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Carbon balance of a partially harvested mixed conifer forest following mountain pine beetle attack and its comparison to a clear-cut

A. Mathys[1,*], T. A. Black[1], Z. Nesic[1], G. Nishio[2], M. Brown[1,3], D. L. Spittlehouse[4], A. L. Fredeen[5], R. Bowler[5], R. S. Jassal[1], N. J. Grant[1], P. J. Burton[5,6], J. A. Trofymow[6], and G. Meyer[1]

[1]Faculty of Land and Food Systems, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada
[2]FPInnovations, Vancouver, British Columbia, V6T 1W5, Canada
[3]Department of Geography and Environmental Studies, Carleton University, Ottawa, Ontario, K1S 5B6, Canada
[4]Ministry of Forests, Lands and Natural Resource Operations, Victoria, British Columbia, V8W 9C2, Canada
[5]Ecosystem Science and Management Program, University of Northern British Columbia, Prince George, British Columbia, V2N 4Z9, Canada
[6]Pacific Forestry Centre, Canadian Forest Service, Victoria, British Columbia, V2N 4Z9, Canada
[*]now at: Department of Forest Resource Management, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada

Correspondence to: A. Mathys (amathys@alumni.ubc.ca)

Abstract. The recent mountain pine beetle (MPB) outbreak has had an impact on the carbon (C) cycling of lodgepole pine forests in British Columbia. This study examines how partial harvesting as a forest management response to MPB infestation affects the net ecosystem production (NEP) of a mixed conifer forest (MPB-09) in Interior BC. MPB-09 is a 70-year-old stand that was partially harvested in 2009 after it had been attacked by MPB. Using the eddy-covariance technique, the C dynamics of the stand were studied over two years and compared to an adjacent clear-cut (MPB-09C) over the summertime. The annual NEP at MPB-09 increased from $-108 \, \mathrm{g\,C\,m^{-2}}$ in 2010 to $-57 \, \mathrm{g\,C\,m^{-2}}$ in 2011. The increase of NEP was due to the associated increase in annual gross ecosystem photosynthesis (GEP) from $812 \, \mathrm{g\,C\,m^{-2}}$ in 2010 to $954 \, \mathrm{g\,C\,m^{-2}}$ in 2011, exceeding the increase in annual respiration (R_e) from $920 \, \mathrm{g\,C\,m^{-2}}$ to $1011 \, \mathrm{g\,C\,m^{-2}}$ during the two years. During the four month period between June and September 2010, NEP at MPB-09C was $-103 \, \mathrm{g\,C\,m^{-2}}$, indicating high C losses in the clear-cut. MPB-09 was a C sink during the growing season of both years, increasing from $9 \, \mathrm{g\,C\,m^{-2}}$ in 2010 to $47 \, \mathrm{g\,C\,m^{-2}}$ in 2011. The increase of NEP in the partially harvested stand amounted to a recovery corresponding to a 26 % increase in the maximum assimilation rate in the second year. This study shows that retaining the healthy residual forest can result in higher C sequestration of MPB-attacked stands compared to clear-cut harvesting.

1 Introduction

Forest management practices in response to insect outbreaks have an impact on the forest carbon (C) balance. In British Columbia (BC) the mountain pine beetle (MPB) outbreak began in the late 1990s and has affected a total area of 18.1 million ha of pine-leading stands with a recent expansion into Alberta (B.C. Ministry of Forests, Lands and Natural Resource Operations, 2012). The unprecedented scale of the outbreak has killed 710 million m^3 or 53 % of the merchantable pine volume in BC from 1999 to 2011 (Walton, 2012). Reasons for the expansion of the outbreak include climate change, which has been attributed to increasing atmospheric concentrations of carbon dioxide (CO_2) and other greenhouse gases on a global scale (IPCC, 2007).

