The impact of climate variation and disturbances on the carbon balance of forests in Hokkaido, Japan

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Abstract

We evaluated the long-term effect of climate, disturbance, and subsequent recovery on the carbon balance of temperate-boreal forest using the process-based ecosystem model VISIT. The study sites are artificial larch forests, which were planted after clear-cutting of mixed forest, in Hokkaido, Japan. In this study, three experimental simulations were conducted. First, we performed a baseline simulation of carbon dynamics and compared these values with those observed across a wide range of stand ages (old mixed forest and young and middle-aged larch forests). Second, we ran attribution simulations to investigate how disturbance and several climate factors affect long-term carbon fluxes. Third, we analyzed the sensitivity of carbon balance to the amount of disturbance-generated residues. By taking into account seasonal variation in the understory leaf area index, which played an important role especially in the initial stage of recovery, simulated net ecosystem production (NEP), gross primary production, ecosystem respiration, and biomass for the three types of forests were consistent with observed values. The effect of disturbances such as clear-cutting, land-use conversion, and thinning on the long-term trend of NEP was larger than that of climate variation, even several decades after clear-cutting. In contrast, interannual variation in the carbon balance was primarily attributable to climate variation. These findings indicate that disturbance controlled the long-term trend of the carbon balance, whereas climate factors controlled yearly variation in the carbon balance. Among the meteorological factors considered, temperature and precipitation mainly affected NEP and its interannual variation. The carbon balance in the initial post-disturbance period, which is strongly affected by the amount of residues, influenced the subsequent long-term carbon budget, implying the importance of residue management. Consequently, carbon release just after disturbance and the length of the recovery period required to pay back the carbon debt are controlled by the amount of residues.
1 Introduction

Changes in carbon flux and storage in forest ecosystems are influenced by climate at various temporal and spatial scales, whereas carbon flux and storage are affected instantaneously and heterogeneously by artificial and natural disturbances at the local scale. The time course of net ecosystem production (NEP) is affected by climate conditions, because biochemical processes such as photosynthesis, respiration, phenology, and allocation all respond to climate (Hirata et al., 2008; Saigusa et al., 2008; Reichstein et al., 2013). Disturbance events also drastically change NEP and carbon storage. Forests in boreal and tropical regions have frequently lost large carbon stocks due to wildfires (Pan et al., 2011; Hirano et al., 2012; Ueyama et al., 2013), and damage by insects has had a similar impact on forest ecosystems (Kurz et al., 2008a). Several years after disturbance, however, regenerated forests become carbon sinks because the net production of a young forest is higher than that of an old forest (Pan et al., 2011). After several decades, NEP tends to approach an equilibrium state (Janisch and Harmon, 2002; Goulden et al., 2011). The drastic changes of carbon flux caused by disturbance in forest ecosystems affect global climate (Dale et al., 2001; Turner, 2010). Although large carbon emissions caused by disturbance may accelerate global warming, enhanced carbon sinks after disturbance mitigate global warming (Pan et al., 2011). Despite these previous findings, the effects of forest disturbance on global climate remain to be clarified (Kurz et al., 2008b).

The effects of disturbance and subsequent recovery on the carbon balance are attributable to carbon uptake by regrowing trees and carbon loss by decomposition of dead wood (residues; Janisch and Harmon, 2002; Grant et al., 2010; Goulden et al., 2011). Therefore, controlling the degree of disturbance and recovery of forest vegetation and managing residues are expected to mitigate global warming by reducing carbon emission and enhancing carbon absorption (Liu and Han, 2009). By clarifying the mechanisms underlying the carbon balance in forest ecosystems and the effects of carbon management practices, researchers can apply these lessons to mitigate climate change.
change, as outlined in the Kyoto Protocol, Clean Development Mechanism (CDM) and Reducing Emissions from Deforestation and Forest Degradation, improve conservation, devise sustainable management techniques for forests, and enhance forest carbon stocks in developing countries (REDD-plus). From a long-term perspective, it is easier to maintain or enhance the function of carbon sinks in managed forests than in unmanaged forests, and the management of carbon sinks was adopted by the Kyoto Protocol and the subsequent international framework under the Durban platform.

The eddy covariance technique is a useful tool for investigating the interaction between terrestrial ecosystems and the atmosphere and evaluating the carbon balance. Despite the technique’s utility, understanding these systems requires continuous and long-term measurement of fluxes. The longest-running measurement of eddy flux was started in 1990 in Harvard forest (Urbanski et al., 2007), and the measurement period at most sites in Asia is less than 10 yr (Mizoguchi et al., 2008). In addition, eddy flux measurements just after disturbance have been conducted at only a few forest sites (Kowalski et al., 2004; Takagi et al., 2009). However, understanding the effect of disturbance on the carbon balance requires data gathered over several decades, from the time the disturbance occurred until the forests reached the mature stage (Janisch and Harmon, 2002; Grant et al., 2010; Goulden et al., 2011). The changes in carbon stock and carbon flux caused by disturbance have been investigated using the chronosequence approach, in which flux measurements are made in similar forest stands that differ in age (Howard et al., 2004; Amiro et al., 2006, 2010; Zha et al., 2009; Goulden et al., 2011). Numerical simulation using ecosystem models also has been used to evaluate the long-term effect of disturbance and recovery on the carbon balance (Janisch and Harmon, 2002; Taylor et al., 2008; Ito, 2012). Studies combining the chronosequence approach and ecosystem models also have been conducted (Law et al., 2004; Grant et al., 2010).

The objective of this study was to evaluate the long-term effect of disturbance and subsequent recovery on the carbon balance of forest ecosystems. We hypothesize that (1) the carbon balance of a forest ecosystem is controlled by the amount of residues,
that is, the dead biomass produced by the disturbance and left at the site; and (2) the period required for the carbon balance to be restored can be controlled by the management of residues. The study sites were artificial larch (Larix spp.) forests in Hokkaido, Japan, that were planted after clear-cutting of mixed stands. First, we validated the ecosystem model using flux data obtained from a wide range of stand ages, including an old forest before disturbance, a young forest just after disturbance, and a middle-aged forest. Second, we used the model to investigate which factors influence the long-term carbon balance from a young stage to a middle-aged stage. Finally, we analyzed the sensitivity of the carbon balance to the amount of residues.

2 Materials and methods

2.1 Site description

Carbon flux data were obtained from two temperate larch forests at different ages in Hokkaido, which is the northernmost island in Japan. One was a young larch forest planted after clear-cutting a conifer–hardwood mixed forest in the Teshio Experimental Forest of Hokkaido University (TSE site, 45°03′ N, 142°06′ E; Fig. 1), and the other was a middle-aged larch forest at the Tomakomai flux research site (TMK site, 42°44′ N, 141°31′ E). The characteristics of the Teshio and Tomakomai sites are listed in Table 1. The Gleyic Cambisol soil of the Teshio site is more fertile than the volcanogenic regosol soil of the Tomakomai site. At both sites, the forest floor is covered with a thick understory, which mainly consists of evergreen dwarf bamboos at Teshio and ferns at Tomakomai. The details of the Teshio and Tomakomai sites were described by Takagi et al. (2009) and Hirata et al. (2007), respectively.

