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windthrow  
disturbance on the  
carbon balance of a  
forest**

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# Effects of a windthrow disturbance on the carbon balance of a broadleaf deciduous forest in Hokkaido, Japan

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## Abstract

Forests play an important role in the terrestrial carbon budget, with most being in a carbon sequestration stage. The net carbon releases that occur result from forest disturbance, and windthrow is a typical disturbance event affecting the forest carbon balance in eastern Asia. The carbon budget has been measured using the eddy covariance method in a deciduous broadleaf forest (Japanese white birch, Japanese oak, and castor aralia) in Hokkaido, where accidental damage by the strong typhoon, Songda, in 2004 occurred. We also used the biometrical method to demonstrate the carbon flow within the forest in detail. Damaged trees amounted to 40 % of all trees, and they remained on site where they were not extracted by forest management. Gross primary production (GPP), ecosystem respiration (Re), and net ecosystem production were 1350, 975, and 375 gC m<sup>-2</sup> yr<sup>-1</sup> before the disturbance and 1262, 1359, and -97 gC m<sup>-2</sup> yr<sup>-1</sup> 2 years after the disturbance, respectively. Before the disturbance, the forest was an evident carbon sink, and it subsequently transformed to net a carbon source. Because of light enrichment at the forest floor, the leaf area index and biomass of the undergrowth (*Sasa kurilensis* and *S. senanensis*) increased by factors of 2.4 and 1.7, respectively, in 3 years subsequent to the disturbance. The photosynthesis of *Sasa* increased rapidly and contributed to the total GPP after the disturbance. The annual GPP only decreased by 6 % just after the disturbance. On the other hand, the annual Re increased by 39 % mainly because of the decomposition of residual coarse-wood debris. The carbon balance after the disturbance was controlled by the new growth and the decomposition of residues. The forest management, which resulted in the dead stands remaining at the study site, strongly affected the carbon budget over the years. When comparing the carbon uptake efficiency at the study site with that at others, including those with various kinds of disturbances, we emphasized the importance of forest management as well as disturbance type in the carbon budget.

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# 1 Introduction

Forests play a particularly important role in terrestrial carbon sequestration because almost 90 % of all biomass is stored in trees and 50 % of terrestrial organic matter is stored in forest (Körner, 2003). A net carbon uptake or release by forests has an impact on the atmospheric CO<sub>2</sub> concentration. Therefore, to determine the carbon budget in various forest ecosystems, eddy covariance measurements have been performed (Valentini et al., 2000; Law et al., 2002; Hirata et al., 2008). These measurements indicated that most forests are in a carbon sequestration stage when forest destruction is not taken into account. The carbon budget in such forests is stable, with anomalies occurring in relation to interannual weather conditions. The net carbon uptake is a slow phenomenon because of tree growth and carbon accumulation into the soil is tied to forest age. In contrast, net carbon releases tend to result from forest disturbances. Schulze (2006) classified ecosystem disturbances as follows: (1) continuous forcing of the C and N cycles, e.g., by temperature or CO<sub>2</sub> increase, (2) disturbances that act as a disruption of C and N cycles, e.g., by insects or windthrow, or (3) disturbances where the C and N are exported from the ecosystem, e.g., by fire and harvesting. The first disturbance type may impose continual stresses on the ecosystem, gradually changing the carbon budget. The second type may impose damage within a day, e.g., by windthrow, or within a few months, e.g., by impact by insects. All dead-wood matter resulting from the impact may remain on site if not extracted by forest management. The third type may impose impacts within a few hours, e.g., by fire, or within a few months, e.g., by forest harvesting, and bypass the heterotrophic chain of respiration. For example, in a fire, carbon fixed over a period of a few decades to 300 years may be released within a few hours. In cases of disturbance, except for fire, most carbon release occurs with some delay, but the release is nevertheless rapid relative to the net carbon uptake. Magnani et al. (2007) demonstrated the age-related dynamics of the carbon balance following a disturbance (harvesting) in five forest ecosystems across Europe. After each event, the forest is typically a net source of carbon over the initial

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years, followed by a broad peak in carbon sequestration. Amiro et al. (2010) summarized more than 180 site years of eddy covariance measurements of carbon flux made at forest chronosequences after disturbances including fire, harvest, thinning, insect infestations, and windthrow in North America. Net ecosystem production (NEP) showed a carbon loss from all ecosystems following a stand-replacing disturbance, only returning to a carbon sink after 20 years for all ecosystems and by 10 years for most. Goetz et al. (2012) assessed the forest carbon dynamics following disturbances of fire, insects, and harvest in North America. They identified disturbance severity and history as key factors but recognized that there are highly uncertain factors driving post-disturbance carbon source–sink dynamics across all disturbance types. Therefore, the long-term carbon budget is affected by a disturbance regime, which shows special and temporal dynamics and is composed of frequency, return interval, rotation period, size, intensity, severity, and residuals (Turner, 2010).

Although many types of disturbance have an influence on the carbon budget, windthrow is one of the most influential ones. However, few reports have described the direct quantification of the change in the carbon budget caused by windthrow. In the USA, windthrow events by hurricanes are intensive and frequent. Chambers et al. (2007) estimated that Hurricane Katrina in 2005 destroyed 320 million large trees, corresponding to a total biomass loss of 105 Tg C. This amount is equivalent to 50–140 % of the net annual carbon sink in US forests. In western Europe, windthrow storm events are important forest disturbances (Nilsson et al., 2004; Usbeck et al., 2010). Lindroth et al. (2009) reported that storm Gudrun, which hit Sweden in 2005, resulted in approximately 66 million m<sup>3</sup> of windthrown stem wood over an area of approximately 272 000 ha. The reduction in the carbon sink scaled to the whole windthrown area was estimated at approximately 3 MtC during the first year. Storm Lothar in 1999 reduced the European carbon balance by approximately 16 Mt C, equating to approximately 30 % of the net biome production in Europe. In European Russia, the spruce forests released 180 gCm<sup>-2</sup> (Schulze et al., 1999) and 192 gCm<sup>-2</sup> (Knohl et al., 2002) over a 3-month period in summer 2 years after a windthrow event.

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Windthrow is the most significant disturbance in eastern Asia, which is a humid region. Typhoons are a typical windthrow event in Japan, causing catastrophic damage to forest ecosystems. For example, Typhoon Toyamaru, which was the most severe typhoon event in Japan's recorded history, damaged 750 000 ha of forest area and 27 million m<sup>3</sup> of stem wood in Hokkaido, the northernmost island of Japan, in 1954 (Tamate et al., 1977). In 2004, Typhoon Songda (the trigger event for this study) also hit Hokkaido and damaged 37 000 ha of forest area, which caused dramatic damage but only 5 % of that of Typhoon Toyamaru (Hokkaido Forest Research Institute, 2004). There are few reports detailing long-term monitoring of the carbon budget using the eddy covariance method in wind-disturbed forest ecosystems. Sano et al. (2010) reported that the net carbon balance during the growing season changed from 159 before to  $-80 \text{ g C m}^{-2}$  after disturbances of the Japanese larch forest. Ito (2010) evaluated the impact of defoliation caused by a typhoon event on the carbon budget in a deciduous broadleaf forest. The biomass of leaves decreased by 10–20 %, lowering the canopy carbon gain by nearly  $200 \text{ g C m}^{-2} \text{ yr}^{-1}$ . As the impacts to forest ecosystems will increase because of projected more frequent and intensive winds under future climate change scenarios, intermittent large windthrow events may partly affect the interannual variation in the terrestrial carbon balance. Although a disturbance is a complicated process associated with temporal and spatial variation, it is uncommon for flux measurement to continue for an extended period both before and after a disturbance.

In this study, the uptake and release of CO<sub>2</sub> by a forest ecosystem has been measured from the year 2000 using the eddy covariance technique. Kitamura et al. (2012) reported on the carbon budget of this forest for the first 4 years (2000–2003). Seasonal and interannual variations in carbon uptake and release in the forest were evaluated and characterized. We used the biometrical method with the eddy covariance method to demonstrate the detailed carbon flow in the forest. By coincidence, the monitored forest was damaged by the strong typhoon, Songda, in 2004. Subsequently, we focused on the change in the carbon budget under the ecosystem recovery process resulting from the windthrow disturbance.