In Northern BC, minimum air temperature in the winter has increased by 3.5 °C in the past century (Moore et al., 2010; Rodenhuis et al., 2009) allowing the beetle to survive through the winter to the following year (Carroll et al., 2006; Safranyik and Wilson, 2006). Furthermore, fire suppression in BC has led to a large abundance of even-aged mature lodgepole pine stands that provide a favorable habitat for the MPB (Taylor and Carroll, 2004). In response to the outbreak, the provincial government increased the annual allowable cut by 15 million m^3 to about 67 million m^3 per year in Interior BC (Bogdanski et al., 2011; Snetsinger, 2011). The most common forest management strategy in BC is to clear-cut the entire stand. As an alternative practice, partial harvesting can be undertaken to reduce the disturbance of the forest. This can help maintain the forest's role of providing environmental services such as sustaining energy, water and nutrient cycles, providing habitat for wildlife, and reducing runoff to rivers and streams. Furthermore, protecting the non-pine secondary structure provides opportunities for mid-term timber harvest that can help reduce the predicted shortage in 15–50 yr (Nishio, 2010). Coates et al. (2006) define secondary structure as all the non-pine canopy and subcanopy trees as well as seedlings and saplings that survive the beetle outbreak. Accordingly, the stands that contain healthy residual vegetation can already constitute the next generation of forest cover without having to be planted (Burton, 2006; Coates et al., 2006). About 20–30 % of pine-leading stands in north-central BC have been found to have abundant secondary structure that can contribute to the mid-term timber supply (Coates et al., 2006). Local efforts in the Prince George region of BC have attempted to minimize the disturbance on forest soils and vegetation cover through partial harvest operations and improving the sustainability of forest management practices (Nishio, 2010).

Disturbances such as insect infestation, harvesting and fire have been shown to shift Canada's forests from C sinks to C sources (Amiro et al., 2010; Kurz et al., 2008). Currently, there is limited information available on how post MPB-outbreak disturbance affects stand C dynamics. Monitoring forest net ecosystem production (NEP) over the long term has been recommended to help provide a better understanding of how management decisions on insect control affect forest productivity (Amiro et al., 2010; Kurz and Apps, 1999). NEP is the balance of C uptake through gross ecosystem photosynthesis (GEP) and C loss resulting from ecosystem respiration (R_e) over a period of time and is an indicator of whether the stand is sequestering or losing C to the atmosphere. It is obtained as −NEE, the net ecosystem exchange between the land surface and atmosphere, and can be measured using the eddy-covariance (EC) technique (Baldocchi, 2003).

Studies have recently been examining the effects of the MPB on the C dynamics of forests that are left to recover naturally (Brown et al., 2012; Edburg et al., 2011; Kurz et al., 2008). EC measurements were made in two MPB-attacked lodgepole pine stands located approximately 20 and 120 km north of the current study sites (Brown et al., 2010; Brown et al., 2012). The recovery of the two stands occurred faster than previously assumed (Kurz et al., 2008) with C neutrality reached within 3 to 5 yr following the beetle attack (Brown et al., 2012). This was attributed to the compensatory C uptake of the surviving trees and understory vegetation (Bowler et al., 2012), increased light penetration and reduced competition for soil nutrients and water due to tree mortality. Furthermore, growing season C flux measurements of lodgepole pine stands that were clear-cut harvested were found to remain annual C sources for at least 10 yr (Brown et al., 2010). A similar general outcome was reported by Edburg et al. (2011), who used the Community Land Model to determine how long-term C fluxes are affected after MPB outbreaks, with particular outcomes depending on the severity of the outbreak and the snagfall transfer rate (the fall and transfer to coarse woody debris). They predicted a secondary decrease in NEP once the dead standing trees fall, increasing heterotrophic respiration (R_h) due to a greater amount of coarse woody debris available to decompose. Edburg et al. (2011) also simulated NEP responses to clear-cut harvesting of beetle-killed trees and found the harvested stands to be an annual C source for 25 yr before returning to a C sink. Overall they found management decisions to have a major impact on the C balance in post-outbreak stands. Kurz et al. (2008) used the C budget model of the Canadian Forest Sector (CBM-CFS3) to determine the cumulative impact of the MPB outbreak in BC's forests. They predicted a loss of 270 Tg C over a 374 000 km^2 forest area from 2000 to 2020 with the removal of beetle-killed and healthy trees contributing an additional loss of 50 Tg C during salvage harvest operations.