The Teshio site had been a mature (∼200 yr old) mixed forest in the late successional stage. In December 1972, it was damaged by strong wind caused by a blizzard and some trees were blown down. From January to March 2003, the trees at the site were clear-cut, with 55% of the logs removed and the residual biomass remaining in the
forest. The Sasa understory was then strip-cut into 4 m wide strips, and 2 yr old hybrid larch trees were planted in the spaces between the strips (Takagi et al., 2009). At the Tomakomai site, Japanese larch was planted in 1958 after the forest was devastated by strong wind caused by typhoon Toyamaru in 1954. Thinning was conducted in 1970, 1985, and 2004.

2.2 Data processing

In the model simulations (for model description, see Appendix A), we used CO₂ flux data collected by using the eddy covariance method at flux towers as well as climate data gathered at the Teshio and Tomakomai sites. The details of tower equipment and instruments were described by Takagi et al. (2009) for Teshio and Hirata et al. (2007) for Tomakomai. The eddy covariance method provided half-hourly NEP measurements, which were partitioned into gross primary production (GPP) and ecosystem respiration (RE). RE was obtained from the relationship between nighttime NEP and temperature, and GPP was obtained by subtracting RE from NEP. The data processing, quality control, gap-filling, and partitioning into GPP and RE were described by Hirata et al. (2008) and Takagi et al. (2009). In this study, we used 1 yr of data (2002) for ~ 200 yr old mixed forest at the Teshio site; 10 yr of data (2003–2012) for young larch forest at Teshio, which ranged in age from 1 to 10 yr old during that period; and 3 yr of data (2001–2003) for the middle-aged larch forest at the Tomakomai site, which ranged in age from 44 to 46 yr (Table 1).

2.3 Model application

To simulate the carbon cycles of the larch forests at Teshio and Tomakomai, we adapted the Vegetation Integrative Simulator for Trace Gases (VISIT) model (Ito, 2010), which was developed based on a simple carbon cycle model (Sim-CYCLE; Ito and Oikawa, 2002) and subsequently improved (Ito et al., 2005). Details of the VISIT were described in Appendix A.
The VISIT model has been modified by using flux tower data obtained from the AsiaFlux database, including middle-aged larch forest at the Tomakomai site and mature mixed forest at the Teshio site, and carbon fluxes simulated with the amended model showed good agreement with observed values (Ito, 2008; Ichii et al., 2010, 2013). However, the VISIT model has not been validated for young forest during the initial stage of growth. Takagi et al. (2009) reported that understory played an important role in the carbon balance of young larch forest at the TSE site. Under the scheme of the conventional VISIT model (Ito et al., 2006), however, the understory was treated as evergreen vegetation and it did not show apparent seasonal variations. Before we conducted the analysis, we modified the model to correct the problem noted by Takagi et al. (2009).

To strengthen the role of the understory in the carbon balance, we modified the phenology of the understory by treating it as deciduous plants and changing the parameter values of specific litter fall rate (A. 6). As a result, in the modified VISIT model, LAI of the understory showed seasonal variation and the understory absorbed more CO₂ and grew faster than in the conventional model.

The model was initialized by a spin-up run for 2000 yr to create the dynamic equilibrium of soil organic matter and vegetation components using the observational climate data from 2002 to 2012 for the Teshio site and from 2001 to 2003 for the Tomakomai site, respectively. To simulate long-term carbon fluxes at the Tomakomai site, we used long-term daily meteorological data derived from a reanalysis of a global climate dataset produced from 1948 to 2010 based on merging the US National Centers for Environmental Prediction and the US National Center for Atmospheric Research (NCEP/NCAR; Kistler et al., 2001) and Climatic Research Unit time-series datasets (CRU TS3.1; Mitchell and Jones, 2005) corrected by in situ observational data. Details of climate dataset were described in Ichii et al. (2013). CO₂ concentrations were constant from the first year of observation. After the spin-up run, an actual simulation was conducted for the observation period for each site and for the long-term period for Tomakomai. The atmospheric CO₂ concentration was gradually increased from 378 ppm in 2002 to 404 ppm in 2012 for Teshio, from 375 ppm in 2001 to 380 ppm in
2003 for Tomakomai and from 312 ppm in 1948 to 398 ppm in 2010 for long-term simulation for Tomakomai. We implemented disturbance events following the site histories as much as possible. In the case of Teshio site, mix forest was devastated and regrown in 1800 so that 90% of foliage and stem and 80% of root were exported and residues were moved to litter compartments as dead vegetation. Because of blizzard in 1972, half of trees were exported. In order to simulate conversion of mix forest to larch forest (clear-cutting and planting larch) in 2003, 55% of stem were removed as wood harvest and the residues remained in forest floor as dead stem (Takagi et al., 2009). Whole foliage and root were also moved to litter compartments. In the case of Tomakomai, the information before the larch plantation was initiated in 1958 and the manner of thinning are not clear. Therefore, we applied the same conditions as at the TSE site to the Tomakomai site before plantation initiation. Mix forest was devastated and regrown in 1760. We implemented a disturbance in 1930 and half of trees were exported. Mix forest was converted to larch forest (clear-cutting and planting larch) in 1958. When thinning was implemented in 1970, 1985 and 2004, 30% of lived stem was exported and 30% of lived foliage and root were moved to litter compartments. The intensity of thinning followed the general manner in Japan.

2.4 Attribution experiment

A series of scenarios was designed to examine the attribution of long-term carbon fluxes to disturbance and individual climate factors at the Tomakomai site. We compared carbon fluxes calculated using historical climate data with constant scenarios, which was an ensemble average of 1948–2010 and the same seasonal variation from 1958, when clear-cutting occurred and the plantation was initiated. In this study, we focus on three types of disturbances: (1) clear-cutting; (2) conversion, in which the mixed forest was clear-cut and larch was planted; and (3) thinning, in which 30% of forest biomass was cut and exported. VISIT was run for 10 scenarios (Table 2). The effect of climate, temperature, precipitation, solar radiation, VPD, CO$_2$, conversion, and clear-cutting were evaluated by subtracting $S_{\text{const-climate}}$, $S_{\text{const-Ta}}$, $S_{\text{const-rain}}$, $S_{\text{const-Sd}}$, $S_{\text{const-Conv}}$, $S_{\text{const-Cc}}$. 
$S_{\text{const-VPD}}, S_{\text{const-CO}_2}, S_{\text{non-conv}}$ and $S_{\text{non-cut}}$ from $S_{\text{non-thin}}$. The effect of thinning was evaluated by subtracting $S_{\text{non-thin}}$ from $S_{\text{full}}$.

2.5 Ecosystem compensation points

To evaluate the recovery of carbon fluxes after clear-cutting disturbance, we used three indices of ecosystem compensation points. These indices provide useful information for carbon management related to disturbance.

To understand when the ecosystem reverts to absorbing carbon in the recovery phase on an annual basis, we used the ecosystem compensation point for annual NEP (ECP$_{\text{NEP}}$), which is the number of years until the ecosystem shifts from being an annual carbon source caused by disturbance to being an annual carbon sink. Kowalski et al. (2004) first used this term, but Thornton et al. (2002) called it the “length of the source period.”