## 2 Materials and methods

### 2.1 Site description

This study was conducted at the Sapporo forest meteorology research site (42°59' N, 141°23' E; 182 m a.s.l.; AsiaFlux site code: SAP) in Sapporo, Japan. The site is located within the Hitsujiigaoka Experimental Forest (147 ha) of the Hokkaido Research Center, Forestry and Forest Products Research Institute (FFPRI). The mean annual temperature is 7.3 °C, and the monthly mean temperature ranges from -5.1 °C in January to 20.1 °C in August. The annual precipitation is 945 mm, and maximum snow depth was 1.37 m in February 2000 (Mizoguchi et al., 2014a). The terrain gently slopes to the northwest, with an average inclination of 6.5°. The soil parent material of this area is predominantly volcanic ash, and the soil type is Andosol (Ishizuka et al., 2006). The forest type is mature secondary deciduous broadleaf forest, regenerated after wild-fires in the late 19th century (1874, 1883, 1887, and 1888). The forest represents the transition stage from an early successional Japanese white birch (*Betula platyphylla* var. *japonica*) to mid- and late-successional species (Japanese oak (*Quercus mongolica* var. *grosseserrata*), castor aralia (*Kalopanax septemlobus* (Thunb.) Koidz), painted maple (*Acer mono*), and Japanese linden (*Tilia japonica*) forest. The first two species accounted for > 75 % of the basal area in 2003 (Utsugi et al., 2005). Dwarf bamboo (*Sasa kurilensis* and *S. senanensis*) dominantly covered the forest floor and some herbaceous species partly covered it. The stand density and mean tree height over 5 cm diameter at breast height (DBH) were 672 trees ha<sup>-1</sup> and 18.3 m in 2003, respectively. The oldest white birch was 90 years old in 2002.

The strong Typhoon Songda (18th of the season) struck northern Japan on 8 September 2004. Many canopy trees were uprooted or broke off by strong winds at the SAP site (Fig. 1). Prior to the windthrow disturbance, the canopy was almost closed with the dominant tree species. The subsequent typhoon removed 33 % of the tree canopy and 28 % of tree biomass (Takahashi et al., 2009; Utsugi et al., 2009). Large canopy gaps were formed at the site. However, the damage was heterogeneously dis-

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tributed throughout the forest. All dead trees remained on site and were not extracted by forest management. The forest began recovering under the natural mechanisms of the ecosystem.

## 2.2 Flux and meteorological measurements

CO<sub>2</sub> flux was measured using an eddy covariance system at a height of 28.5 m on a 41 m tall scaffold tower at the center of the SAP site. The system consisted of a three-dimensional sonic anemometer (SAT: DA600-3T or DA600-3TV, SONIC, Japan) that measured wind vector components and a closed-path infrared gas analyzer (IRGA: LI-6262, LI-COR, USA) that measured atmospheric CO<sub>2</sub> concentrations. An aspirated thermohygrometer (HMP-45A, Vaisala, Finland) that measured relative humidity and air temperature was mounted at the same height as the SAT. The air inlet was installed behind the SAT, and air was drawn to the IRGA in a cabin located at the ground level. The inlet and IRGA were connected by a polytetrafluoroethylene tube of 40 m in length and 6 mm in inner diameter. Sample air was pushed into a mass flow controller at a flow rate of approximately 9.5 L min<sup>-1</sup> and was regulated at 2.0 L min<sup>-1</sup>. The residual air was released from an exhaust port. Water vapor in the sample air was removed with an air dryer (MD-110-48F, Perma Pure, USA). The IRGA was calibrated automatically once a day using zero and CO<sub>2</sub> (450 ppm) standard gases in an air balance. The sensor signals were recorded every 0.2 s (5 Hz) using a digital data logger (DRM3, TEAC, Japan). Details of the flux system are reported in the study by Yasuda and Watanabe (2001). The system in FFPRI FluxNet sites, including the SAP site, was subsequently modified for long-term flux monitoring (Ohtani et al., 2001). Vertical profiles of the CO<sub>2</sub> concentration were measured using another IRGA (LI-6262, LI-COR) with a multisampling system at five sampling heights (3.6, 10.5, 16.3, 20.1, and 29.6 m). The sampling interval of each height was 2 min, and, therefore, one cycle of the system equated to 10 min. Dehumidification and calibration of the sampling air for the IRGA were the same as those for the eddy covariance system.

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Meteorological conditions were measured in and above the forest canopy. Air temperature and humidity were measured using an aspirated thermohygrometer (HMP-45D, Vaisala) at 29.6 m. Photosynthetically active radiation (PAR) was measured using quantum sensors (LI-190, LI-COR) at the top of the tower (41.3 m) and above the undergrowth (2.4 m).

The observations commenced in August 1999. The observational infrastructure was destroyed by the typhoon in 2004 and reconstructed in the spring of 2005 (Nakai et al., 2004). The studies by Kitamura et al. (2012) and Mizoguchi et al. (2014a) provide a more detailed description and additional information regarding the meteorological measurements.

### 2.3 Data processing and analysis

The CO<sub>2</sub> flux above the canopy (F<sub>c</sub>) was calculated every 30 min using the eddy covariance technique. Three-dimensional coordinate rotation (McMillen, 1988), corrections for the effects of lateral wind on sonic velocity and of water vapor on temperature (Kaimal and Gayner, 1991; Hignett, 1992), and the density correction theory of Webb et al. (1980) (WPL correction) were applied. The attenuation loss of high-frequency fluctuations in the CO<sub>2</sub> concentration in the closed-path system (Leuning and Moncrieff, 1990) was corrected with an empirical transfer function. Linear trends were removed. The lag time of the sampling of air from the inlet to the cell of the IRGA was determined by maximizing the covariance between the vertical wind velocity and the CO<sub>2</sub> concentration. Tests were run on all data to screen for data quality; one method used was visual inspection of the raw data, whereas the other was a series of tests in accordance with the quality control procedure (Foken and Wichura, 1996; Vickers and Mahrt, 1997). The proportion of missing observations due to instrument malfunction and maintenance was 10 %, and the amount of data rejected by the quality test mentioned above was 12 %. Using the CO<sub>2</sub> profile data, the rate of change in CO<sub>2</sub> storage in the canopy (S<sub>c</sub>) was calculated every 30 min from the temporal change in CO<sub>2</sub> stor-

age in an air column between the ground level and the height of the eddy covariance systems.

Net ecosystem exchange (NEE) is defined as the sum of  $F_c$  and  $S_c$  during the average period and net ecosystem production (NEP) is equal to negative NEE:

$$5 \quad \text{NEP} = -\text{NEE} = -(F_c + S_c). \quad (1)$$

NEE was underestimated during low-turbulence atmospheric conditions, such as stable night periods. We applied data screening using the threshold of friction velocity ( $u_*$ ) to exclude flux under such conditions (Massman and Lee, 2002). To determine the  $u_*$  threshold, we examined NEE at night, which decreased greatly with the depression of  $u_*$ . In this study, we selected  $0.29 \text{ m s}^{-1}$  before the disturbance and  $0.31 \text{ m s}^{-1}$  after the disturbance as the  $u_*$  threshold. NEE was equal to ecosystem respiration ( $R_e$ ) during the night. We expressed  $R_e$  in terms of air temperature ( $T_a$ ):

$$10 \quad R_e = R_0 Q_{10}^{T_a/10} = R_0 \exp(k \cdot T_a), \quad (2)$$

where  $R_0$  is the respiration rate at  $0^\circ\text{C}$  and  $Q_{10}$  is the increase in respiration for every  $10^\circ\text{C}$  rise in temperature.  $R_0$ ,  $Q_{10}$ , and  $k$  were derived for three periods in a year (growth period, defoliation period without snow, and defoliation period with snow) and were constants in each period. Daytime  $R_e$  was also calculated using Eq. (2), with the assumption that Eq. (2) is valid during the day. Daytime was defined as the period from sunrise to sunset.