There is a need to understand how forest management practices affect the C exchange processes of forests attacked by MPB. This study determines the impact of partial harvesting on the NEP of a 70-year-old stand using the EC technique and compares the summertime C balance of the partially harvested stand with a nearby clear-cut, harvested at the same time. It is hypothesized that partial harvesting will lower CO$_2$ emissions of the forest compared to clear-cut harvesting. Retaining biomass can maintain the photosynthetic capacity resulting in continued C sequestration in the residual stand. Furthermore, a reduced amount of dead roots, coarse woody debris and litter are left behind to decompose and contribute to R_h compared to a clear-cut. Partial harvesting helps provide a continuous supply of litter fall, which can shade the soil surface and reduce soil temperature and hence R_h, which increases with soil temperature (Taylor et al., 2008). This choice of harvesting practice can increase the forest's capability for C uptake, while at the same time preserve habitats for ecosystem biodiversity and maintain the future economic viability of the forest to meet society's needs by providing a mid-term timber supply within 20–40 yr, compared to approximately 80 yr required for a clear-cut. The objectives of this study were (1) to measure the annual clear-cut NEP of

a partially harvested mixed-conifer stand following an MPB attack, (2) to determine GEP and R_e and how they are affected by environmental factors, (3) to compare NEP, GEP and R_e of the partially harvested stand with values from a nearby clear-cut.

2 Methods

2.1 Site description

The study site (MPB-09) was located on generally level ground in the Interior of BC near Summit Lake, 46 km north of Prince George (Table 1). Following MPB attacks in 2005 and 2006, the 70-year-old stand was partially harvested in a 40 ha cutblock (Nishio, 2010). Harvesting operations occurred from February to March 2009. The beetle-killed lodgepole pine trees were removed along manually selected trails, and the non-pine tree species (i.e. secondary structure) were retained (Fig. 1). In the process, the trees were felled by a feller-buncher and then skidded to roadside landings. This technique reduces the impact of soil compaction by restricting the movement of the logging equipment to the designated trails. Furthermore, deep snow conditions in the winter protected 13–30 % more understory than when harvesting occurred after snow melt (Nishio, 2009). The harvested volume of the partially harvested stand was 152 m³ ha⁻¹ with a total volume of 6022 m³ (Nishio, 2010). He found that overstory basal area was reduced from 39.6 m² ha⁻¹ prior to harvesting to 7.6 m² ha⁻¹ after harvesting in 2009. The residual canopy was composed of a combination of black spruce (*Picea mariana*), hybrid white spruce (*Picea engelmannii × glauca*) and subalpine fir (*Abies lasiocarpa*) trees. The understory consisted of small tree and shrub species, including pink spiraea (*Spiraea douglasii* ssp. *menziesii*), bearberry honeysuckle (*Lonicera involucrata*) and willow (*Salix* spp.). In May 2010, the stand was replanted with tree seedlings consisting of 57 % lodgepole pine and 43 % hybrid white spruce at a planting density of 1370 stems ha⁻¹ within both the harvested trails and retention areas. Soil, vegetation and overstory characteristics were also measured in 2010 at MPB-09 on three National Forest Inventory (NFI, 2008) ground plots within 50 m of the flux tower. Measurements indicated that stand density and overstory basal area were 308 ± 113 (mean and standard deviation) stems ha⁻¹ and 5.6 ± 1.0 m² ha⁻¹, respectively. The groundcover consisted of mosses, grasses and ferns. Coarse woody debris, plant litter and exposed soil were also found on the forest floor as a result of the harvesting activities. The soil is classified as an Orthic Gray Luvisol with a silty clay loam texture derived from glaciolacustrine deposits (P. Sanborn, personal communication, 2012). The surface organic layer (LFH) had an average thickness of 8 cm. Site characteristics are summarized in Table 1. Adjacent to MPB-09 was a 4.2 ha clear-cut (MPB-09C), which had the same understory composition and soil type as in