Despite the ecosystem reverting to net CO$_2$ fixation at the ECP$_{\text{NEP}}$, the ecosystem was still under a carbon debt because carbon was released after the disturbance prior to the ECP$_{\text{NEP}}$. Therefore, we need to account for the carbon release before the ECP$_{\text{NEP}}$ when we consider carbon management after disturbance. Here, we use the ecosystem compensation point for cumulative NEP (ECP$_{\text{CNEP}}$), which is the number of years until cumulative NEP shifts from negative to positive after the disturbance, and this represents how long it takes to pay back the carbon released after the disturbance.

If cut logs or fallen trees burn and the carbon is released into the atmosphere immediately, we also need to take this carbon into account. The third index is the ecosystem compensation point for cumulative net ecosystem carbon balance (NECB) (ECP$_{\text{CNECB}}$), which is the number of years until cumulative NECB shifts from negative to positive after the disturbance. NECB is calculated by subtracting exported carbon from NEP and adding imported carbon.
2.6 Sensitivity test

We conducted a sensitivity test for the strength of disturbance. The proportions of the carbon emission were set to three scenarios; (1) emission of logs is 0% and that of residue is 100% ($S_{E0R100}$); (2) emission of logs is 50% and that of residue is 50% ($S_{E50R50}$); and (3) emission of logs is 100% and that of residue is 0% ($S_{E100R0}$).

3 Results

3.1 Model validation

The results of the simulation were compared with observed NEP, GPP, and RE. Modeled carbon fluxes calculated from all of three forest types, the mature mixed forest (2002 in Teshio, Fig. 2), young larch forest (2003–2012 in Teshio), and middle-aged larch forest (2001–2003 in Tomakomai), matched well with those derived from field observations. Model output of monthly carbon fluxes also agreed well with observed values (Fig. 3).

The mature mixed forest absorbed CO$_2$ during the growing season, but NEP shifted from positive to negative after clear-cutting and planting of larch trees in 2003 because of an abrupt decrease in GPP. After that, CO$_2$ release from the ecosystem decreased with the increase of GPP. Based on field observations, apparent CO$_2$ absorption during the growing season began in 2008, and the ecosystem reverted to fixing CO$_2$ annually (0.5 tCha$^{-1}$ yr$^{-1}$) in 2010. The NEP derived from the model was similar to the observed seasonal and interannual patterns, although annual NEP changed from negative to positive in 2009 (1.6 tCha$^{-1}$ yr$^{-1}$). GPP showed a drastic change after clear-cutting, whereas the change in RE was small according to both observations and the simulation (Teshio in Fig. 2). At the Tomakomai site, the peak of NEP occurred in early summer and then a rapid decrease was observed in midsummer (Hirata et al., 2007), and the model successfully simulated seasonal and interannual patterns of NEP, GPP,
and RE observed at Tomakomai. Overall, the model output was consistent with observed fluxes, so we used the model to evaluate the long-term effect of disturbance on carbon fluxes.

The simulated biomass of trees (56 tCha\(^{-1}\)) of the middle-aged larch forest at Tomakomai was close to that observed (52 tCha\(^{-1}\)). Simulated plant biomass of the mature mixed forest (90 tCha\(^{-1}\)) was also close to the observed value (99 tCha\(^{-1}\); Aguilos et al., unpublished data). Simulated vegetation carbon increment of the young larch forest at Teshio from 2003 to 2009 was 22 tCha\(^{-1}\), which was a bit larger than the observed value (17.2 tCha\(^{-1}\); Aguilos et al., unpublished data).

### 3.2 Attribution experiment

Simulated long-term NEP is shown in Fig. 4a. There was an abrupt shift from carbon sink to source after clear-cutting and conversion of the mixed forest to a larch plantation at the Tomakomai site, followed by a decrease of carbon release, and the return to being a carbon sink. This pattern was similar to the interannual pattern of NEP observed in the young larch forest at Teshio from 2002 to 2012. After that, NEP increased asymptotically, with fluctuations.

We analyzed how carbon fluxes were affected by climate, CO\(_2\), clear-cutting, conversion, and thinning (Fig. 4, Table 3). The effect of disturbance and climate factors on annual NEP and long-term trends of each effect were evaluated by time-averaging the effect for each decade after clear-cutting in 1958 (Table 3). However, by calculating the time-average, we found that the positive and negative fluctuations of the effects compensated each other; therefore, the standard deviation of the effect was also used for evaluating the effect of interannual variation in each factor (Table 3). NEP declined immediately after clear-cutting (Fig. 4a), and the effect of this disturbance was much larger than the effect of climate variation (Fig. 4b, Table 3). In the second decade after clear-cutting, the effects of clear-cutting on NEP shifted from negative to positive (Fig. 4b, Table 3). Clear-cutting still affected the average NEP, and the effect was larger than that of climate even 50 yr after this disturbance (Fig. 4b, Table 3). However, climate
had a relatively large effect on the interannual variation of NEP at 30 yr after clear-cutting (Table 3), which indicates that the amplitude of the annual NEP was driven by climate variation, whereas the long-term trend in NEP resulted from the disturbance that had occurred several decades previously.

The effect of clear-cutting on GPP approached zero about 15 yr after the disturbance (Fig. 4c), suggesting that after this period, the growth rate of post-harvest forest was similar to that of intact forest. The effect of clear-cutting on RE was continuously negative, even after 50 yr (Fig. 4d). Even though the GPP (or NPP) of clear-cut forest was similar to that of intact forest, there was less dead biomass, which determines RH (A.5), in the disturbed forest. Consequently, clear-cutting reduced RH (Fig. 4e). Thus, although CO₂ absorption by plants recovered to a level similar to that of intact forest several decades after clear-cutting, the decomposition rate was reduced because the amount of litter decreased.

The effect of conversion to a plantation on all carbon fluxes was positive a decade after clear-cutting (Fig. 4b–e, Table 3). Conversion to a larch plantation had a large effect on GPP, RE, and RH because GPP and RH in larch forest were larger than these values in mixed forest. However, the effect of conversion on NEP was less than those on other flux components because increased GPP was offset by increased RE.

Only the second and third thinning in 1985 and 2004 enhanced NEP (Fig. 4b, Table 3). The reason is that thinning events decreased RE and RH in 1985 and 2004 (Fig. 4d and e), whereas the effect on GPP was small (Fig. 4c). Each thinning event reduced the decomposition rate because the litter supply was reduced. However, the extra growth of the remaining trees compensated for the removed trees, such that GPP did not change drastically. When the first thinning was implemented, tree biomass was still small (14 t C ha⁻¹), which may explain the smaller effect of the initial thinning as compared to those of the second and third thinning.

The anomaly of the effect of climate can be separated into each meteorological component (Table 3). The abrupt decrease in NEP in 1984 (Fig. 4b) was caused by much less precipitation than normal (694 mm vs. the average of 1000 mm; Table 3), and the
interannual variation in NEP 50 yr after clear-cutting was mainly caused by air temperature (Table 3). The effects of CO$_2$ on productivity and respiration gradually increased because of elevated ambient CO$_2$ (Fig. 4, Table 3).