20 Data gaps during the nighttime NEP were infilled with  $R_e$  values calculated using Eq. (2), and those during the daytime were filled with NEP calculated as follows:

$$\text{NEP} = (a' \cdot \text{Pd} \cdot \text{Ag}_{\text{max}}) / (\text{Ag}_{\text{max}} + a' \cdot \text{Pd}) + c, \quad (3)$$

where  $a'$  is the light-use efficiency,  $\text{Pd}$  is the downward PAR above the canopy,  $\text{Ag}_{\text{max}}$  is the light-saturated NEP, and  $c$  is the daytime respiration rate. The variables  $a'$ ,  $\text{Ag}_{\text{max}}$ ,

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and  $c$  are constants and were derived daily for the previous 5 days. Gross primary production (GPP) was estimated as follows:

$$\text{GPP} = \text{NEP} + \text{Re}. \quad (4)$$

## 2.4 Biometric measurements

5 The plots for biometric measurement were established near the observation tower. We used a 0.25 ha (50 m × 50 m) plot established in 1978 before the disturbance and set up a 1.6 ha plot composed of 40 subplots (20 m × 20 m) after the disturbance. The DBH of all trees that were > 5 cm in the plots were measured every year from 2000 to 2012. Tree heights ( $H$ ) of all trees in the plot were measured in 2002. The relationships  
10 between  $H$  and DBH for each species were formulated. During the summer of 2001 and 2003, 26 sample trees were subjected to destructive analysis. Eight stands of birch, 10 of oak, and 8 of castor aralia were used to determine the allometrics between biomasses and tree dimensions. The sample trees were felled at a height of 0.3 m, and DBH and  $H$  were measured. The crowns were divided into 1 m thick strata from the  
15 stump height (0.3 m) to the treetop. Each stratum was divided into the tree biomass components of stem, branch, and leaf, and the fresh weight of each component was immediately measured. The dry weights of each component were calculated from the fresh weight and water content. These weights were summed for the entire tree, and the total dry weight of each component scaled positively with tree dimensions, i.e.,  
20  $\text{DBH}^2 \times H$  for stem and branch and  $\text{DBH}$  for leaf in the allometric equations.

Biomass production at the stand level was estimated by summing up the biomass production of individual trees, which was obtained by inventorying the dimensions of trees in the study plots. The litterfall was collected monthly using 50 traps of 0.48 m<sup>2</sup> from 2000 to 2003 in the growing seasons. In the snowy seasons, a large plastic sheet  
25 (20 m × 20 m) was set up on the ground. All branches that had dropped on to the sheet were collected as representative of litterfall during the snowy seasons. The litterfall was oven-dried at 70 °C and separated into leaf, branch, and other components (seed, flower, and bud) for weighing.

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estimated by substituting values of PAR and LAI obtained by leaf litter measurements in 2000 and 2001.

Six small plots (2 m × 2 m) under different disturbance intensities were selected to measure the biomass and the leaf area index of *Sasa* in 2006, 2008, 2009, and 2012.

Therefore, the plots were influenced by the different light conditions. All aboveground biomass of *Sasa* in the plot was separated into leaf and culm, and the root of *Sasa* was collected from a part of the plot. All samples were dried and weighed. The area of 10 leaves that were randomly selected was measured. Values of  $Pd_0$  were measured above *Sasa* at each plot. The leaf area index of *Sasa* ( $LAI_{sasa}$ ) and the biomass of *Sasa* (SBM) were increased with the transmittance ( $Pd_0 / Pd$ ) linearly (Utsugi et al., 2013; Mizoguchi et al., 2014b) and were estimated at all the subplots.

### 3 Results

#### 3.1 Seasonal changes in carbon flux

At the study site, the bud burst started at the end of April and the beginning of May, and all leaves of canopy trees turned yellow during October. *Sasa* undergrowth was buried in snowpack from mid-December to the beginning of April. Seasonal changes in GPP,  $Re$ , and NEP before the disturbance, represented by the monthly means of the daily fluxes, are shown in Fig. 2. GPP increased after bud burst, was almost constant from June to mid-August, and decreased gradually in autumn. GPP peaked in July and was 0 during the snowy defoliation period.  $Re$  increased after snow thaw with rising air temperature, peaked in August, and maintained an almost constant value of  $1.3 \text{ gCm}^{-2} \text{ day}^{-1}$  during the snowy defoliation period from December to March. NEP increased rapidly in May and peaked in June, decreasing gradually from mid-summer to autumn. A positive NEP value was observed from May to September and a negative value from October to April, with the positive and negative values representing  $\text{CO}_2$  uptake to and release from the forest, respectively. During the defoliation period, the

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forest was a weak source of CO<sub>2</sub>, at a rate of  $-1.4 \text{ gCm}^{-2} \text{ day}^{-1}$ . Maximum values of the monthly means of GPP, Re, and NEP were 10.2, 4.7 and  $6.0 \text{ gCm}^{-2} \text{ day}^{-1}$ , respectively.

The seasonal changes in the CO<sub>2</sub> budgets after the disturbance are shown in Fig. 3. The shapes of seasonal trends in GPP and Re after the disturbance were similar to the trends before the disturbance. Averaged maximum GPP and Re from 2006 to 2008 were  $10.0$  and  $7.6 \text{ gCm}^{-2} \text{ day}^{-1}$ , respectively, and they were 1.0 and 1.6 times greater, respectively, than those before the disturbance. During the snowy defoliation period, the average Re from 2006 to 2008 was  $2.0 \text{ gCm}^{-2} \text{ day}^{-1}$ , 1.5 times greater than Re before the disturbance. The disturbed forest absorbed CO<sub>2</sub> for 3 to 4 months after the disturbance as opposed to 5 months before the disturbance. In particular, CO<sub>2</sub> sequestration only occurred for 2 months in 2012. The average NEP during the defoliation period from 2006 to 2008 was  $-1.8 \text{ gCm}^{-2} \text{ day}^{-1}$ .

### 3.2 Interannual changes in carbon flux

Figure 4 shows interannual variation in GPP, Re, and NEP from 2000 to 2012. The observations were suspended because of the windthrow disturbance in 2004. Ten months of observations are missing from September 2004 to June 2005; however, 2 years of observations are shown in Fig. 4. The 4-year average annual GPP, Re, and NEP before the disturbance were 1350, 975, and  $375 \text{ gCm}^{-2} \text{ yr}^{-1}$ , respectively. In 2006, 2 years after the disturbance, the annual GPP decreased to  $1262 \text{ gCm}^{-2} \text{ yr}^{-1}$  and annual Re increased to  $1359 \text{ gCm}^{-2} \text{ yr}^{-1}$ , being 6% smaller and 39% greater, respectively. The annual NEP changed from a positive value (CO<sub>2</sub> uptake) to a negative value (CO<sub>2</sub> release) and was  $-97 \text{ gCm}^{-2} \text{ yr}^{-1}$ . The carbon balance was greatly altered by the disturbance. After the disturbance, these fluxes changed year after year; Re increased gradually and GPP varied in a temporally heterogeneous and complicated manner. NEP represented a weak CO<sub>2</sub> release in 2006 and 2007, which subsequently decreased

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gradually and bottomed out at  $-365 \text{ g C m}^{-2} \text{ yr}^{-1}$  in 2010. NEP increased slightly under the forest restoration processes in 2011 and 2012.

### 3.3 Changes in biomass for canopy trees and *Sasa*

Changes in total aboveground woody biomass (AGB) and the details of the increments are shown in Fig. 5. The carbon pools are summarized in Table 1. For a 4-year period from 2000 to 2003, the mean AGB was  $9.37 \text{ kg C m}^{-2}$ , including leaf and branch biomass. The mean AGB of Japanese white birch was 51.6% and that of Japanese oak was 33.5% of the mean total AGB before the disturbance. As shown in Table 1, the root biomass was 31.7% of stem biomass (Utsugi et al., 2007) and soil carbon was  $18.0 \text{ kg C m}^{-2}$  (Sakata et al., 2010). We assumed that the ratio of root to stem biomass and the soil carbon content after the disturbance were the same as that before the disturbance. After the disturbance, AGB decreased by 40.4% in 2005 and had evidently stabilized by 2012.

The increment of aboveground biomass in living trees ( $\Delta y$ : growth and recruitment in Fig. 5b) ranged from  $0.092$  to  $0.164 \text{ kg C m}^{-2} \text{ yr}^{-1}$ , with a mean value of  $0.140 \text{ kg C m}^{-2} \text{ yr}^{-1}$  before the disturbance. The interannual value of ANBI hovered around 0, with a mean value of  $0.017 \text{ kg C m}^{-2} \text{ yr}^{-1}$  before the disturbance. This marginally positive value of the mean ANBI was attributed to the negative ANBI of Japanese white birch that occurred over the 4-year period, excluding 2001. This negative ANBI value demonstrated that the dead-tree biomass ( $L_d$ ) was greater than  $\Delta y$  for Japanese white birch. However, The ANBI value for Japanese oak and that for the other surveyed species was positive and significantly greater than that for Japanese white birch during the 4-year period. After the disturbance,  $\Delta y$  increased and ranged from  $0.092$  to  $0.197 \text{ kg C m}^{-2} \text{ yr}^{-1}$ . The small number of recruitments became countable after the disturbance. On the other hand, the mortality fluctuated irregularly and was greater in 2010 because of minor crown snow damage. No clear differences in ANBI values before and after the disturbance were evident.

