range of species-age combinations and various successional stages, there was an abundance of observed data for comparing simulated forest composition and structure at year 10.

The simulation experiment

We designed four simulation scenarios: (1) succession-only (fire and harvest were not included); (2) fire-only (wherein fire and succession were simulated with the fire regime approximating current fire suppression practices); (3) harvest-only (whereby harvest and succession were simulated, with harvest regime reflecting current forest harvest practices); and (4) fire-and-harvest (wherein fire, harvest, and succession were simulated to reflect current conditions). Each scenario was simulated from year 2000 to 2300 at 5-year time steps with five replicates used to account for model stochasticity.

Using tree biomass as the response variable for the five species, the succession-only scenario was compared to the fire-only, harvest-only, and fire-and-harvest scenarios for short-, medium-, and long-term periods using the mean comparison. To assess the simulated results of harvest events with the forest inventory data, paired t-tests were used to compare differences between observed and simulated basal areas in different management areas. To evaluate effects of fire and harvest on predicted biomass for the different scenarios, we used analysis of variance (ANOVA) to test for differences among simulation results derived from the fire-only, harvest-only, fire-and-harvest, and succession-only scenarios; the Least Significant Difference (LSD) method was used for post hoc analyses. We also tested the spatial biomass dynamics among different landtypes under four simulated scenarios using Tukey's Honest Significant Difference method for post hoc analysis. SPSS 16 software was use for all statistical analyses.

Evaluating the initial forest composition

To compare the simulated landscapes with forest inventory data for year 2000 and for year 2010 respectively, we used a scatter plot of observed tree density and basal area with simulated density and basal area (BA). To do this, we first randomly selected 652 raster cells from the simulated landscape for year 2000 and 322 raster cells for 2010. Then tree densities and basal areas were extracted from selected cells for comparing the 652 forest inventory plots for year 2000 and the 322 relatively undisturbed plots for year 2010, respectively.

Using forest inventory data to verify fire and harvest

To verify simulated forest responses to fire, we randomly selected 80 fires from different years and locations on the output maps of simulated results within the succession-and-fire scenario. These fires were all of low intensity, which characterized more than 90 % of the fires occurring on the study area. We also inventoried 40 field sites (8 field sites/age group) that were burned by low-intensity fires 5, 10, 15, 20 and 25 before the year they were inventoried. We first created five 20 m × 20 m plots and within each recorded individual trees with DBH > 1 cm. We then statistically compared tree density and basal area of the 80 simulated fires at 5, 10, 15, 20, and 25 post-fire years with 40 corresponding fires sampled in the field.

To verify the simulated basal area responses, we calculated the mean basal area of field plots in two management areas (harvest-restricted and harvest-permitted areas) at years 2000 and 2010, respectively. We then ran the tree harvest simulation for 10 years

(2000–2010), and adjusted the harvest parameters to ensure that the simulated basal area harvests matched the field data in both management areas.

Results

Evaluating the initial forest species composition

Our simulations indicated that the initialized forest composition and structure constructed from forest inventory data for year 2000 adequately represented the forest composition and structure for that year (stand density: $R^2 = 0.81$, Pearson correlation test: $p < 0.01$; basal area: $R^2 = 0.82$, $p < 0.01$) (Fig. 2a, b). Likewise, simulated density and basal area by species for year 2010 adequately represented the forest inventory data for that year (stand density: $R^2 = 0.81$, $p < 0.01$; basal area: $R^2 = 0.81$, $p < 0.01$) (Fig. 2c, d).

Verifying the effects of simulated fire and harvest using experimental data

The simulated post-fire responses showed that observed tree density at year 5 was relatively high (13,012 trees/ha > 1 cm DBH), and that the density of trees increased during the first 10 years. The increase largely was attributable to the death of trees from fire and the associated release of growing space that provided for the establishment of seedlings of pioneer species (e.g., birch and aspen). After post-fire stands reached the stem exclusion stage (after year 15), mortality from self-thinning then reduced numbers of trees in following years (Fig. 3a). Post-fire basal area increased steadily throughout the first 25 years (Fig. 3b). Simulated trends in tree density and basal area dynamics closely followed the observed data.

The simulations and observed stand basal areas were similar in harvest-restricted and harvest-permitted areas (Table 4). Observed data and simulations at year 2000 and year 2010 did not differ significantly (Table 4, $p > 0.05$). A comparison of basal areas before and after harvest showed that the simulations and observed data at years 2000 and 2010 were in agreement, indicating that tree harvest effects were adequately characterized.