### 3.3 Ecosystem compensation points

The ecosystem shifted from a net carbon source to a sink (ECP$_{\text{NEP}}$) at 6 yr after clear-cutting (Fig. 4a). The total amount of carbon released before ECP$_{\text{NEP}}$ was 19 t C ha$^{-1}$ yr$^{-1}$, and 9 yr were required for the ecosystem to regain this carbon, so ECP$_{\text{CNEP}}$ was 15 yr. 8 yr were required to compensate for the carbon emission as logs, so ECP$_{\text{CNECB}}$ was 23 yr.

### 3.4 Sensitivity test

We examined the sensitivity of carbon flux to the residual biomass left at the site after clear-cutting. Figure 5 shows the results of the sensitivity analysis of carbon balance in terms of changes in the proportions of the residual debris as foliage, stems, and roots. Short-term effects are given in Table 4, which lists the annual values just after clear-cutting in 1958, and long-term effects are also shown in Table 4, which gives the cumulative annual values of carbon fluxes from 1958 to 2010.

When all of the logs were left on the forest floor ($S_{\text{E0R100}}$), the ecosystem released more carbon immediately after clear-cutting as compared with the other two scenarios ($S_{\text{E50R50}}$ and $S_{\text{E100R0}}$), and the least carbon was released when all the logs were exported ($S_{\text{E100R0}}$; Fig. 5a, NEP of $S_{\text{E100R0}}$ in Table 4). Therefore, the longest and the shortest ECP$_{\text{NEP}}$ were found in the scenarios $S_{\text{E0R100}}$ (9 yr) and $S_{\text{E100R0}}$ (5 yr), respectively (Fig. 5a, ECP$_{\text{NEP}}$ in Table 4). ECP$_{\text{NEP}}$ of $S_{\text{E50R50}}$ had an intermediate value of 6 yr.

Over the 52 yr, cumulative NEP in $S_{\text{E100R0}}$ was almost twice that in $S_{\text{E0R100}}$ (Fig. 5b, NEP in Table 4). This is attributed to the difference of RH through RE, even though RH in $S_{\text{E100R0}}$ was only 13 % larger than that in $S_{\text{E0R100}}$ (RH in Table 4). Cumulative
NEP strongly affected $ECP_{\text{CNEP}}$. The $ECP_{\text{CNEP}}$ of $S_{E0R100}$ and that of $S_{E100R0}$ were the longest (24 yr) and the shortest (11 yr), respectively, showing the same order as cumulative NEP (Fig. 5b, $ECP_{\text{CNEP}}$ in Table 4). However, $ECP_{\text{CNECB}}$ showed the opposite order: $ECP_{\text{CNECB}}$ of $S_{E100R0}$ and $S_{E0R100}$ were the longest (35 yr) and shortest (24 yr), respectively (Fig. 5c, $ECP_{\text{CNECB}}$ in Table 4).

4 Discussion

According to our simulations of temperate-boreal forest using the VISIT model, the effect of disturbance such as clear-cutting, conversion, and thinning on the long-term trend of NEP is larger than that of climate variation, even several decades after clear-cutting. Ito (2012) also reported that the effect of disturbance on NEP is larger than of climate factors in deciduous broad-leaf forest in Japan. We found that interannual variation in the carbon balance was primarily attributed to climate variation. These findings indicate that disturbance controlled the long-term trend of the carbon balance, whereas climate factors controlled the yearly variation.

4.1 The role of disturbance

In most cases, observation using the eddy covariance method detects carbon fluxes at one point within a long-term temporal sequence. Although the VISIT model could successfully simulate the carbon balance during several decades after disturbance without correct information about the amount of the residues as the initial condition (Fig. 5a), residual biomass strongly affected the carbon balance in the first decade after disturbance (Fig. 5, Table 4). When we evaluate carbon debt and compensation periods for proper carbon management, we must consider not only the short-term carbon balance during the observation period but also the long-term sequential carbon balance after disturbance. The carbon balance in the initial period, which is strongly affected by the amount of residues, is important for long-term sequential carbon fluxes.
In addition, even several decades after the disturbance, the effect of clear-cutting on NEP was ascribed to decreased RH because the production of dead biomass decreased, which was consistent with the findings of Noormets et al. (2012). Therefore, treatment of residues plays an important role in long-term carbon balance and carbon management. Using a Monte Carlo simulation in a forest ecosystem in Washington State, Janisch and Harmon (2002) showed that the length of the NEP recovery period, which ranged from 0 to 57 yr after disturbance, depended on the amount of residues. By applying the Biome-BGC model to a forest damaged by harvest and wildfire, Thornton et al. (2002) also showed that the NEP recovery period and carbon lost during this period depended on woody debris remaining on the site after the disturbance.

Thinning is useful for enhancing NEP by decreasing RH, especially in middle-aged forests. By applying a carbon budget model to eastern Canadian red spruce forests, Taylor et al. (2008) reported that thinning enhanced carbon assimilation because of increased productivity and reduced decomposition rate, which is consistent with our results. Dore et al. (2012) showed that thinning stimulated carbon sink of ponderosa pine forest in northern Arizona 3 or 4 yr after thinning because thinning mitigated drought stress for carbon uptake. They indicated that the effect of thinning was smaller than that of wildfire, which is similar to our results. They also mentioned that it was difficult to detect the effect of thinning by using eddy covariance measurements, which is similar to the observational results of Scots pine forest presented by Vesala et al. (2005). Vesala et al. (2005) indicated the reason of unaltered CO₂ flux by thinning is that increased carbon absorption canceled out increased heterotrophic respiration, which is opposite to our results. In their study, logging waste by thinning increased on the forest floor, whereas the effect of additional litter produced by thinning was small in our simulation. Although our simulation clearly showed the effect of thinning, it might difficult to detect it using field observation.
4.2 The role of climate factors

Variations of temperature and precipitation especially affected interannual variation of NEP. Both of them directly affect both GPP (or NPP) and RH via their effects on photosynthesis and respiration, whereas solar radiation and VPD directly affect only GPP. However, RH is indirectly influenced by solar radiation and VPD via biomass change, because RH is influenced by the amount of dead biomass, which is influenced by NPP via the change in live biomass.

Less annual precipitation critically decreased annual NEP, as supported by the attribution experiments. In the late 2000s, NEP decreased as temperature increased. This finding suggests that global warming might reduce carbon uptake by larch forest at the Tomakomai site because enhanced RE would be larger than enhanced GPP.