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Using the linear relation between the SBM and the light transmittance ( $Pd_0 / Pd$ ), the three components of SBM were estimated as follows:

$$SBMc = 1.039 \times Pd_0/Pd + 0.1717, \quad (7)$$

$$SBMI = 0.244 \times Pd_0/Pd + 0.0598, \quad (8)$$

$$5 \quad SBMr = 0.709 \times Pd_0/Pd + 0.3631, \quad (9)$$

where SBMc, SBMI, and SBMr were the culm, leaf, and root (including rhizome) biomass of *Sasa*, respectively. The total biomass change of *Sasa* is shown in Fig. 6 assuming that the turnovers of culm, leaf, and root were 9, 3, and 3 years, respectively (Oshima, 1961a, 1961b). The mean SBM before the disturbance was  $0.715 \text{ kg C m}^{-2}$ .  
10 SBM increased sharply during the first 3 years after the disturbance and reached  $1.408 \text{ kg C m}^{-2}$  by the year 2012.

### 3.4 Changes in leaf area index for canopy trees and *Sasa*

The leaf area index for canopy tree ( $LAI_{tree}$ ) and *Sasa* ( $LAI_{sasa}$ ) were also estimated from the light transmittance quoted from Mizoguchi et al. (2014b). For the canopy,  
15 the transmission coefficients ( $F$ ) as calculated using Eq. (6) in 2000 and 2001 were 2.91 and 2.41, respectively. We assumed  $F$  was constant throughout a year and used a mean value of 2.66 over all the years. For *Sasa*, we derived a linear correlation between  $LAI_{sasa}$  and the transmittance as follows:

$$LAI_{sasa} = 5.71 \times Pd_0/Pd + 1.40. \quad (10)$$

20 For *Sasa*, the maximum leaf area index of each year was estimated as the mean of  $LAI_{sasa}$  over the former 3 years with the turnover of leaves in mind. Because  $Pd_0$  was measured at only one point near the observation tower, where the disturbance was more severe, LAI may not have been rigorously measured after the disturbance.

Interannual changes in the maximum leaf area indexes are shown in Fig. 7, quoted  
25 from Mizoguchi et al. (2014b). The value of  $LAI_{tree}$  after 2005 fell to below a quarter

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dropped by only 6% after the disturbance. The increases in LAI<sub>sasa</sub> had a significant effect on GPP in the years immediately following the disturbance.

## 4.2 Relationship between monthly mean Re and air temperature

Figure 9 shows the exponential functions between air temperature and Re in the snow-free season. The value of Re after the disturbance at 5 and 20 °C increased by factors of 1.50 and 1.61, as compared with that before the disturbance. The coarse-wood debris (CWD) of 4.82 kg C m<sup>-2</sup> (41% of the biomass before the disturbance) supplied to the forest floor resulted in a CO<sub>2</sub> source after the disturbance. Utsugi et al. (2010) indicated that the decomposition rate of CWD is 0.04 yr<sup>-1</sup>. The fallen biomass decomposed into 0.916 kg C m<sup>-2</sup> in the first 5 years after the disturbance. Therefore, the mean decomposition rate was 183 g C m<sup>-2</sup> yr<sup>-1</sup>. The annual Re increased from 978 g C m<sup>-2</sup> yr<sup>-1</sup> before the disturbance to 1359 g C m<sup>-2</sup> yr<sup>-1</sup> in 2006, and this increased rate was 2.1 times greater than the decomposition rate of CWD. The decomposition of soil organic matter may constitute half of the increased annual Re. The forest management policy of not extracting dead trees will have a significant effect on the change in Re after the disturbance.

Because the soil surface did not freeze and the soil temperature reached nearly 0 °C under the snow cover, most of the carbon was released as soil respiration through the snow cover. The value of Re in the snowy season agreed with that in the snow-free season at an air temperature equal to 0 °C (Fig. 9). In the snowy season, the value of Re was constant over a period of 4 months and a considerable amount of Re was released.

## 4.3 Carbon flows before and after the disturbance

Net primary production was calculated by adding together ANPP and the changes in root and SBM. Autotrophic (Ra), heterotrophic (Rh), and soil (Rs) respiration were separated from Re. The Ra values of leaves, branches, and stems were estimated using

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chambers (Utsugi et al., 2008). The  $R_a$  value of coarse roots was assumed to be in proportion to the stem respiration and the biomass ratio of the root and stem. The  $R_a$  of fine roots and  $R_h$  of soil decomposition were estimated using incubation tests (T. Sakata, personal communication, 2010). The  $R_h$  value of CWD was estimated as mentioned above. The carbon that flowed within the SAP forest before and after the disturbance as estimated by the biometrical methods is integrated into Table 2 and was compared with the flux measured by the eddy covariance method. In Table 2, the periods before and after the disturbance were 2000–2003 and 2006–2008, respectively.

Carbon fluxes measured by the two methods were in reasonable agreement with each other. In general, the measurements by the eddy covariance method gave smaller values. However, the changes before and after the disturbance showed the same tendency. Specifically, GPP decreased by only a few percentage points,  $R_e$  increased at a rate of  $> 30\%$ , and NEP changed from a positive value to a negative value.

The  $R_a$  of the canopy trees decreased drastically, but the increased  $R_a$  of *Sasa* had a compensatory effect. After the disturbance, a slight reduction in  $R_a$  occurred. On the other hand, the value of  $R_h$  was increased by a factor of 1.9 after the disturbance. The increases in the decomposition of CWD and soil organic matter were estimated to be 186 and 187  $\text{g C m}^{-2} \text{yr}^{-1}$ , respectively. Because about 80% of the fallen CWD remained in 2009, CWD continued to decompose for long periods. A steady increase in the value of the annual  $R_e$  after the disturbance, as shown in Fig. 4, suggested that the decomposition rate of CWD was increasing year by year. The change in the  $R_h$  value after the disturbance plays an important role in the carbon budget in the forest.

Because SBM and  $\text{LAI}_{\text{sasa}}$  were limited by the availability of light above the undergrowth in 2008 (Figs. 6 and 7), *Sasa* rapidly grew during the first 3 years after the disturbance, with a maximum growth rate of 0.213  $\text{kg C m}^{-2} \text{yr}^{-1}$ , greater than the growth rate of trees shown in Fig. 5. Increases in  $\text{LAI}_{\text{sasa}}$  and the light at the forest floor resulted in a compensatory slight decrease in the annual GPP. NEP values in 2006 and 2007 were constant, as shown in Fig. 4, because a remarkable growth of *Sasa* caused a gentle increase in carbon release. Therefore, after SBM and  $\text{LAI}_{\text{sasa}}$  became saturated, car-

bon release increased steadily and stabilized in 2010. Because the recruitment of trees increased in 2012 (Fig. 5b), carbon release decreased slightly under forest restoration.

#### 4.4 Comparison with other disturbed and mature forest ecosystems

The carbon fluxes measured by the eddy covariance method were summarized in Table 3. Data at 75 sites were selected with a focus on the history of a disturbed forest and a stand age of a mature forest. The disturbances included forest fires, insect infestation, windthrow events, harvest, tree thinning, and plantation. Some mature forests with an identified stand age were also included. The measurements that included periods both before and after disturbances were taken at eight sites. Only two sites (sites TSE and SAP) included measurements from a period longer than 10 years. Because the carbon budget changed drastically in the years after the disturbance, it is very important to maintain measurements over a long term.

The calculation of carbon uptake efficiency ( $GPP / Re$ ) in the forest is shown in Table 3 and plotted with years since the last disturbance for the disturbed forest or stand age for the mature forest in Fig. 10. The  $GPP / Re$  with years  $\leq 0$  (data before disturbance) is plotted on the left axis. Similarly, the  $GPP / Re$  with years greater than or equal to 100 is plotted on the right axis. Because the  $GPP / Re$  changed with the type and intensity of the disturbance, they were scattered around the line equal to 1. The  $GPP / Re$  plotted on the left axis was greater than 1 (carbon sink), and all values were derived from the mature forest before the disturbance. The mature or older forests are also expressed on the right side in Fig. 10. The  $GPP / Re$  for the forests were  $> 1$  except for Norunda, De Inslag, and F77 listed in Table 3. Norunda, in central Sweden, has been shown to have an unusual carbon balance (Lagergren et al., 2008). Valentini et al. (2000) pointed out that the carbon is being lost in Norunda as a result of past soil drainage, plowing and fertilization. De Inslag in Belgium was losing carbon as a result of intensive thinning during the 1980s (Carrara et al., 2003). The cause of the carbon source in F77, Saskatchewan, Canada, where there was a burnt forest as reported by Mkhabela et al. (2009), unknown. As show in Fig. 10, carbon

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uptake occurred in the forest ecosystem after a long period and in most of the mature or older forests. For example, Knohl et al. (2003) showed a large carbon uptake by an unmanaged 250-year-old forest in central Germany. The GPP / Re in this case was 1.46, demonstrating a considerable carbon sink. The net carbon uptake evident in the study by Knohl et al. (2003) agreed with the hypothesis of Luysaert et al. (2008) and contradicted the hypothesis of Kira and Shidei (1967).