Table 1. Site description for MPB-09 after partial harvesting. Values in parentheses indicate standard deviations (±S.D.) from the mean.

	MPB-09
Stand age (yr)	$\sim 70 \, (\pm 10)$[a]
Site location	54°13′25.4″ N
	122°36′53.5″ W
Elevation (m)	680
Canopy height (m)	$\sim 16 \, (\pm 4)$
Stand density (stems ha⁻¹)	435[b]
Overstory basal area (m² ha⁻¹)	7.6[c]
Dominant tree species	*Picea mariana*, *Picea engelmannii × glauca*, *Abies lasiocarpa*
Understory vegetation	*Spiraea douglasii*, *Lonicera involucrata*, *Salix* spp.
Overstory LAI (m² m⁻²)	1.3
Soil classification	Orthic Gray Luvisol[d]
Litter-fibric-humus (LFH) C (kg ha⁻¹)	30.6–42.6
Average ($n = 3$) LFH thickness (cm)	8 (± 4)
Mineral soil C (0–55 cm) (kg ha⁻¹)	75.6–158.9
Fine mineral soil bulk density (kg m⁻³)	1247–1495[e]
Soil texture	Silty clay loam

[a] Age determined from 52 samples.
[b] Values for the tower footprint area.
[c] Value for the full partial cut block (Nishio, 2010).
[d] P. Sanborn (UNBC, personal communication, 2012).
[e] Volumetric coarse fraction was < 1 %.

the partially harvested stand (Nishio, 2010). It lies approximately 1 km north of MPB-09 and was harvested at the same time. The harvested volume of the clear-cut was 474 m³ with a smaller average tree size than MPB-09. It was replanted with the same seedlings as the partially harvested stand in the spring of 2010. Both MPB-09 and MPB-09C are in the Sub-Boreal Spruce Biogeoclimatic Zone (SBSmk1) (Meidinger and Pojar, 1991).