In deciduous broad-leaf forest in central Japan, Ito (2012) reported that temperature was the meteorological factor with the largest effect on NEP, which is similar to our results. However, in that study increasing temperature increased NEP, whereas we found the opposite, and precipitation did not affect NEP, also in contrast to our result. By applying an ecosystem model to future climate scenarios in aspen and jack pine forests in Saskatchewan, Canada, Wang et al. (2012) projected higher NEP under wet conditions than under dry conditions, which is consistent with our results. Yi et al. (2013) analyzed the effect of climate and fire on the carbon flux in a boreal and arctic ecosystem using field and satellite observations and a satellite-oriented model. They found that NEP recovery after wildfire was enhanced under warmer conditions and was reduced under drought conditions, which is similar to our results. However, they also reported that the effect of drought and temperature on NEP was larger than that of wildfire in most boreal and arctic areas, which was the opposite of our results. Sensitivity analysis using the Biome-BGC model showed that spring temperature and summer solar radiation were the primary factors that affected NEP based on three-year data (2001–2003) at the Tomakomai site (Ueyama et al., 2010), as also noted in our study, but precipitation did not influence NEP. Ueyama et al. (2010) added biases each season, whereas we found
a most severe drought year in 1984 (694 mm), which was lowest precipitation in this six decades. Thus, we noted a critical effect on carbon balance. In monsoonal Asia, it might be difficult to detect reduced carbon uptake caused by severe droughts based on observation because there are few severe drought events (long-term-mean annual precipitation is about 1000 mm at the Tomakomai and Teshio sites) compared with North America or Europe. Saigusa et al. (2005) indicated that moderate droughts condition may not reduce GPP but enhance it because of prolonged growing season. However, our results indicated that severe droughts strongly effected on carbon balance similar to tropical forest in East Asia (Saigusa et al., 2008), and the effect of a severe drought in 1984 was larger than that of thinning.

4.3 The ecosystem compensation points

The simulated $ECP_{NEP}$ of the Tomakomai site (6 yr) was close to observational $ECP_{NEP}$ calculated by eddy flux data, which was 7 yr at the Teshio site. $ECP_{CNEP}$ and $ECP_{CNECB}$ were 8–34 and 20–91 yr, respectively based on observational and previously published data for the Teshio site (Aguilos et al., unpublished data). The simulated $ECP_{CNEP}$ (16 yr) and $ECP_{CNECB}$ (31 yr) of the Tomakomai site were within these ranges. According to Aguilos et al. (unpublished data), $ECP_{NEP}$ in disturbed forests in cool temperate or boreal regions ranges from 7 yr (clear-cut boreal upland forest in Canada; Howard et al., 2004) to 20 yr (wildfire-damaged boreal forests in North America; Amiro et al., 2010; Grant et al., 2010) and $ECP_{CNEP}$ is from 3–17 yr (clear-cut boreal upland forest in Canada; Howard et al., 2004) to 11–92 yr (wildfire-damaged boreal forest in Canada; Goulden et al., 2011). The both $ECP_{NEP}$ and $ECP_{CNEP}$ values of the Tomakomai and Teshio sites were smaller than these values or at the lower limit. The reasons for this are that larch forests have a high photosynthetic capacity (Hirata et al., 2007), and the sites’ dense understories contributed to a large GPP in the initial period after disturbance (Takagi et al., 2009), such that the recovery period tends to be faster than in other forest types.
The ecosystem compensation point is controlled by the amount of residues and annual NEP after disturbance. As residual biomass increases, the ecosystem compensation point becomes longer. As annual NEP increases, the ecosystem compensation point becomes shorter. Therefore, not only ecosystem productivity but also residues related to forest practice are key factors in the carbon recovery period.

If logs are used as semi-permanent wood products, such as houses or furniture, fixed carbon should be considered when determining \(ECP_{\text{CNEP}}\). However, if carbon is emitted into the atmosphere immediately when logs are burned at the site, or when wildfire occurs instead of clear-cutting, \(ECP_{\text{CNECB}}\) should include such carbon emissions. Ideally, to pay back carbon emissions as soon as possible, all logs should be used for wood production (Liu and Han, 2009). If logs are used as biofuel, this compensates for the effects of fossil fuel consumption (Taylor et al., 2008; Reinhardt and Holsinger, 2010). The ecosystem compensation point is a useful index when considering the optimal carbon management like life cycle assessment (Petersen and Solberg, 2005).

When disturbance occurs, leaving logs on the forest floor \(S_{\text{EO}}R_{100}\) is a better management practice than releasing carbon by burning logs \(S_{\text{E100R0}}\). When logs are left as dead trees in the forest, recalcitrant organic matter remains and increases soil organic matter for several decades, whereas easily decomposable organic matter oxidizes into \(\text{CO}_2\) in a relatively short period. In contrast, all the carbon is emitted to the atmosphere in the case of \(S_{\text{E100R0}}\). This difference in the treatment of logs causes an 11 yr difference between \(S_{\text{E100R0}}\) and \(S_{\text{EO}}R_{100}\). In most cases, it is difficult to know the correct amount of residues to leave at the site, but \(ECP_{\text{CNECB}}\) is assumed to be the value between \(S_{\text{E100R0}}\) and \(S_{\text{EO}}R_{100}\).

5 Conclusion

We hypothesize that the carbon balance of a forest ecosystem is controlled by the amount of residues and the recovery period can be controlled by the management
of residues. The amount of residues strongly affected carbon release just after clear-cutting as well as the recovery period for NEP. These findings suggest that reducing the amount of residues could suppress negative NEP in the post-harvest forest and shorten the NEP recovery period if logs could be used as semi-permanent wood products. Leaving logs on the forest floor is a better management practice than burning the logs, which immediately releases the carbon into the atmosphere.

Appendix A

Model description

VISIT simulates carbon, water, and nutrient cycles of terrestrial ecosystems, including vegetation and soil, and evaluates the exchange of greenhouse gases (CO₂, CH₄, N₂O) between the atmosphere and terrestrial ecosystems. The model can provide daily components of the carbon balance, including NEP, GPP, RE, net primary production (NPP), biomass, and soil organic matter, by simulating biogeochemical and hydrologic processes. Input daily meteorological data are air temperature, precipitation, solar radiation, and the vapor-pressure deficit (VPD). The structure of VISIT is a simplified compartment scheme representing vegetation and soil carbon stocks. The vegetation compartment is composed of canopy tree and understory compartments, each of which consists of foliage, stem, and root compartments. The soil compartment is composed of litter and humus pools. The litter pool is divided into dead leaf, dead stem, and dead root compartments, and the humus pool is divided into active, intermediate, and passive organic decomposed carbon pools.

The GPP of an ecosystem is calculated as the sum of canopy and understory GPP as a result of photosynthetic activity, as based on dry-matter production theory (Monsi and Saeki, 1953). The attenuation of incident light intensity in the canopy is expressed
as follows:

\[ I = I_0 \exp(-KL_{\text{A}}) \]  
(A1)

where \( I \) and \( I_0 \) are the photosynthetic photon flux density (PPFD) within and above the canopy, respectively; \( L_{\text{A}} \) is leaf area index; and \( K \) is the extinction coefficient. Forest canopy receives the full irradiance of PPFD, whereas the understory receives an attenuated irradiance of PPFD because it is shaded by the forest canopy.