The effects of fire and harvest on tree species biomass

Biomass responses to fire and timber harvest differed among species. In the fire-only, harvest-only, and fire-

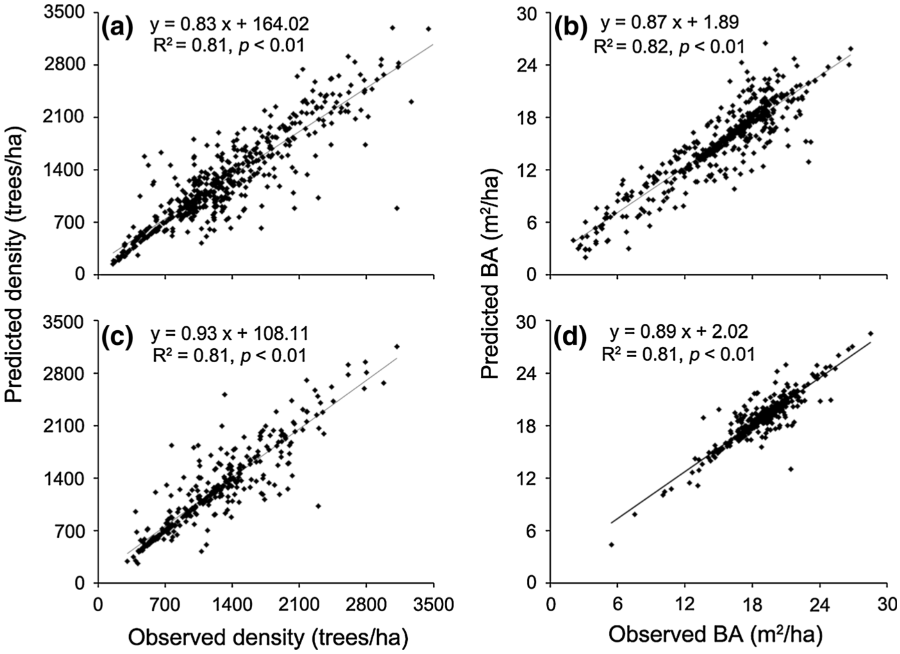


Fig. 2 Scatter plot showing the relation between observed and predicted values for stand density (**a**) and basal area (**b**) at year 2000; and stand density (**c**) and basal area (**d**) at year 2010 (Pearson correlation test: $p < 0.01$)

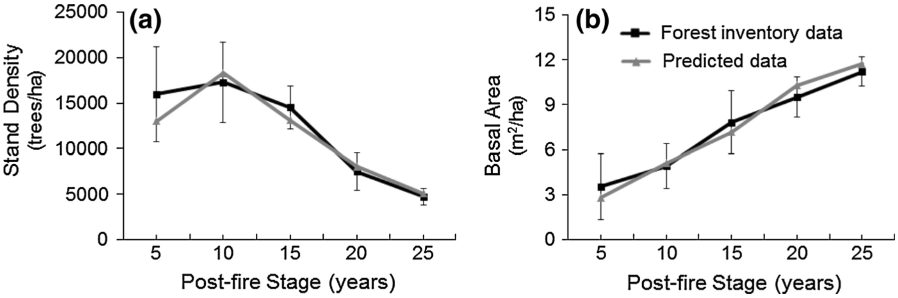


Fig. 3 Changes in predicted and observed stand density (**a**) and basal area (**b**) in burned areas in relation to post-fire year

Table 4 Mean landscape-scale values of basal area (BA) for years 2000 and 2010 by data source and management area

Management area	Observed or predicted value	Mean BA at year 2000 (m^2/ha + SD)	Mean BA at year 2010 (m^2/ha + SD)	BA removed (%)
Harvest-restricted area	Observed	21.7 (±1.36)	18.8 (±1.15)	13.1
	Predicted	20.9 (±1.02)	18.1 (±0.84)	13.4
Harvest-permitted area	Observed	17.9 (±1.12)	14.4 (±1.31)	19.6
	Predicted	18.5 (±1.07)	14.9 (±0.97)	19.4