2.2 Flux and climate measurements

Eddy-covariance and climate measurements have been continuously made since October 2009 at MPB-09. Instruments were mounted on a scaffold tower that was 2.1 m long, 1.5 m wide and 32 m high. An ultrasonic anemometer (model CSAT3, Campbell Scientific Inc. (CSI), Logan, Utah, USA) was installed at a height of 26 m to measure components of the wind vector and air temperature, along with an open-path infrared gas analyzer (IRGA, model LI-7500, LI-COR Inc., Lincoln, Nebraska, USA) to measure CO_2 and water vapor densities at a frequency of 10 Hz. The tower was located near the SE edge of the cut block with the EC sensors mounted on the west side of the tower. This ensured that the flux footprint lay mainly within the partially harvested stand since the prevailing wind direction was from the NW to SW. Instrument calibrations were performed in the laboratory prior to
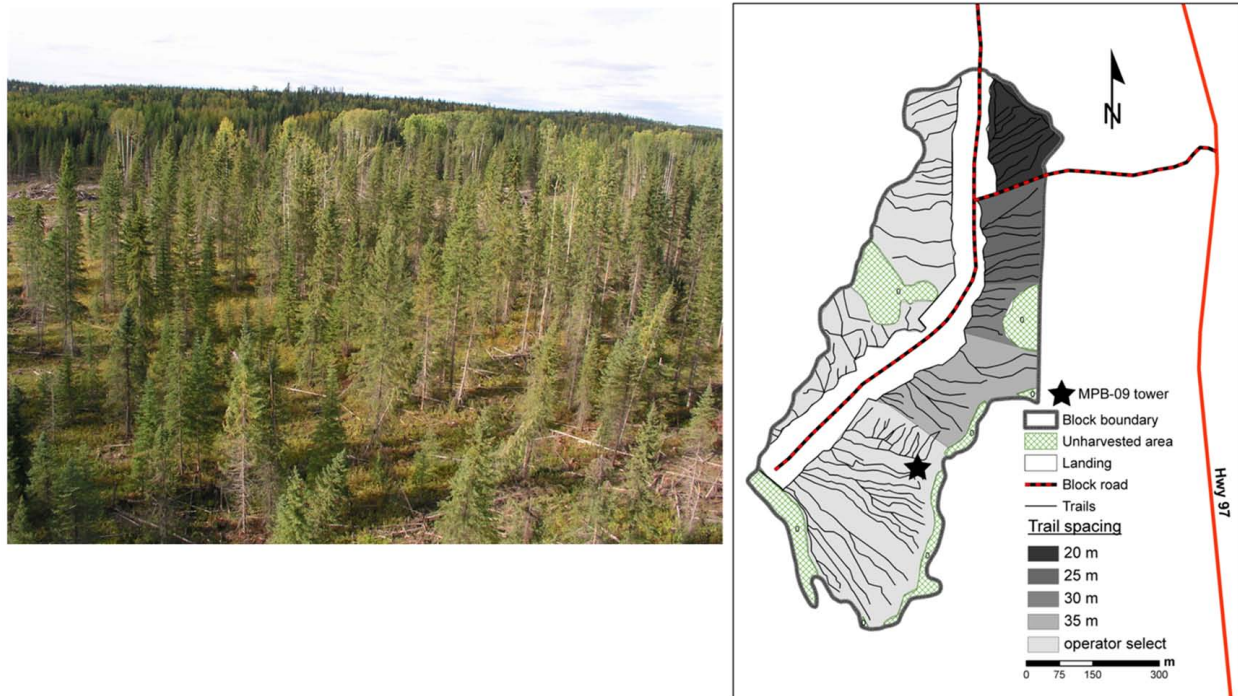
Fig. 1. Photograph and schematic diagram of the partially harvested stand with locations of the MPB-09 flux tower and harvesting trails. The clear-cut, MPB-09C, is located 1 km north of MPB-09. Source: Nishio (2010).

installation at the site. The IRGA was replaced in 2011. The calibration of the replaced IRGA was checked in the laboratory and found to show little change in both the sensitivity and offset. Climate measurements included air temperature and relative humidity (model HMP45C, Vaisala Oyj, Helsinki, Finland). Comparison of calculated specific humidity from the IRGA water vapor density with the HMP45C showed that the measurements were in good agreement during the two years of the study. Downwelling and upwelling shortwave radiation and longwave radiation were measured with a net radiometer (model CNR1, Kipp and Zonen B.V., Delft, the Netherlands) above the canopy at the 30 m height and below the canopy upwelling shortwave radiation was measured with a Black & White Pyranometer (model 8-48, Eppley Laboratory Inc., Newport, Rhode Island, USA) at the 3 m height. Quantum sensors (model LI-190AS, LI-COR Inc.) were used to measure downwelling and upwelling photosynthetically active radiation (PAR) above the canopy as well as below-canopy downwelling PAR. Rainfall was measured with a tipping-bucket rain gauge (model 52203 R.M. Young Co., Traverse City, MI) at the 5 m height, providing an adequate angle of catch in an open area where interception by the canopy was negligible. Wind speed was recorded with a propeller-vane anemometer (model 05103 R.M. Young Co.). Two soil profiles were established to measure soil temperature at depths of 3, 10, 20, 50 and 100 cm using soil thermistors (model ST100, Apogee Instruments Inc. Logan, Utah,