The GPP / Re after the disturbance changed rapidly and widely, as shown in Fig. 10. At most disturbed sites, the greatest decreases appeared just after the disturbance, whereas the GPP / Re dropped gently at the SAP site. The management procedure adopted after the disturbance at the SAP site, where all dead trees remained on site, played an important role in the distribution of decomposable organic matter. An increase in Rh from CWD and a remarkable growth of *Sasa*, as mentioned above, will surely affect the carbon balance. We compared the GPP / Re at the SAP site with that at the TSE site, where trees were clear-cut and half the biomass was removed as logs (Aguilos et al., 2014). The ecosystem carbon compensation point at which carbon flow changed from a carbon source to a sink at the TSE site was after 8 years compared with over 10 years at the SAP site. The greater residual CWD at the SAP site resulted in later restoration. Consequently, the amount of the residues plays an important role in the disturbance chronosequences. Figure 10 demonstrates that the GPP / Re crosses the compensation point after approximately 20 years at all disturbed sites. We estimate that the GPP / Re crosses the compensation point after approximately 15 years at the SAP site.

## 5 Conclusions

We performed measurements of the carbon budget over a 4-year period before the windthrow disturbance and over 8 years thereafter in a deciduous broadleaf forest in Hokkaido, Japan. Before the disturbance, the forest fulfilled the role of an evident carbon sink, and it changed to a carbon source after the disturbance. Because of light en-

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richment at the forest floor after the disturbance, the photosynthesis of *Sasa* increased rapidly, ultimately contributing to the total GPP. The annual GPP only decreased by 6 % just after the disturbance. On the other hand, the annual Re increased by 39 %, mainly because of the decomposition of residual CWD. A steady increase in the annual Re after the disturbance suggested that the decomposition rate of the CWD was increasing year after year. Consequently, the carbon balance after the disturbance was controlled by the new growth and the decomposition of residues.

We characterized the SAP site by the impact caused by the windthrow and the subsequent forest management adapted after the disturbance. The observations of a forest damaged by windthrow are novel. In particular, the measurements reported here include periods before and after the disturbance. The forest management, which resulted in the dead stands remaining at the study site, strongly affected the carbon budget over the years. When comparing the carbon uptake efficiency at the SAP site with that at others, including sites with various kinds of disturbances, we emphasized the importance to the carbon budget of forest management as well as the disturbance type.

*Author contributions.* K. Yamanoi and Y. Mizoguchi designed and carried out the meteorological experiments. H. Utsugi designed the biometrical experiments, and all authors carried them out. K. Yamanoi prepared the manuscript with contributions from coauthors.

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**Table 1.** Carbon pools at the SAP site before and after the windthrow disturbance.

Carbon pool	Before disturbance <sup>1</sup>	After disturbance <sup>2</sup>
Aboveground woody biomass	9.37	5.61
Stem	7.47	4.39
Branch	1.73	1.12
Leaf	0.17	0.10
Root biomass <sup>3</sup>	2.37	1.39
<i>Sasa</i> biomass	0.72	1.20
Soil carbon <sup>4</sup>	18.	18.

<sup>1</sup> Mean stocks ( $\text{kg C m}^{-2}$ ) from 2000 to 2003. <sup>2</sup> Mean stocks ( $\text{kg C m}^{-2}$ ) from 2006 to 2008.

<sup>3</sup> Root biomass is 31.7% of stem biomass (Utsugi et al., 2007). <sup>4</sup> Soil carbon is quoted from Sakata et al. (2010).

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**Table 2.** Carbon flows at the SAP site before and after the windthrow disturbance. Gross primary production (GPP), ecosystem respiration (Re), and net ecosystem production (NEP) were measured by biometric and eddy covariance methods. Net primary production (NPP) and soil respiration (Rs) were measured, and autotrophic (Ra) and heterotrophic (Rh) respiration were separated from Re biometrically.

	Before disturbance <sup>1</sup>		After disturbance <sup>2</sup>	
	Biometric	Eddy cov.	Biometric	Eddy cov.
GPP	1552	1349	1517	1293
NPP	678		660	
Re	1285	978	1641	1424
Ra	875		858	
Rh	410		783	
Rs	730		984	
NEP	267	374	-123	-131

<sup>1</sup> Mean annual rates ( $\text{gCm}^{-2}\text{yr}^{-1}$ ) from 2000 to 2003. <sup>2</sup> Mean annual rates ( $\text{gCm}^{-2}\text{yr}^{-1}$ ) from 2006 to 2008.

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**Table 3.** Characteristics of the eddy covariance measurement in forest sites. Sites were selected with a focus on disturbance or management history. Some mature forest sites of a certain stand age were added.

Site location name or symbol	Forest type <sup>1</sup>	Disturbance history	Years <sup>2</sup>	GPP <sup>3</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	Re <sup>3</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	NEP <sup>3</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	GPP/Re	References
North America								
AL, USA, Poker Flat	ENF	Fire	5	299	229	70	1.31	Iwata et al. (2011)
AL, USA, Delta Junction	ENF	Fire	3, 15	193, 436	234, 322	-41, 114	0.82, 1.35	Weip et al. (2006)
BC, Canada, MPB-06, -03	ENF	Mature	ca. 80	499	426	70	1.16	
BC, Canada, MPB-09	ENF	Insect	1, 2, 4, 5	439, 522, 432, 522	521, 555, 488, 518	-82, -33, -56, 4	0.84, 0.94, 0.89, 0.94	Brown et al. (2010)
BC, Canada, DF49	ENF	Insect–harvest	1, 2, 3	812, 954, 922	920, 1011, 974	-108, -57, -52	0.88, 0.94, 0.95	Mathys et al. (2013)
BC, Canada, HDF88, HDF00	ENF	Harvest–burn	53	1991	1737	254	1.15	Humphreys et al. (2006)
SK, Canada, F98	ENF	Harvest–burn–plant	14, 3	1214, 435	1347, 1041	-133, -606	0.90, 0.41	
SK, Canada, F89	ENF	Fire	6, 7	388, 456	385, 499	3, -43	1.01, 0.91	Mkhabela et al. (2009)
SK, Canada, F77	ENF	Fire	15, 16	903, 902	787, 849	115, 53	1.15, 1.06	
SK, Canada, OJP	ENF	Fire–mature	27, 28	752, 906	791, 984	-39, -78	0.95, 0.92	
SK, Canada, HJP02	ENF	Harvest	88, 89	560, 594	556, 558	4, 36	1.01, 1.06	
SK, Canada, HJP94	ENF	Harvest	2, 3	89, 99	245, 222	-155, -123	0.36, 0.46	
SK, Canada, HJP75	ENF	Harvest	10, 11	353, 410	360, 376	-7, 34	0.98, 1.09	
MB, Canada, UCI-1998, -1989, -1981, -1964, -1930, -1850	ENF	Fire	5, 15	380, 450	443, 446	63, 4.5	0.86, 1.01	Goulden et al. (2011)
QC, Canada, EOBS	ENF	Fire	23, 40	710, 640	580, 478	131, 62	1.23, 1.34	
QC, Canada, HBS00	ENF	Fire	75, 154	630, 720	490, 667	140, 52	1.29, 1.08	
OR, USA, YS	ENF	Harvest–scarf–plant	ca. 100	586	586	6	1.01	Bergeron et al. (2008)
OR, USA, MS	ENF	Harvest–mature	4, 5	274, 359	440, 483	-167, -124	0.62, 0.74	
WI, USA, Willow Creek	DBF	Harvest	23, 24	704, 809	659, 696	45, 113	1.07, 1.16	Schwarz et al. (2004)
WI, USA, MHW	DBF	Insect	ca. 90	1360	989	371	1.38	
WI, USA, MRP	ENF	Plant–thin–Mature	0, 1, 2	1099, 898, 1202	776, 821, 778	323, 77, 422	1.42, 1.09, 1.54	Cook et al. (2008)
WI, USA, PB	ENF	Fire	65	1047	387	655	2.71	Noormets et al. (2007)
WI, USA, YRP	ENF	Harvest	63	1153	514	648	2.24	
WI, USA, YHW	DBF	Harvest	12	673	470	195	1.43	
WI, USA, Willow Creek	DBF	Harvest	8	1059	739	313	1.43	
MI, USA, Sylvania	DBF	Mature	3	697	827	-128	0.84	
MI, USA, UMBS	MXF	Mature	ca. 70	1149	686	464	1.68	Desai et al. (2005)
OH, USA, Toledo	DBF	Mature	> 300	1034	924	110	1.12	Desai et al. (2005)
MA, USA, Harvard Forest	MXF	Harvest–burn	85	1400	1240	160	1.13	Gough et al. (2008)
NJ, USA, Pine Barrens	DBF	Mature	45	1148	845	303	1.36	Noormets et al. (2008)
	MXF	Windthrow–Mature	75–110	1400	1150	242	1.22	Urbanski et al. (2007)
	MXF	Insect	0, 1	1153, 491	1007, 785	146, 294	1.14, 0.63	Clark et al. (2010)
	MXF	Insect	0, 1, 2	877, 804, 702	740, 907, 831	137, -103, -129	1.19, 0.88, 0.84	
	MXF	Insect	0, 1	1370, 1170	1187, 1153	183, 17	1.15, 1.01	