Instantaneous GPP is estimated by integrating single-leaf photosynthesis expressed by a Michaelis-type function of PPFD for \( L_{\text{A}} \) using Eq. (1). Daily GPP is calculated by integrating instantaneous GPP over day length as follows:

\[
GPP = \int_0^{L_{\text{A}}} \left( \frac{P_{\text{max}} \alpha I}{P_{\text{max}} + \alpha I} \right) dL_{\text{A}} dt 
= \frac{2P_{\text{max}}}{K} \ln \left\{ 1 + \sqrt{1 + \frac{K + \alpha I_{\text{mid}}}{P_{\text{max}}}} \right\} - \ln \left\{ 1 + \sqrt{1 + \frac{K \alpha I_{\text{mid}} \exp(-KL_{\text{A}})}{P_{\text{max}}}} \right\} 
\]  
(A2)

where \( l \) is day length, \( P_{\text{max}} \) is the maximum single-leaf photosynthetic rate under light saturation, \( \alpha \) is the light-use efficiency, \( I_{\text{mid}} \) is the irradiance of PPFD at midday, and \( t \) is time since sunrise. \( P_{\text{max}} \) is calculated from potential maximum \( P_{\text{max}} (P_{\text{max}^*}) \) suppressed by daily environmental factors, namely temperature, intercellular \( CO_2 \) concentration, and soil moisture, where the total suppression is calculated to multiply the effect of the three suppressions. \( \alpha \) is calculated from potential maximum \( \alpha (\alpha^*) \) suppressed by temperature and intercellular \( CO_2 \) concentration, where the total suppression is calculated to multiply the effect of the two suppressions. Each suppression function ranges from 0 to 1, with 0 meaning complete suppression and 1 no suppression. Air temperature is directly substituted for temperature. Intercellular \( CO_2 \) concentration is calculated from atmospheric \( CO_2 \), single-leaf photosynthetic rate, and stomatal conductance (Leuning,
1990), the last of which is derived from single-leaf photosynthetic rate, atmospheric CO$_2$, and VPD. Soil moisture is derived from the water balance of precipitation, transpiration, evaporation, interception of rainfall, and lateral flow. The details of the suppression functions were given by Ito and Oikawa (2002).

RE is calculated as the sum of autotrophic respiration (RA) and heterotrophic respiration (RH). The RA is composed of maintenance respiration (RM) and growth respiration (RG). The carbon from RH is released from two compartments: the litter and humus carbon pools.

RM is the sum of maintenance respiration of foliage, stems, and roots. Each compartment’s RM is represented by an exponential function of temperature and the amount of biomass:

$$RM_x = SRM_x \exp \left( \frac{\ln(Q_{10})}{10}(T - 15) \right) B_x$$  \hspace{1cm} (A3)

where $x$ denotes the compartments (foliage, heartwood, sapwood, coarse roots, and fine roots), $SRM$ is the specific maintenance respiration rate per unit biomass at 15°C, $Q_{10}$ is the rate of increase with a 10°C rise in temperature, $T$ is temperature, and $B$ is plant biomass.

RG represents the cost to produce new biomass and is the sum of growth respiration of foliage, stems, and roots. Each compartment’s RG is proportional to its increase of biomass:

$$RG_x = SRG_x \Delta B_x \approx SRG_x \frac{PT_x}{1 + SRG_x}$$  \hspace{1cm} (A4)

where $x$ denotes the compartments (foliage, stems, and roots), $SRG$ is specific growth respiration, and $PT$ is photosynthate translocation to each compartment. PT is the result of allocation of effective photosynthate (GPP – RM) to each compartment (foliage, stems, and roots). The details of this allocation were given by Ito and Oikawa (2002).

RH is respired carbon as a result of decomposition of litter and soil organic matter by microbial activities. RH is regulated by the soil carbon content, temperature, and soil
moisture conditions, as follows:

\[ RH_y = SRH_y C_y T_{scalar} W_{scalar} \]  \hspace{1cm} (A5)

where \( y \) indicates each compartment in litter and humus pools, \( SRH \) is specific heterotrophic respiration, \( C \) is the soil carbon content of each compartment, \( T_{scalar} \) is the modified Arrhenius-type equation (Lloyd and Taylor, 1994), and \( W_{scalar} \) is the minimum of two suppression terms: soil moisture and soil air space. The details of the functions were described by Ito and Oikawa (2002).

In the case of deciduous vegetation, such as larch forests, phenology is an important process. In the scheme of VISIT, there are four phenological periods: dormancy (from defoliation to leaf-out), emergence of new leaves, vegetative growth, and defoliation. The number of days between the beginning and end of leaf flush are determined by growing degree-days, which is the cumulative temperature above 1 °C. The number of days between the beginning and end of leaf shedding are determined by cumulative coolness (degree-days below 12 °C). In the case of evergreen vegetation, the entire period is the vegetative growth period. The details of phenology and turnover were described by Ito and Oikawa (2002) and Ito et al. (2005).

The process of litter fall or turnover brings carbon in the live vegetation compartments to the soil litter compartments. The litter fall (\( L \)) of each vegetation compartment is represented as follows:

\[ L_x = S_L x B_x \]  \hspace{1cm} (A6)

where \( S_L \) is the specific litter fall rate or turnover rate per unit biomass.

Daily NPP is the difference between GPP and RA, whereas daily NEP is the difference between NPP and RH. In this study, positive NEP represents carbon uptake by the ecosystem and negative NEP represents carbon release from the ecosystem. The biophysical process of carbon allocation, hydrological processes, and meteorological calculations were described by Ito and Oikawa (2002).
When we simulated a disturbance such as clear-cutting or thinning, all or some of the carbon in vegetation compartments was exported out of the ecosystem and the residues were moved to litter compartments. When we take exported carbon into account, it is necessary to use the net ecosystem carbon balance (NECB), which is NEP minus the exported carbon, so we performed this calculation. Because clear-cutting is often accompanied by land-use conversion (Adachi et al., 2011), ecophysiological parameters were changed from those of the former vegetation type to those of the subsequent one when a conversion event occurred. Representative ecophysiological parameters of mixed and deciduous needle-leaf forests and understory are presented in Table A1.

The VISIT model has been validated by using several flux datasets covering tropical to subarctic biomes including mature mixed forest in Teshio and middle aged larch forest in Tomakomai (Ito, 2008; Ichii et al., 2010, 2013). Parameters in Table A1 were obtained from these studies. $P_{\text{max}}$ of deciduous needle leaf forest was modified with referring maximum GPP of Tomakomai obtained form eddy covariance method (Hirata et al., 2007).