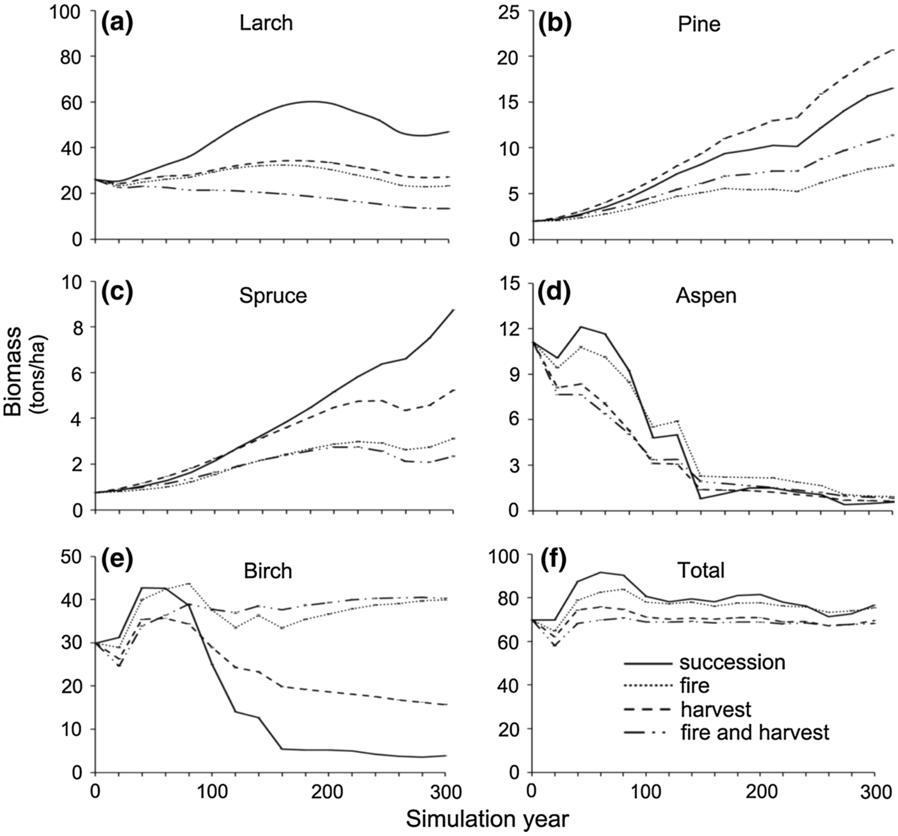


Fig. 4 Change in biomass density at the landscape level in relation to simulation year by species for fire and timber harvest scenarios

and-harvest scenarios, the biomass of larch decreased during all simulation periods (Fig. 4a), whereas the biomass of pine and spruce increased (Fig. 4b, c). Under the fire-only, harvest-only, and fire-and-harvest scenarios, biomass of aspen (an early successional species) was lower than that under the succession-only scenario during the first 100 years (Fig. 4d). In contrast, the biomass of larch, pine, and spruce responded positively to fire and timber harvest and their interactions. An exception was birch, an early successional species that was already abundant in the landscape (Fig. 4e). There was a significant decrease of total biomass in fire-only, harvest-only and fire-and-harvest scenarios compared to the succession-only scenario (Fig. 4f). Among all scenarios, the fire-and-harvest combination reduced the biomass of larch, spruce, aspen, and birch the most.

Biomass for larch in the fire-only scenario differed significantly from the succession-only scenario during all time intervals ($p < 0.05$, Fig. 5); it decreased between 8 and 48 % across the short- to long-term range. For pine and spruce, biomass did not differ significantly between succession-only and fire-only scenarios for the short-term interval ($p > 0.05$, Fig. 5). But pine and spruce in both of those scenarios differed significantly from the succession-only scenario for the long-term interval, where their biomass was 45 and 53 % greater, respectively, than that in the succession-only scenario.

Larch biomass under the harvest-only scenario also differed significantly from the succession-only scenario for all three simulation periods ($p < 0.05$, Fig. 5). Larch biomass in the harvest-only scenario was 4, 29, and 44 % lower than that in the succession-only scenarios across short-, medium-, and long-term periods, respectively. Biomass of both birch and aspen during the short-term period differed significantly from that in the succession-only scenario, and was 14 and 23 % less, respectively, than that in the succession-only scenario (Fig. 5). The increase in pine biomass was 8, 8, and 20 % greater than that in the succession-only scenario across short-, medium- and long-term periods, respectively.

In the fire-and-harvest scenario, the biomass of all species (with the two exceptions noted below) differed significantly from the succession-only scenario across all three simulation periods. Exceptions occurred during the short-term period where pine and spruce biomass was only 4 and 3 % lower, respectively, than in the succession-only scenario. Collectively, our results indicate that in our study area and for most species, the combined effects of fire and timber harvest had the greatest impact on reducing tree biomass (Fig. 5).