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Table 3. Continued.

Site location name or symbol	Forest type <sup>1</sup>	Disturbance history	Years <sup>2</sup>	GPP <sup>3</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	Re <sup>3</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	NEP <sup>3</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	GPP/Re	References
NC, USA, Duke Forest	ENF	Plant	17	1808	1203	605	1.50	Lai et al. (2002)
AZ, USA, Flagstaff	MXF	Mature	> 100	879	786	110	1.12	Dore et al. (2010)
	ENF	Thin	0, 1	909, 826	811, 902	118, -51	1.12, 0.92	
	GS	Fire	10, 11	372, 401	480, 453	-109, -45	0.78, 0.88	
CA, USA, Blodgett	ENF	Plant–thin	0, 1–3	1462, 1260–1777	1261, 1254–1604	201, -13–172	1.16, 0.99–1.11	Misson et al. (2005)
FL, USA, Gainesville	ENF	Harvest–plant	1, 2	705, 1504	1974, 2386	-1269, -882	0.36, 0.63	Clark et al. (2004)
	ENF	Harvest–plant	10, 11	2922, 2605	2346, 2002	576, 603	1.25, 1.30	
	ENF	Harvest–plant	24, 25	2695, 2517	1956, 1907	741, 610	1.38, 1.32	
<b>Europe</b>								
European Russia, Tver	MXF	Windthrow	2	109	218	-109	0.50	Knohl et al. (2002)
Hyttälä, Finland, SMEAR II	ENF	Plant	36	949	720	228	1.32	Markkanen et al. (2001)
Central Sweden, Norunda	ENF	Harvest–drain	50–100	1075	1127	-52	0.95	Lagergren et al. (2008)
Zealand, Denmark, Sore	DBF	Mature	80	1303	1120	184	1.16	Pilegaard et al. (2001)
Oxford, UK, Wytham Woods	DBF	Coppice–mature	40	2110	1980	130	1.07	Thomas et al. (2011)
UK	ENF	Harvest–mature	41	1970	1385	496	1.42	Kowalski et al. (2004)
	ENF	Harvest–plant	3	988	1100	-112	0.90	
Eisenach, Germany, Hainich	DBF	Coppice–mature	ca. 250	1560	1068	492	1.46	Knohl et al. (2003)
Brasschaat, Belgium, De Inslag	MXF	Plant–thin	71	1234	1326	-91	0.93	Carrara et al. (2004)
Hesse, France, FR02	DBF	Mature–thin	30	1128	891	238	1.27	Grarnier et al. (2000)
Bordeaux, France, Bray	ENF	Plant	28	2255	1680	575	1.34	Berbigier et al. (2001)
Les Landes, France, Bilos	ENF	Harvest	2	727	996	290	0.73	Kowalski et al. (2003)
Central Italy	DBF	Coppice–mature	10	1600	1160	381	1.38	Kowalski et al. (2004)
	DBF	Coppice	2	1420	2220	-427	0.64	
<b>Asia</b>								
Mongonmorit, Mongolia, SKT	DNF	Thin–fire–insect	70–150	525	440	85	1.19	Li et al. (2005)
Gwangneung, Korea, GDK	DBF	Mature	80–200	835	746	87	1.12	Kwon et al. (2009)
Teshio, Japan, TSE	MXF	Harvest–plant	0, 1–9	1439, 481–1238	1395, 1035–1229	44, -569–52	1.03, 0.46–1.05	Agiolos et al. (2014)
Sapporo, Japan, SAP	DBF	Windthrow	0, 2–8	1349, 1214–1460	975, 1360–1741	374, -82 to -365	1.38, 0.77–0.94	This study
Tomakomai, Japan, TMK	DNF	Windthrow–plant	48	1673	1461	212	1.15	Hirata et al. (2007)
Appi, Japan, API	DBF	Harvest–mature	ca. 90	1177	899	278	1.31	Yasuda et al. (2012)
Kawagoe, Japan, KWG	DBF	Coppice–insect	ca. 25	1453	1190	263	1.22	Yasuda et al. (1998)
Fujiyoshida, Japan, FJY	ENF	Coppice–mature	ca. 90	1802	1413	388	1.28	Mizoguchi et al. (2012)
Takayama, Japan, TKY	DBF	Mature	ca. 50	978	742	237	1.32	Saigusa et al. (2005)
Kiryu, Japan, KEW	ENF	Plant	43	1539	1060	523	1.45	Takanashi et al. (2005)
Pasoh, Malaysia, PSO	EBF	Mature	> 100	3243	3119	124	1.04	Kosugi et al. (2008)
Kalimantan, Indonesia, DB	BS	Drain–fire	2–6	1071–1428	1662–1871	-318 to -591	0.64–0.82	Hirano et al. (2012)

<sup>1</sup> DBF: deciduous broadleaf forest; DNF: deciduous needle forest; ENF: evergreen needle forest; EBF: evergreen broadleaf forest; MXF: mixed forest; GS: grasses and shrub. <sup>2</sup> Years since last disturbance or stand age. <sup>3</sup> Some data older than 30 years are averaged.

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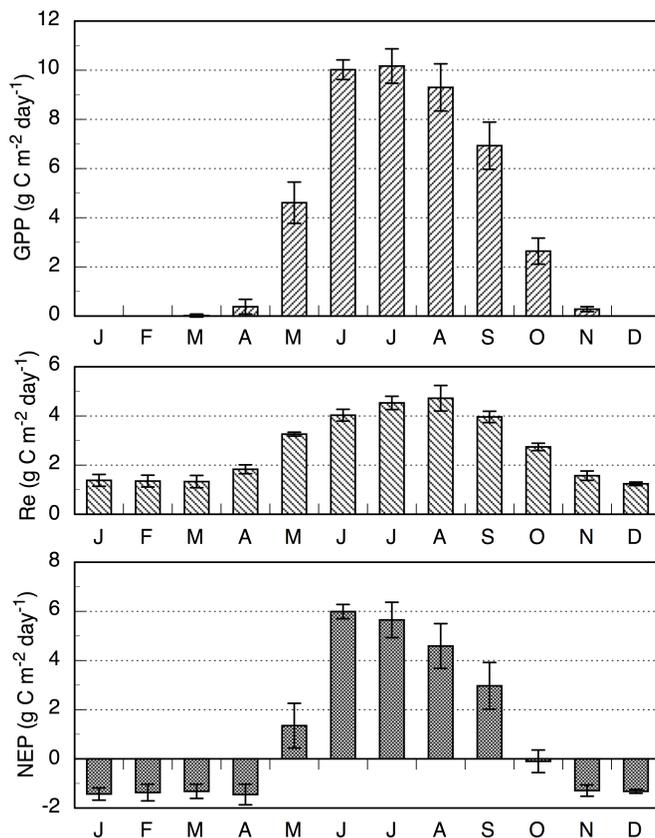


**Figure 1.** Southeast-facing aspect at a deciduous broadleaf forest in Sapporo, Japan. This forest was disturbed by strong wind in September 2004. The picture was taken on 12 May 2005.