USA). Volumetric soil water content was also measured in two soil profiles at 3, 20, 50 and 100 cm depths with water content reflectometers (model CS615 and CS616, CSI). Soil heat flux was measured at the 3 cm depth with 4 soil heat flux plates that were homemade (using Peltier coolers) and calibrated at UBC, and was corrected for heat storage in the 3 cm soil surface layer. The surface temperature of the forest floor was measured with a downward-facing infrared radiometer (model Apogee SI-111, CSI) and snow depth with an acoustic distance sensor (model SR50A, CSI) mounted at 3.6 m height. Snowfall was estimated by converting changes in snow depth to snow-water equivalent using a density of $100 \, \text{kg} \, \text{m}^{-3}$. The climate measurements were sampled at a rate of 0.5 Hz. Climate and flux data were recorded on two data loggers (model CR1000, CSI). The half-hour averages and covariances used to derive the turbulent fluxes were calculated and sent to UBC Biometeorology Laboratory via cell-phone connection on a daily basis. A compact flash card stored the high frequency data and was replaced every 2–4 weeks. The system was powered by three 100 W solar panels and an 800 Ah battery unit as described in Brown et al. (2010).

The forest leaf area index (LAI) was measured in 2011 using a LI-COR Plant Canopy Analyzer (model LAI-2000, LI-COR Inc.) and a Tracing Radiation and Architecture of Canopies (TRAC) system (Third Wave Engineering, Nepean,

Ontario, Canada) following the procedure outlined by Chen et al. (2006).

At MPB-09C, EC measurements were made during the summer of 2010 (10 June–22 September), using the same instruments as above but mounted on a tripod at 2.2 m above the ground. The EC and climate data were recorded on a data logger (model CR5000, CSI) and the system was powered by a 100 W solar panel.

2.3 Data analysis and quality control

2.3.1 Flux calculations

Fluxes of CO_2 (F_c) and water vapor (i.e., evapotranspiration) (E) were calculated by multiplying the dry air density by the covariances of the vertical wind speed (w) and the CO_2 and water vapor mixing ratios, respectively. The covariances were block-averaged in 30 min intervals with no detrending applied. Three coordinate rotations were performed on each half-hour average to align the vertical wind velocity measurement normal to the mean wind streamlines, bringing the mean vertical ($\bar{w}$) and lateral ($\bar{v}$) wind vector components as well as the covariance between these components ($\overline{w'v'}$) to zero (Tanner and Thurtell, 1969). Half-hour averaged data points were removed when instruments malfunctioned during events such as snow, rain and frost by setting limits of average, minimum, maximum and standard deviations on CO_2 and water vapor fluxes. The data were also visually inspected and the high frequency data were examined before removing data points that deviated from the general course of the time series. NEE was calculated using:

$$\text{NEE} = F_c + S_t, \tag{1}$$

where S_t is the rate of change of CO_2 storage in the air column below the EC system. The storage term was calculated using the difference between the mean mixing ratio for the following and previous half hour at EC sensor height (Morgenstern et al., 2004). To deal with the questionable nighttime flux measurements in calm conditions, data were rejected when the friction velocity (u_*) fell below a threshold (u_{*th}) of 0.2 m s^{-1}. This value was determined by sorting increasing nighttime NEE according to u_* into bin averages of 100 data points each and identifying at what u_* value NEE no longer increased. Flux measurements were also removed when the wind direction was from NE to SE (45–135°), as the footprint extended outside the partially harvested stand. This also removed data points corresponding to when the wind blew through the tower before reaching the EC system that was oriented in a westward direction.