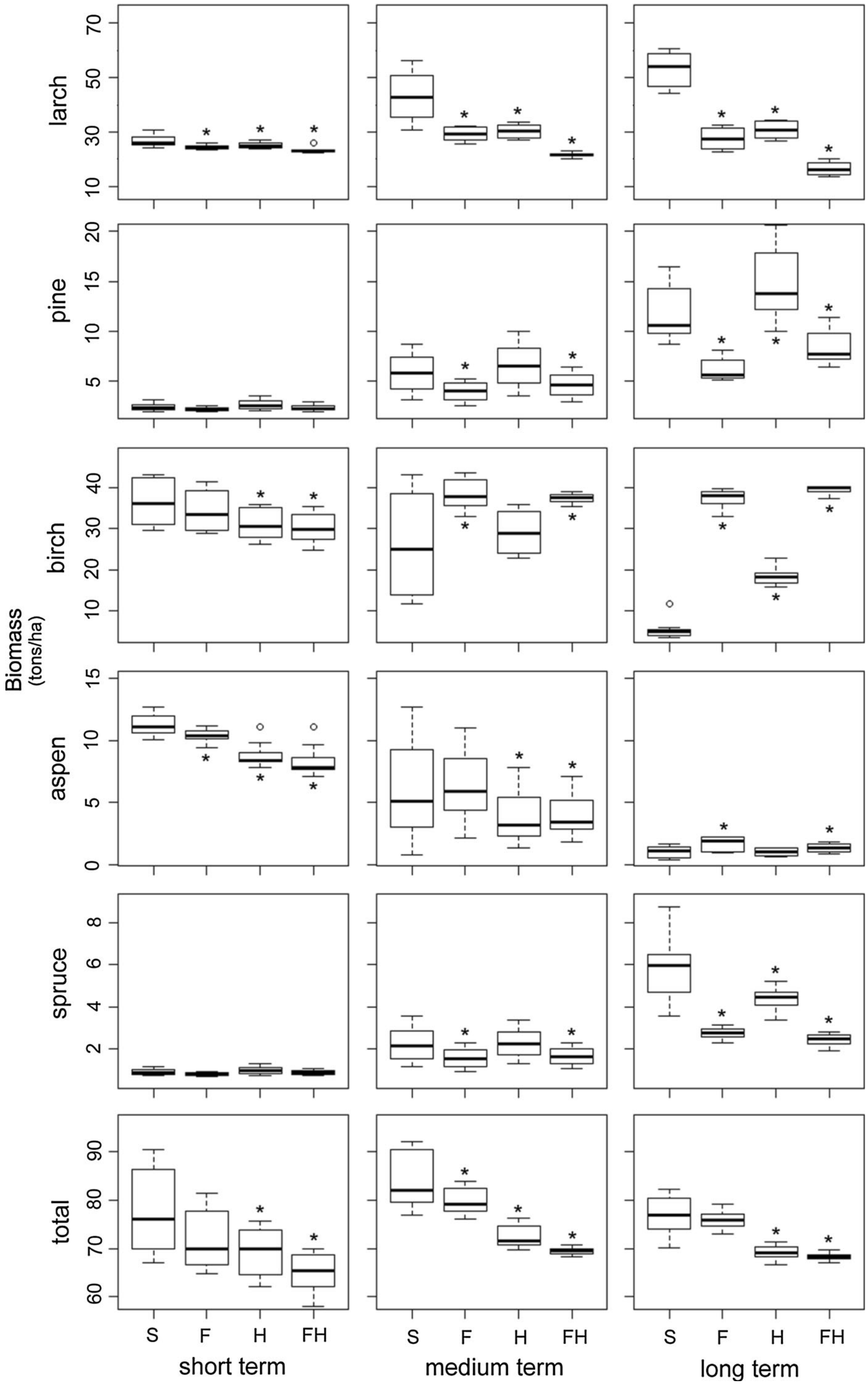
The spatial patterns of biomass over time

The model output created thousands of maps by species for each time step of the simulations. We selected graphical snapshots of total biomass distribution for the three simulation periods to illustrate how spatial variation of biomass responds to fire and timber harvest (Fig. 6). The four illustrated scenarios show how biomass distribution varied significantly among simulation periods and landtypes ($p < 0.05$, Figs. 6 and 7). In the terrace landtype, fire-only, harvest-only, and fire-and-harvest scenarios significantly decreased in biomass whereas the succession-only scenario at year 50 and 300 did not differ significantly from the fire-only scenario at year 150 (Fig. 7a). Across 300 years of simulation, biomass differences diminished in succession-only and fire-only scenarios (Fig. 7b, c). In the ridge top landtype, the biomass of the fire-only scenario was lower than in the harvest-only scenario (Fig. 7d). For all four landtypes at years 50, 150 and 300, total biomass under the fire-only, harvest-only, and fire-and-harvest scenarios were below those in the succession-only scenario. Tree biomass under the four scenarios we observed thus represent a wide range of landtypes and temporal variation occurring in our study area (Fig. 7).

Discussion

Validation of projected results of FLMs is a challenge. Because independent spatio-temporal data for validating FLM predictions often do not exist, model validation in the traditional sense is inapplicable to FLMs (Rykiel 1996). Previous research on model validation usually has compared simulation results with those using other simulation models, sporadic empirical studies, experimental data (e.g., flux tower data), or are qualitatively based on ecological and biological principles (Gustafson et al. 2000; Chen 2002; Thompson et al. 2011; Liu et al. 2012). In contrast to those studies, the novelty of our results lies in their quantitative expression. Both fire intensity and timber harvest disturbances were spatially explicit and stochastic events that were simulated as their interactions based on tree-level information at the pixel scale. To our knowledge, no previous research using forest landscape models has validated or verified the simulation results

Fig. 5 Mean biomass density in relation to time interval for the four scenarios considered: succession-only (S); fire-only (F); harvest-only (H); and fire-and-harvest (FH). The time intervals are: 0–50 years for short term, 50–150 years for medium term, and 150–300 years for long term; *indicates that a given scenario differs significantly from the succession-only scenario ($p < 0.05$)



of fire or timber harvest against field data as rigorously as has this study. Results showed that our simulations of fire and timber harvest effects were comparable to the field data (Figs. 2, 3; Table 4). Predicted biomass under the succession-only scenario (68 ± 2.3 tons/ha) was similar to observed data from another study in northeastern China (42–95 tons/ha) (Fang et al. 1998, 2001). Although the latter results are comparatively close to ours, they are based on plot data that are limited with respect to capturing the full extent of fire and harvest,