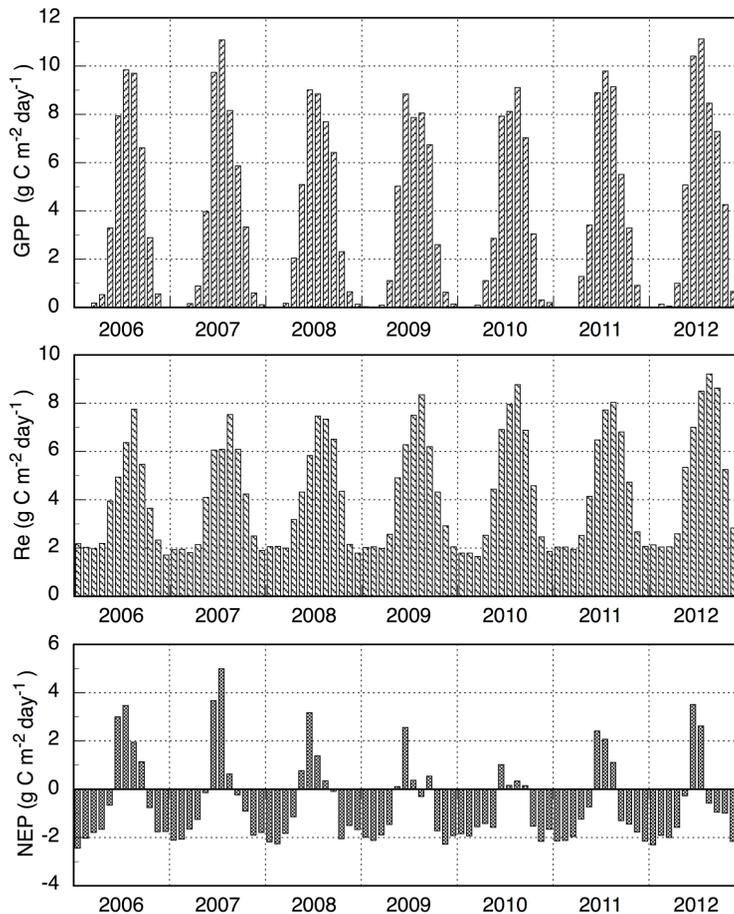
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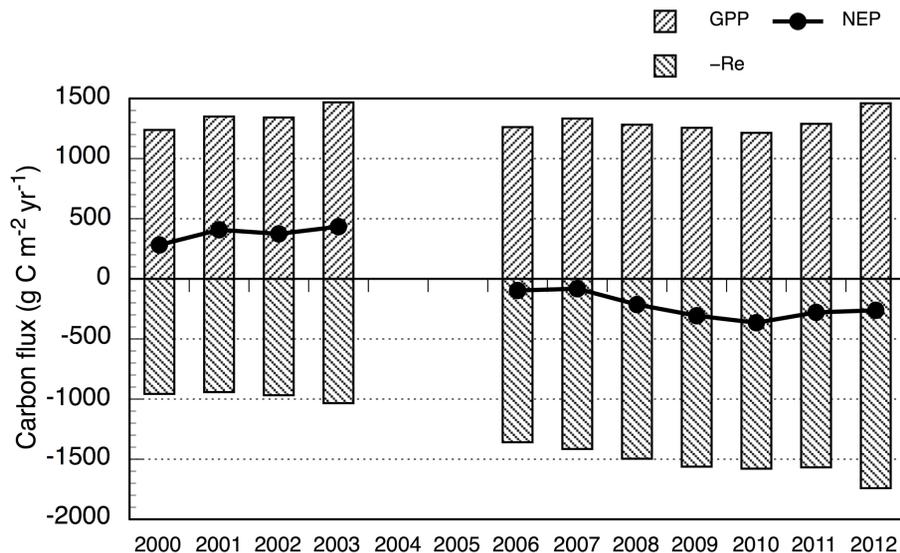
**Figure 2.** Seasonal variations in gross primary production (GPP), ecosystem respiration (Re), and net ecosystem production (NEP) before the disturbance between 2000 and 2003. The fluxes represent 4-year monthly means and standard deviations of daily values ( $\text{g C m}^{-2} \text{ day}^{-1}$ ).



**Figure 3.** Seasonal and interannual variations in gross primary production (GPP), ecosystem respiration (Re), and net ecosystem production (NEP) after the disturbance between 2006 and 2012.

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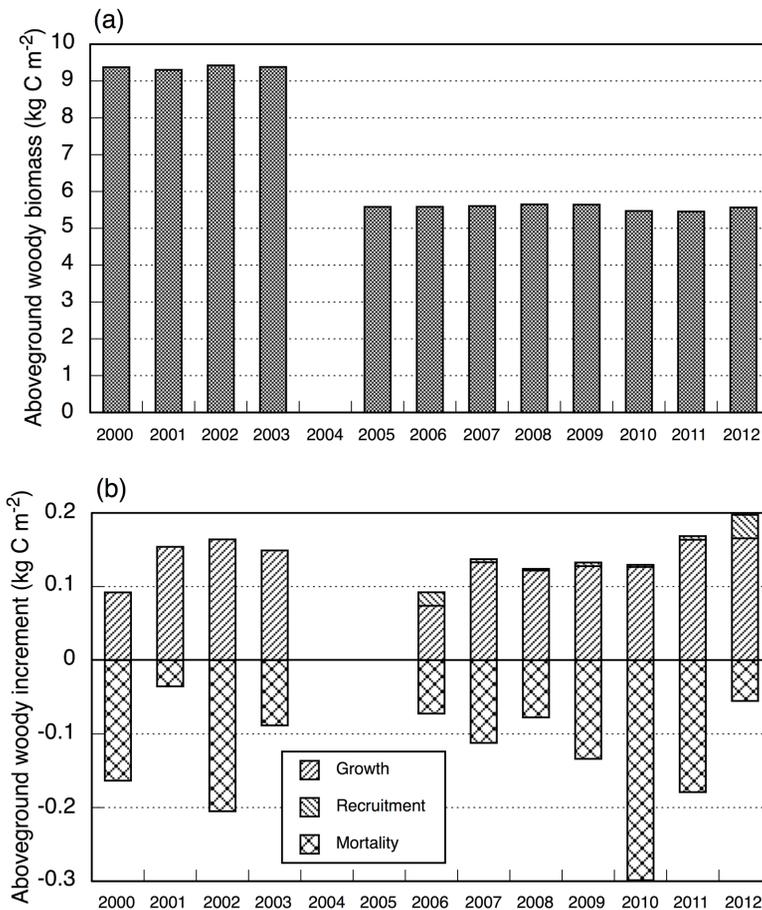


**Figure 4.** Interannual carbon flux changes in gross primary production (GPP), ecosystem respiration (Re), and net ecosystem production (NEP) before and after the disturbance. The values for the annual sums are missing in 2004 and 2005.

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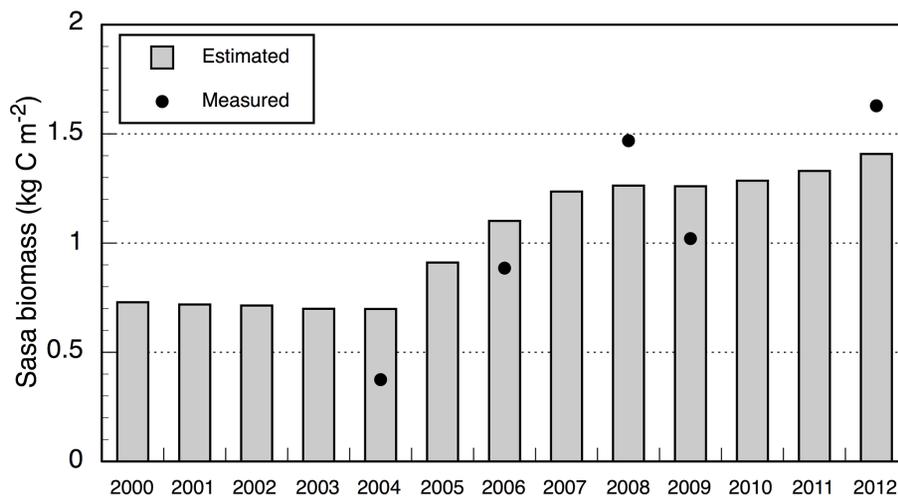
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**Figure 5.** Interannual carbon storage changes in **(a)** aboveground woody biomass and **(b)** the details of increments. The growth components from 2000 to 2004 include the recruitment.