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References


### Table 1. Site descriptions.

<table>
<thead>
<tr>
<th>Site name (Site code)</th>
<th>CC-LaG experiment site, Teshio (TSE)</th>
<th>Tomakomai Flux Research Site (TMK)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>45°03’ N, 142°06’ E</td>
<td>42°44’ N, 141°31’ E</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>66</td>
<td>70</td>
</tr>
<tr>
<td>Annual mean air temperature (°C)</td>
<td>5.7</td>
<td>6.2</td>
</tr>
<tr>
<td>Annual precipitation (mmyr⁻¹)</td>
<td>1000</td>
<td>1043</td>
</tr>
<tr>
<td>Soil type</td>
<td>Gleyic Cambisol</td>
<td>Volcanogenic regosol</td>
</tr>
<tr>
<td></td>
<td>Before clear-cutting</td>
<td>After clear-cutting</td>
</tr>
<tr>
<td>Forest type</td>
<td>Conifer–Hardwood mixed forest</td>
<td>Young larch forest</td>
</tr>
<tr>
<td>Dominant species</td>
<td>Oak (<em>Quercus crispula</em>),</td>
<td>Hybrid larch</td>
</tr>
<tr>
<td></td>
<td>Birch (<em>Betula ermanii</em>),</td>
<td>(Larix <em>gmelinii</em> (Rupr.))</td>
</tr>
<tr>
<td></td>
<td>Sakhalin fir (<em>Abies sachalinensis</em>),</td>
<td>Kuzen. var. <em>japonica</em> (Maxim. ex Regel)</td>
</tr>
<tr>
<td></td>
<td>Bamboo grass (<em>Sasa senanensis</em> Rehd. and <em>Sasa kurlensis</em> (Rupr.) Makino et Shibata)</td>
<td>Plig. x <em>Larix kaempferi</em> (Lamb.) Carrière), Bamboograss (Sasa <em>senanensis</em>)</td>
</tr>
<tr>
<td>LAI (m² m⁻²)</td>
<td>7.3 (PAI) (Canopy 3.2, Forest floor 4.1)</td>
<td>9.7 (PAI) (Canopy 1.7, Forest floor 8)</td>
</tr>
<tr>
<td></td>
<td>Tree height (m)</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Flux measurement period</td>
<td>2002</td>
</tr>
<tr>
<td>Forest age (yr)</td>
<td>About 200</td>
<td>1–12</td>
</tr>
</tbody>
</table>

*Note: The abbreviations are not explained in the table.*
Table 2. Scenarios for the attribution experiment.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Temperature</th>
<th>Precipitation</th>
<th>Solar radiation</th>
<th>VPD</th>
<th>CO₂ concentration</th>
<th>Clear-cutting</th>
<th>Forest type</th>
<th>Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td>S_all</td>
<td>Full</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>occur</td>
</tr>
<tr>
<td>S_const-climate</td>
<td>Constant climate</td>
<td>constant</td>
<td>constant</td>
<td>constant</td>
<td>constant</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_const-Ta</td>
<td>Constant temperature</td>
<td>constant</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_const-ppt</td>
<td>Constant precipitation</td>
<td>historical</td>
<td>constant</td>
<td>historical</td>
<td>historical</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_const-Sd</td>
<td>Constant solar radiation</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_const-VPD</td>
<td>Constant VPD</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_const-CO₂</td>
<td>Constant CO₂ concentration</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_non-conv</td>
<td>No conversion</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>not occur</td>
<td>Larch forest continues to exist</td>
<td>not occur</td>
</tr>
<tr>
<td>S_non-cut</td>
<td>No clear-cutting</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>not occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
<tr>
<td>S_non-thin</td>
<td>No thinning</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>historical</td>
<td>not occur</td>
<td>Mix forest to larch forest</td>
<td>not occur</td>
</tr>
</tbody>
</table>

VISIT was run for climate constant (S_const-climate) which means temperature, precipitation, solar radiation and VPD were constant, temperature constant (S_const-Ta), precipitation constant (S_const-ppt), solar radiation constant (S_const-Sd), VPD constant (S_const-VPD) and CO₂ constant (S_const-CO₂). These scenarios were run with clear-cutting and conversion of mix forest to larch forest, and without thinning event. We also conducted non-conversion scenario (S_non-conv) which means a mixed forest without clear-cutting continues to exist (both clear-cutting and plantation does not occur), non-clear-cutting scenario (S_non-cut) which means a larch forest exist without clear-cutting continues to exist, and non-thinning scenario(S_non-thin) using historical climate data to examine the effect of disturbance.
Table 3. The average of the effects of climate, air temperature, precipitation, solar radiation, VPD, CO₂, clear-cutting, conversion, and thinning on NEP at the Tomakomai site for each decade after the disturbance in 1958. Positive values represent enhancement effects on each flux and negative values the opposite. Units are tCha⁻¹ yr⁻¹. The values in brackets mean standard deviations.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate</td>
<td>0.04 (0.22)</td>
<td>0.37 (0.36)</td>
<td>−0.96 (1.81)</td>
<td>0.17 (0.69)</td>
<td>0.03 (1.02)</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>−0.14 (0.38)</td>
<td>−0.15 (0.32)</td>
<td>−0.14 (0.79)</td>
<td>0.01 (0.64)</td>
<td>−0.20 (1.12)</td>
<td></td>
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<tr>
<td>Precipitation</td>
<td>0.16 (0.23)</td>
<td>0.44 (0.30)</td>
<td>−0.52 (1.37)</td>
<td>0.50 (0.43)</td>
<td>0.49 (0.48)</td>
<td></td>
</tr>
<tr>
<td>Solar radiation</td>
<td>−0.08 (0.08)</td>
<td>−0.08 (0.11)</td>
<td>0.05 (0.18)</td>
<td>0.01 (0.29)</td>
<td>−0.11 (0.17)</td>
<td></td>
</tr>
<tr>
<td>VPD</td>
<td>0.05 (0.06)</td>
<td>−0.00 (0.10)</td>
<td>−0.29 (0.22)</td>
<td>−0.17 (0.22)</td>
<td>0.01 (0.08)</td>
<td></td>
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<tr>
<td>CO₂</td>
<td>0.26 (0.12)</td>
<td>0.37 (0.06)</td>
<td>0.47 (0.12)</td>
<td>0.60 (0.11)</td>
<td>0.64 (0.10)</td>
<td></td>
</tr>
<tr>
<td>Clear-cutting</td>
<td>−4.06 (3.37)</td>
<td>1.13 (0.55)</td>
<td>1.44 (0.25)</td>
<td>1.24 (0.23)</td>
<td>0.80 (0.13)</td>
<td></td>
</tr>
<tr>
<td>Conversion</td>
<td>−0.85 (1.28)</td>
<td>1.76 (0.25)</td>
<td>0.96 (0.73)</td>
<td>0.91 (0.34)</td>
<td>0.64 (0.56)</td>
<td></td>
</tr>
<tr>
<td>Thinning</td>
<td>0.00 (0.00)</td>
<td>0.01 (0.16)</td>
<td>0.29 (0.17)</td>
<td>0.71 (0.11)</td>
<td>0.87 (0.39)</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. The sensitivity of NEP, GPP, RE, RH (upper table) and ECP (lower table) to changes in residues. In the upper table, the first row shows the values of NEP, GPP, RE, and RH immediately after clear-cutting in 1958. The second row shows the relative percentage as compared to the control experiment ($S_{E100R0}$). The third row shows the cumulative values of NEP, GPP, RE, and RH from the clear-cutting in 1958 to 2010. The forth row shows the relative percentage as compared to the control experiment ($S_{E100R0}$).