Fig. 6 Simulated biomass of all species combined for years 0, 50, 150 and 300

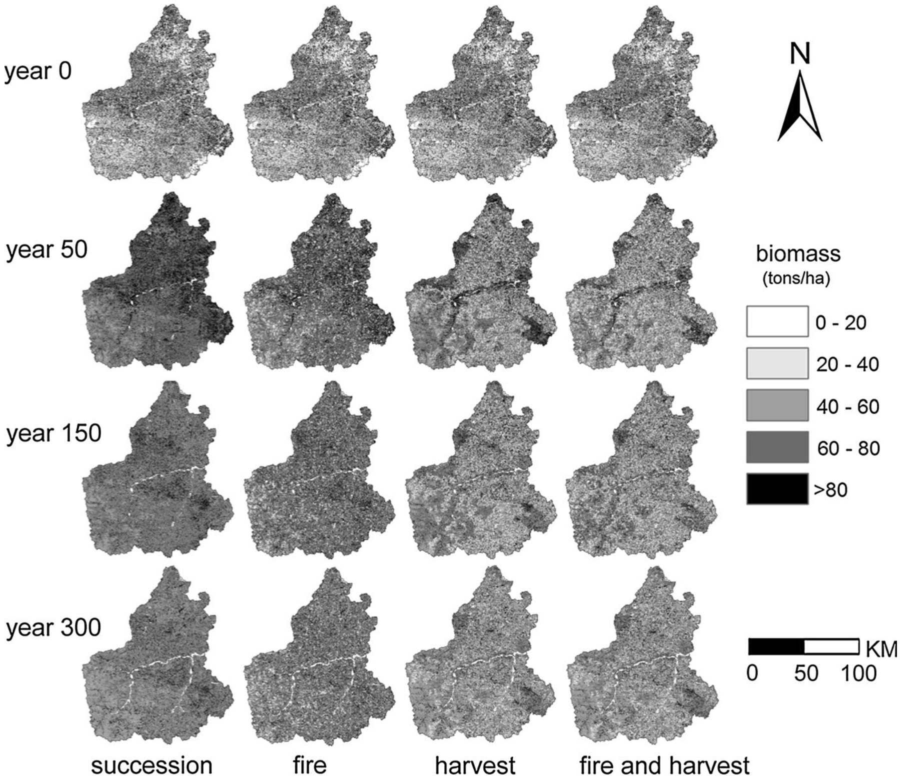
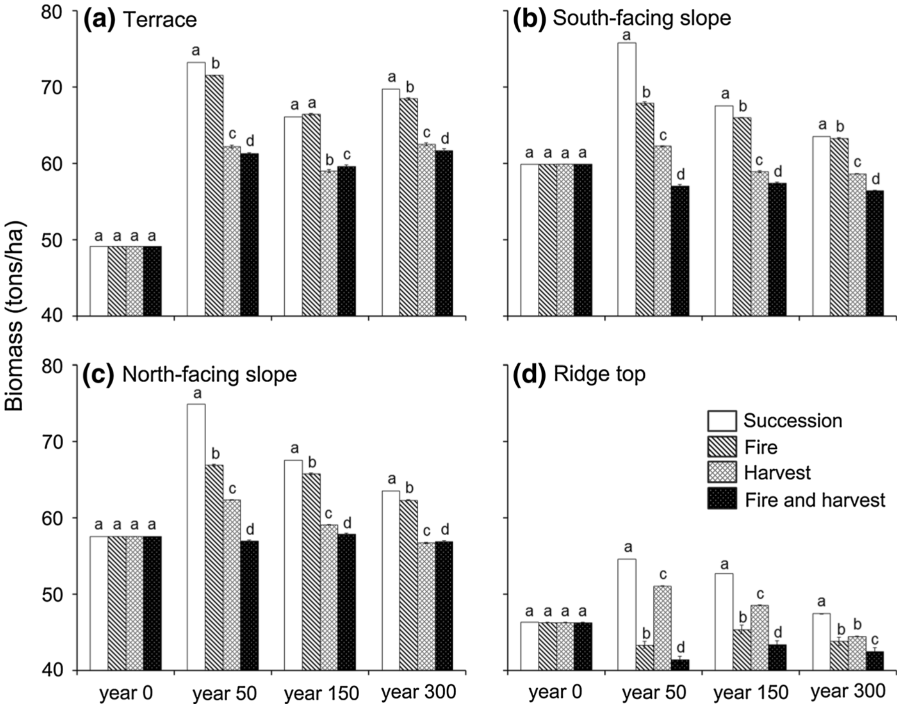


Fig. 7 Species biomass dynamics for different landtypes under four simulated scenarios: **a** terrace, **b** south-facing slope, **c** north-facing slope, and **d** ridge top (different letters indicate significant difference at $\alpha = 0.05$)



and moreover do not account for effects of recurrent fire and harvest on tree biomass. In contrast, our approach to predicting biomass dynamics incorporates effects of harvest and fire from past records. The resulting quantitative agreement thus adds assurance of our modeling approach and predictions. This distinction differs from approaches based only on estimation from inventory data. In addition, this type of verification provides added assurance that simulations under the fire and timber harvest scenarios we observed produced greater accuracy than those observed in previous modeling efforts (e.g., Ward et al. 2005; He 2008; Scheller et al. 2011b; Steenberg et al. 2013).