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**Figure 6.** Interannual changes in carbon storage in dwarf bamboo (*Sasa kurilensis* and *S. senanensis*). *Sasa* biomass is estimated from the light transmittance.

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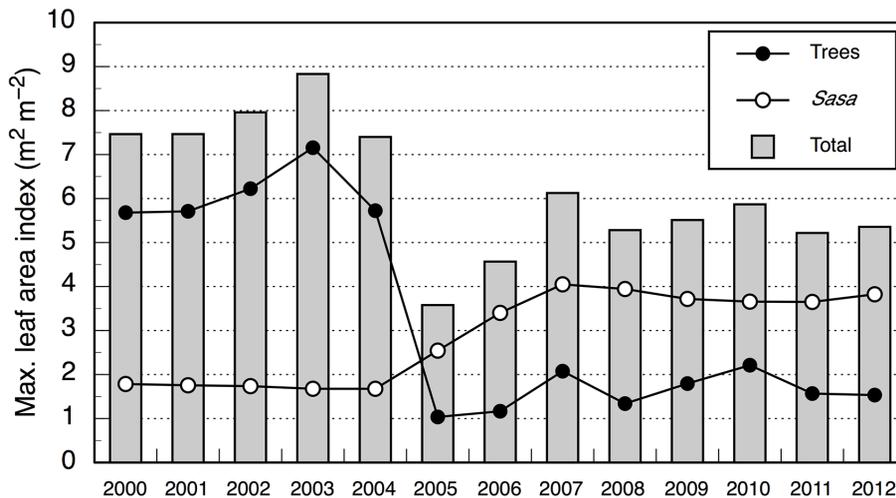
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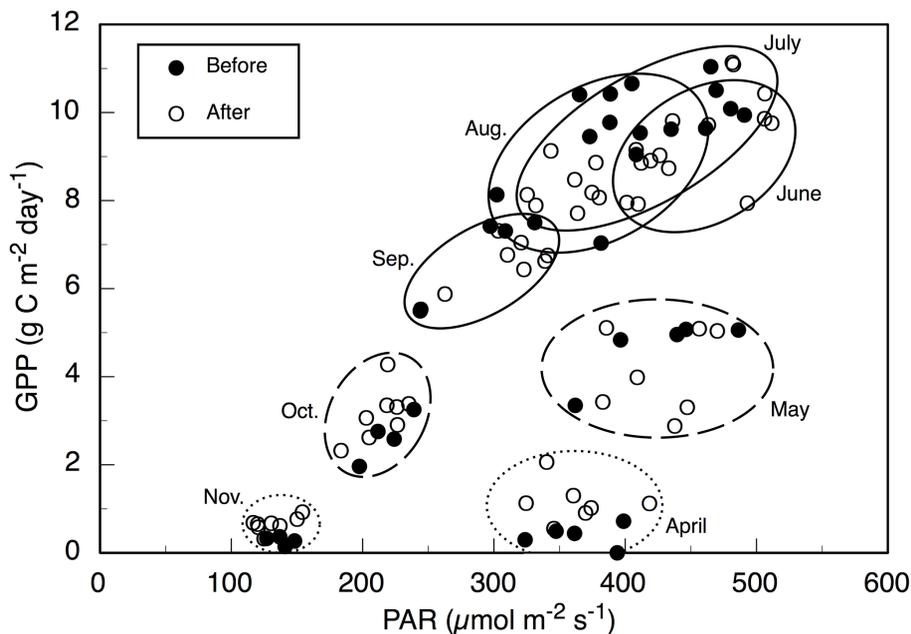


**Figure 7.** Interannual changes in maximum leaf area index in the canopy tree and dwarf bamboo (*Sasa kurilensis* and *S. senanensis*). *Sasa* LAI is estimated from the light transmittance. The data in this figure are quoted from Mizoguchi et al. (2014b).

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**Figure 8.** Relationships between monthly mean gross primary production (GPP) and monthly mean photosynthesis active radiation (PAR) in the snow-free season. Each month's data are enclosed by ellipses. Black and white circles represent monthly data before and after the disturbance, respectively. The snow-free season is separated into three periods. The elliptical solid, broken, and dotted lines indicate the growing season (June–September), transition season (May and October), and leafless season without snow (April and November), respectively.

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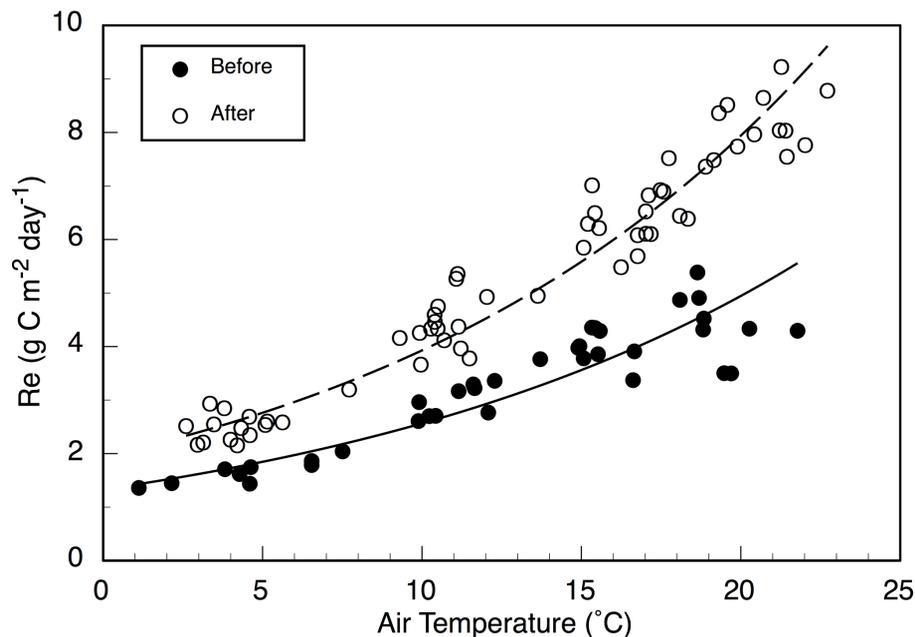
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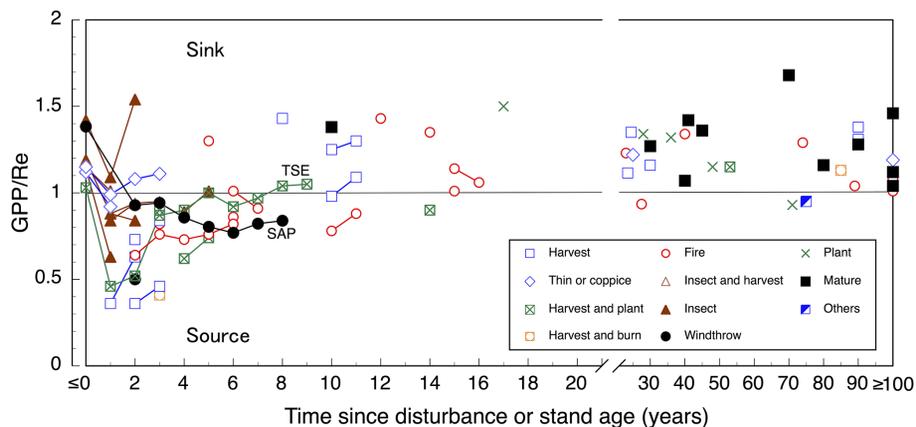
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**Figure 9.** Relationships between monthly mean ecosystem respiration ( $Re$ ) and mean air temperature in the snow-free season. Black and white circles represent values before and after the disturbance, respectively. The solid line indicates the regression equation before the disturbance, i.e.,  $Re = 1.94 \times 2.02^{Ta/10}$ . The broken line indicates the regression equation after the disturbance, i.e.,  $Re = 1.33 \times 1.93^{Ta/10}$ .

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**Figure 10.** The carbon uptake efficiency (GPP/Re) in forest with years since last disturbance in the forest or stand age for the mature forest. The GPP/Re with years  $\leq 0$  (data before disturbance) is plotted on the left axis. Similarly, the GPP/Re with years older than or equal to 100 are plotted on the right axis. Data older than 20 years are averaged. In particular, data of the TSE site (Aguilos et al., 2014) and SAP site (the present study) are indicated. At these two sites, the measurements include periods both before and after the disturbance and were taken for over 10 years.

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