<table>
<thead>
<tr>
<th></th>
<th>$S_{E100R0}$</th>
<th>$S_{ES5R50}$</th>
<th>$S_{ES10R100}$</th>
<th>$S_{ES100R0}$</th>
<th>$S_{ES5R50}$</th>
<th>$S_{ES10R100}$</th>
<th>$S_{ES100R0}$</th>
<th>$S_{ES5R50}$</th>
<th>$S_{ES10R100}$</th>
<th>$S_{ES100R0}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Values in 1958 (tCha$^{-1}$yr$^{-1}$)</td>
<td>-5.4</td>
<td>-7.7</td>
<td>-9.9</td>
<td>6.4</td>
<td>6.4</td>
<td>6.4</td>
<td>11.8</td>
<td>14.1</td>
<td>16.3</td>
<td>9.4</td>
</tr>
<tr>
<td>Ratio (%)</td>
<td>100.0</td>
<td>141.4</td>
<td>182.8</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>119.0</td>
<td>138.0</td>
<td>100.0</td>
</tr>
<tr>
<td>Cumulative values from 1958 to 2010 (tCha$^{-1}$)</td>
<td>135.0</td>
<td>103.5</td>
<td>71.9</td>
<td>1028.6</td>
<td>1028.6</td>
<td>1028.6</td>
<td>893.5</td>
<td>925.1</td>
<td>956.7</td>
<td>496.3</td>
</tr>
<tr>
<td>Ratio (%)</td>
<td>100.0</td>
<td>76.6</td>
<td>53.2</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>103.5</td>
<td>107.1</td>
<td>106.4</td>
</tr>
<tr>
<td>ECP (yr)</td>
<td>ECP$^{\text{NEP}}$</td>
<td>5</td>
<td>6</td>
<td>9</td>
<td>11</td>
<td>16</td>
<td>24</td>
<td>ECP$^{\text{CNEP}}$</td>
<td>35</td>
<td>31</td>
</tr>
</tbody>
</table>
Table A1. Representative parameters of the VISIT model for the mixed and deciduous needle-leaf forests and understory.

<table>
<thead>
<tr>
<th>Definition</th>
<th>Term</th>
<th>Unit</th>
<th>Mixed forest</th>
<th>Deciduous needle leaf forest</th>
<th>Understory</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light attenuation coefficient</td>
<td>eK0</td>
<td>Dimensionless</td>
<td>0.48</td>
<td>0.48</td>
<td>0.7</td>
</tr>
<tr>
<td>Maximum photosynthetic rate</td>
<td>$P_{\text{max}}$</td>
<td>$\mu$molm$^{-2}$s$^{-1}$</td>
<td>13</td>
<td>27</td>
<td>12</td>
</tr>
<tr>
<td>Maximum light use efficiency</td>
<td>$\alpha^*$</td>
<td>molmol$^{-1}$</td>
<td>0.052</td>
<td>0.052</td>
<td>0.055</td>
</tr>
<tr>
<td>Specific maintenance respiration of foliage</td>
<td>SRM$_{\text{foliage}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>1.3</td>
<td>1.3</td>
<td>1.25</td>
</tr>
<tr>
<td>Specific maintenance respiration of sapwood</td>
<td>SRM$_{\text{sapwood}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.033</td>
<td>0.04</td>
<td>0.035</td>
</tr>
<tr>
<td>Specific maintenance respiration of heartwood</td>
<td>SRM$_{\text{heartwood}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.004</td>
<td>0.004</td>
<td>0.011</td>
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<tr>
<td>Specific maintenance respiration of coarse root</td>
<td>SRM$_{\text{coarse root}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.16</td>
<td>0.16</td>
<td>0.14</td>
</tr>
<tr>
<td>Specific maintenance respiration of fine root</td>
<td>SRM$_{\text{fine root}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.525</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Specific growth respiration of foliage</td>
<td>SRG$_{\text{foliage}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Specific maintenance respiration of stem</td>
<td>SRG$_{\text{stem}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.18</td>
<td>0.2</td>
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</tr>
<tr>
<td>Specific maintenance respiration of root</td>
<td>SRG$_{\text{root}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.32</td>
<td>0.35</td>
<td>0.35</td>
</tr>
<tr>
<td>Specific litter fall rate</td>
<td>SL$_{\text{foliage}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.00002</td>
<td>0.00009</td>
<td>0.00027</td>
</tr>
<tr>
<td>Specific litter fall rate</td>
<td>SL$_{\text{stem}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.0000008</td>
<td>0.00006</td>
<td>0.00035</td>
</tr>
<tr>
<td>Specific litter fall rate</td>
<td>SL$_{\text{root}}$</td>
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<td>0.00012</td>
<td>0.00067</td>
</tr>
<tr>
<td>Specific heterotrophic respiration of foliage</td>
<td>SRH$_{\text{foliage}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>1.5</td>
<td>1.4</td>
<td>–</td>
</tr>
<tr>
<td>Specific heterotrophic respiration of litter</td>
<td>SRH$_{\text{litter foli}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
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<tr>
<td>Specific heterotrophic respiration of root</td>
<td>SRH$_{\text{litter stem}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.95</td>
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<td>Specific heterotrophic respiration of active humus</td>
<td>SRH$_{\text{active}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.12</td>
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<td>Specific heterotrophic respiration of intermediate humus</td>
<td>SRH$_{\text{intermediate}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.04</td>
<td>0.15</td>
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<tr>
<td>Specific heterotrophic respiration of passive humus</td>
<td>SRH$_{\text{passive}}$</td>
<td>MgMgC$^{-1}$day$^{-1}$</td>
<td>0.01</td>
<td>0.075</td>
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</tr>
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</table>
Fig. 1. Location of the Teshio (TSE) and Tomakomai (TMK) sites on Hokkaido, Japan.
Fig. 2. Seasonal and interannual variations in NEE, GPP, and RE of the Teshio (TSE) and Tomakomai (TMK) sites. Black and grey lines represent the output of the VISIT model and the observed values, respectively. A 2 week moving window was applied to the daily values of the model and observations.
Fig. 3. The relationship between monthly NEP, GPP, and RE derived from observation and the VISIT model.
Fig. 4. The effect of climate, CO$_2$, thinning, land-use change, and disturbance on (a) annual NEP, (b) $\Delta$NEP, (c) $\Delta$GPP, (d) $\Delta$RE and (e) $\Delta$RH at the Tomakomai site. The $\Delta$ values for climate, CO$_2$, clear-cutting, and conversion were calculated by subtracting each flux of $S_{\text{const-climate}}$, $S_{\text{const-CO}_2}$, $S_{\text{non-cut}}$, and $S_{\text{non-conversion}}$ from each flux of $S_{\text{non-thin}}$. The $\Delta$ values for thinning were evaluated by subtracting each flux of $S_{\text{const-thin}}$ from each flux in the full scenario ($S_{\text{full}}$). Positive $\Delta$ values represent enhancement effects on each flux and negative values the opposite.
Fig. 5. Time course of (a) annual NEP, (b) cumulative NEP, and (c) cumulative NECB at the Tomakomai site. They were simulated based on four treatment scenarios for clear-cutting and residues. Clear-cutting was not implemented in the non-disturbance scenario. $S_{E0R100}$: emission of logs 0 %, that of residues 100 %; $S_{E50R50}$: emission of logs 50 %, that of residues 50 %; $S_{E100R0}$: emission of logs 100 %, that of residues 0 %.