Our results suggest that predictions for boreal forests in northeastern China that do not consider fire and timber harvest may inflate biomass estimates. For example, biomass estimated by several other studies (Zhao and Zhou 2005; Thomas et al. 2007; Zhu et al. 2010) predicted larger values that did our study. This discrepancy may be related to the higher standing biomass in the relatively undisturbed forests of other forests (with their higher stocking volumes and mean diameters >4 cm DBH) than that occurring in our forests (Wang et al. 2001). Under the fire-only scenario, our biomass predictions, which decreased by 3.8 ± 2.1 tons/ha (across all simulation periods) were comparable to field-based studies in other boreal forest regions, which ranged from 2 to 11 tons/ha (Cahoon et al. 1994; Harden et al. 2000; Stocks 1989). However, Ivanova et al. (2011) observed that in central Siberia, low intensity fires reduced biomass by 6.5 ± 2.1 tons/ha. However, that discrepancy may have been related to differences in fire frequency. In the Great Xing'an Mountains of China, Mu et al. (2013) found that, compared to uncut stands, the biomass of harvested stands decreased by 15.4–48.3 tons/ha after 5 years of selective harvest. That biomass reduction was somewhat less than we observed (9.1 ± 3.6 tons/ha), a difference that may be related to the new harvest regimes implemented since 2000 in our study area, which have substantially reduced harvest intensity. Using the EFIMOD model in a transect across their study area, Chertov et al. (2009) simulated combined fire and timber harvest effects on biomass. They found that biomass decreased by 22.5–33.7 tons/ha during the period 1961–2100. That decrease was greater than observed in our simulation (11.2 ± 5.1 tons/ha across all simulation periods). This difference may be the result of lower fire occurrences and harvest intensities in our study area.

Our results revealed that the spatial distribution of biomass changed significantly among different landtypes during different simulation periods. Within the terrace landtype, fire tended to reduce standing tree biomass less so than did timber harvesting by itself or combined harvesting and fire. Such differences could have resulted from the relatively low fire frequency and severity in our region. Our results moreover showed that the direct effects of fires on biomass decline weakened over long periods in three landtypes: terraced, south-facing slope, and north-facing slope. This may have been related to the concentration of biomass in large, old trees that co-occurred with shifts in biomass distribution and the continued growth of those and new trees associated with low intensity fires over long-duration simulations. The current fire regime also increased the patch size of larch, which is the most fire-tolerant tree species in our region (Chang et al. 2007). Our results also revealed that the fire-only scenario reduced more biomass than the harvest-only scenario in the ridge-top landtype, which in turn, may be associated with that landtype (elevation above 1,000 m) and its vulnerability to frequent lightning strikes (Xu 1998).

In summary, our study suggests that FLMs are the preferred tools for predicting the effects of landscape processes on forest biomass dynamics. They also provide insight into species' biomass trends under different scenarios. Our study found that: (1) Total and individual species' biomass were significantly altered by fire, timber harvest, and their interactive effects during all simulation periods; (2) Although the effect of timber harvesting on species biomass was greater than that of fire, their interactive effect had a greater influence on reducing biomass than did any single landscape factor we observed; (3) Biomass prediction models that consider fire and timber harvest appear to be more accurate than models that do not; and (4) Under the scenarios we considered, the spatial distribution of biomass differed significantly ($p < 0.05$) among simulation periods. The evidence from our study indicates that fire and timber harvest strongly influence the spatial distribution of forest biomass.

Acknowledgments Funding for this research was provided by Chinese National Science Foundational Project (Nos. 31300404 and 41371199), "the 973 project" (No. 2011CB403206) and the project of State Key Laboratory of Forest and Soil Ecology (No. LFSE2013-12). We thank the workgroup from the local Forestry Bureau for providing valuable data for this study.

References

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. Global Change Biol 11(9):1504–1513

Bernier PY, Guindon L, Kurz WA, Stinson G (2010) Reconstructing and modelling 71 years of forest growth in a Canadian boreal landscape: a test of the CBM-CFS3 carbon accounting model. Can J Forest Res 40(1):109–118

Bond-Lamberty B, Gower ST, Goulden ML, McMillan A (2006) Simulation of boreal black spruce chronosequences: comparison to field measurements and model evaluation. J Geophys Res 111:G02014

Brown S (2002) Measuring carbon in forests: current status and future challenges. Environ Pollut 116:363–372

Bugmann H (2001) A review of forest gap models. Clim Change 51:259–305

Cahoon DR, Stocks BJ, Levine JS, Cofer WR, Pierson JM (1994) Satellite analysis of the severe 1987 forest fires in northern China and southeastern Siberia. J Geophys Res Atmos (1984–2012) 99(D9):18627–18638

Cavard X, Bergeron Y, Chen HY, Pare D (2010) Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. Can J For Res 40(1):37–47

Chang Y, He HS, Bishop Lan et al (2007) Long-term forest landscape responses to fire exclusion in the Great Xing'an Mountains, China. Int J Wildland Fire 16:34–44

Chang Y, He HS, Hu Y et al (2008) Historic and current fire regimes in the Great Xing'an Mountains, northeastern China: implications for long-term forest management. For Ecol Manage 254(3):445–453

Chen X (2002) Modeling the effects of global climatic change at the ecotone of boreal larch forest and temperate forest in northeast China. Clim Change 55:77–97

Chertov O, Bhatti J, Komarov A, Bykhovets S (2009) Influence of climate change, fire and harvest on the carbon dynamics of black spruce in Central Canada. For Ecol Manage 257:941–950

Conard SG, Sukhinin AI, Stocks BJ et al (2002) Determining effects of area burned and fire severity on carbon cycling and emissions in Siberia. Clim Change 55(1–2): 197–211

Fang J, Wang GG, Liu G-h, Xu S-l (1998) Forest biomass of China: an estimate based on the biomass-volume relationship. Ecol Appl 8:1084–1091

Fang J, Chen A, Peng C, Zhao S, Ci L (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. Science 292(5525):2320–2322

Fraser JS, He HS, Shifley SR, Wang WJ, Thompson FR III (2013) Simulating stand-level harvest prescriptions across landscapes: LANDIS PRO harvest module design. Can J For Res 43(10):972–978

Goodale CL, Apps MJ, Birdsey RA et al (2002) Forest carbon sinks in the Northern Hemisphere. Ecol Appl 12:891–899

Groot W, Bothwell P, Carlsson D et al (2003) Simulating the effects of future fire regimes on western Canadian boreal forests. J Vege Sci 14(3):355–364

Gustafson EJ, Shifley SR, Mladenoff DJ, Nimerfro KK, He HS (2000) Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30:32–43

Gustafson EJ, Zollner PA, Sturtevant BR, He HS, Mladenoff DJ (2004) Influence of forest management alternatives and land type on susceptibility to fire in northern Wisconsin, USA. Landscape Ecol 19:327–341

Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. Ecol Appl 20:700–715

Hagemann U, Moroni MT, Shaw CH, Kurz WA, Makeschin F (2010) Comparing measured and modelled forest carbon stocks in high-boreal forests of harvest and natural-disturbance origin in Labrador, Canada. Ecol Model 221: 825–839

Harden J, Trumbore S, Stocks B et al (2000) The role of fire in the boreal carbon budget. Global Change Biol 6(S1): 174–184

He HS (2008) Forest landscape models: definitions, characterization, and classification. For Ecol Manage 254:484–498

He HS, Mladenoff DJ (1999) Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology 80(1):81–99

He HS, Mladenoff DJ, Gustafson EJ (2002) Study of landscape change under forest harvesting and climate warming-induced fire disturbance. For Ecol Manage 155:257–270

He HS, Shang BZ, Crow TR, Gustafson EJ, Shifley SR (2004) Simulating forest fuel and fire risk dynamics across landscapes—LANDIS fuel module design. Ecol Model 180(1):135–151

He HS, Hao Z, Mladenoff DJ, Shao G, Hu Y, Chang Y (2005) Simulating forest ecosystem response to climate warming incorporating spatial effects in northeastern China. J Biogeogr 32:2043–2056

Holtsmark B (2012) Harvesting in boreal forests and the biofuel carbon debt. Clim Change 112(2):415–428

Houghton R (2005) Aboveground forest biomass and the global carbon balance. Global Change Biol 11(6):945–958

Houghton R, Hall F, Goetz SJ (2009) Importance of biomass in the global carbon cycle. J Geophys Res Biogeo (2005–2012) 114:G00E03

Hu HF, Liu GH (2006) Carbon sequestration of China's National Natural Forest Protection Project. Acta Ecologica Sinica 26(1):291–296

Hurtt G, Pacala S, Moorcroft P et al (2002) Projecting the future of the US carbon sink. Proc Natl Acad Sci 99(3): 1389–1394

Ivanova GA, Conard SG, Kukavskaya EA, McRae DJ (2011) Fire impact on carbon storage in light conifer forests of the Lower Angara region, Siberia. Environ Res Lett 6(4):045203

Lee J, Morrison IK, Leblanc J-D, Dumas MT, Cameron DA (2002) Carbon sequestration in trees and regrowth vegetation as affected by clearcut and partial cut harvesting in a second-growth boreal mixedwood. For Ecol Manage 169:83–101

Li K, Wang S, Cao M (2004) Vegetation and soil carbon storage in China. Sci China Ser D 47(1):49–57

Li X, He HS, Wu Z, Liang Y, Schneiderman JE (2013) Comparing effects of climate warming, fire, and timber harvesting on a boreal forest landscape in Northeastern China. PLoS ONE 8(4):e59747

Liu S, Bond-Lamberty B, Hicke JA et al (2011) Simulating the impacts of disturbances on forest carbon cycling in North America: processes, data, models, and challenges. J Geophys Res 116(G4):G00K08

Liu Z, He HS, Yang J (2012) Emulating natural fire effects using harvesting in an eastern boreal forest landscape of northeast China. J Vege Sci 23(4):782–795

Medvigy D, Moorcroft PR (2012) Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. Philos T Roy Soc B 367(1586):222–235

Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363:234–240

Mkhabela MS, Amiro BD, Barr AG et al (2009) Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests. Agr For Meteorol 149(5):783–794

Mu C, Lu H, Wang B, Bao X, Cui W (2013) Short-term effects of harvesting on carbon storage of boreal *Larix gmelinii—Carex schmidtii* forested wetlands in Daxing'anling, northeast China. For Ecol Manage 293:140–148

Oliver CD, Larson BC (1996) Forest stand dynamics. Wiley, New York

Pennanen J, Kuuluvainen T (2002) A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. For Ecol Manage 164:157–175

Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biol 10(12):2052–2077

Reineke LH (1933) Perfecting a stand density index for even-aged forest. J Agric Res 46:627–638

Running SW (1994) Testing FOREST-BGC ecosystem process simulations across a climatic gradient in Oregon. Ecol Appl 4(2):238–247

Rykiel EJ Jr (1996) Testing ecological models: the meaning of validation. Ecol Model 90:229–244

Scheller RM, Mladenoff DJ (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol Model 180:211–229

Scheller RM, Mladenoff DJ (2007) An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. Landscape Ecol 22:491–505

Scheller RM, Hua D, Bolstad PV, Birdsey RA, Mladenoff DJ (2011a) The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. Ecol Model 222:144–153

Scheller RM, Van Tuyl S, Clark KL, Hom J, La Puma I (2011b) Carbon sequestration in the New Jersey Pine Barrens under different scenarios of fire management. Ecosystems 14(6):987–1004

Schumacher S, Bugmann H, Mladenoff DJ (2004) Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecol Model 180:175–194

Shifley SR, Thompson FR III, Dijak WD, Fan Z (2008) Forecasting landscape-scale, cumulative effects of forest management on vegetation and wildlife habitat: a case study of issues, limitations, and opportunities. For Ecol Manage 254:474–483

Shifley SR, Rittenhouse CD, Millspaugh JJ (2009) Validation of landscape-scale decision support models that predict vegetation and wildlife dynamics. In: Millspaugh JJ, Thompson FR III (eds) Models for planning wildlife conservation in large landscapes. Academic Press, Burlington, MA, pp 415–448

Sitch S, Huntingford C, Gedney N et al (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biol 14(9):2015–2039

Steenberg JW, Duinker PN, Bush PG (2013) Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. Ann For Sci 70(1):61–73

Stocks B (1989) Fire behavior in mature jack pine. Can J For Res 19(6):783–790

Taylor AR, Wang JR, Kurz WA (2008) Effects of harvesting intensity on carbon stocks in eastern Canadian red spruce (Picea rubens) forests: an exploratory analysis using the CBM-CFS3 simulation model. For Ecol Manage 255:3632–3641

Thomas SC, Malczewski G, Saprunoff M (2007) Assessing the potential of native tree species for carbon sequestration forestry in Northeast China. J Environ Manage 85(3):663–671

Thompson JR, Foster DR, Scheller R, Kittredge D (2011) The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. Ecol Appl 21:2425–2444

Wang C (2006) Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. For Ecol Manage 222:9–16

Wang X, Feng Z, Ouyang Z (2001) The impact of human disturbance on vegetative carbon storage in forest ecosystems in China. For Ecol Manage 148:117–123

Wang WJ, He HS, Spetich MA et al (2013) A large-scale forest landscape model incorporating multi-scale processes and utilizing forest inventory data. Ecosphere 4(9):art106

Ward BC, Mladenoff DJ, Scheller RM (2005) Simulating landscape-level effects of constraints to public forest regeneration harvests due to adjacent residential development in northern Wisconsin. For Sci 51(6):616–632

Xu HC (1998) Forest in Great Xing'an Mountains of China. Science Press, Beijing

Xu C, He HS, Hu Y et al (2004) Assessing the effect of cell-level uncertainty on a forest landscape model simulation in northeastern China. Ecol Model 180(1):57–72

Xu C, Güneralp B, Gertner GZ, Scheller RM (2010) Elasticity and loop analyses: tools for understanding forest landscape response to climatic change in spatial dynamic models. Landscape Ecol 25:855–871

Yang J, He HS, Gustafson EJ (2004) A hierarchical fire frequency model to simulate temporal patterns of fire regimes in LANDIS. Ecol Model 180:119–133

Yang J, He HS, Shifley SR (2008) Spatial controls of occurrence and spread of wildfires in the Missouri Ozark Highlands. Ecol Appl 18:1212–1225

Zhao M, Zhou G-S (2005) Estimation of biomass and net primary productivity of major planted forests in China based on forest inventory data. For Ecol Manage 207(3):295–313

Zhu B, Wang X, Fang J et al (2010) Altitudinal changes in carbon storage of temperate forests on Mt Changbai, Northeast China. J Plant Res 123(4):439–452