The use of open-path IRGAs during wintertime has been found to result in unexpected CO_2 uptake (Lafleur and Humphreys, 2007; Burba et al., 2008; Bonneville et al., 2008). Burba et al. (2008) attributed this to the heat generation inside the IRGA, leading to a sensible heat flux inside the open-path array which affects the CO_2 density, and

proposed applying a sensor-heating correction. There is a lack of consensus on the issue because some comparisons of flux measurements using open- and closed-path analyzers (Wohlfahrt et al., 2008; Bowling et al., 2010) have shown much better agreement without the sensor-heating correction. Using an LI-7500, Amiro (2010) also found apparent ecosystem uptake of CO_2 in frozen soil conditions when a small respiratory flux was expected and they found that removing such data followed by gap-filling worked just as well. Burba et al. (2008) found that sensor heating decreased for wind speeds exceeding 6–8 m s^{-1}. Consequently, we discarded all wintertime fluxes when NEE < 0 and daytime winter data when wind speed < 4 m s^{-1} as described in Brown et al. (2010). Although removing only negative NEE values in wintertime would have introduced a bias towards greater CO_2 loss, sensor heating of the LI-7500 would have caused some reduction in measured F_c (i.e., R_e) during winter months.

Missing data during the rest of the year were gap-filled according to standard methods developed by the Fluxnet Canada Research Network (Barr et al., 2004). Respiration was modeled using a logistic equation relating nighttime R_e to soil temperature at the 3 cm depth:

$$R_e = \frac{r_1}{1 + \exp[r_2(r_3 - T_s)]}, \tag{2}$$

where r_1, r_2 and r_3 are model-fitted empirical constants. Equation (2) was used to gap-fill nighttime data and calculate daytime half-hourly R_e (the latter using daytime T_s). Half-hourly GEP values were calculated by adding measured daytime NEP to modeled daytime R_e. Gaps in GEP were filled using the rectangular hyperbolic Michaelis–Menten relationship with PAR (Q):

$$\text{GEP} = \frac{\alpha Q A_{\max}}{\alpha Q + A_{\max}}, \tag{3}$$

where α is the quantum yield and $A_{\max}$ is the photosynthetic capacity. Annual relationships were first used to model R_e and GEP values using Eqs. (2) and (3), which then were adjusted by including an additional parameter. This time-varying parameter was used to make the modeled mean value equal to the mean measured value within a moving window interval, which was 100 points wide and moved at an increment of 20 points at a time (Barr et al., 2004). The gap-filling procedure was slightly altered according to Brown et al. (2010) by not applying the moving window during the wintertime when large data gaps occurred. When high frequency data from the flash card were lost due to technical issues, fluxes were calculated by applying the WPL equation (Webb et al., 1980) to the half-hour averaged covariances sent from the data logger on a daily basis.

2.3.2 Uncertainty analysis

Uncertainties exist in the annual totals of NEP, GEP and R_e, which are caused by random and systematic errors. The

primary systematic error, which is caused by occurrence of low wind speeds at night, was dealt with by applying the u_* threshold of $0.2\,\mathrm{m\,s^{-1}}$ as described above. The effect of random error on the uncertainty of annual NEP was calculated by assigning a random error of 20 % to each half-hourly measurement (Wesely and Hart, 1985; Morgenstern et al., 2004). A Monte Carlo simulation was used to obtain the uncertainty in gap-filling where gaps up to 40 % of the year were generated using a uniformly distributed random number generator with continuous gaps of up to 10 days (Krishnan et al., 2006). The missing data were then filled using the soil temperature and light response functions as described above (Eqs. 2 and 3) and the new annual sums of NEP, GEP and R_e were calculated. The procedure was repeated 500 times in order to determine the 95 % confidence interval. All data analysis and statistical calculations were carried out with Matlab (Version 7.5.0, The MathWorks, Natick, MA, USA).

To assess the quality of the EC measurements, an energy balance closure analysis was conducted but a correction was not applied to the flux data. The sum of the turbulent fluxes of sensible (H) and latent heat (λE), where λ is the latent heat of vaporization, was plotted against the available energy flux, which was computed as net radiation minus soil heat flux minus the rate of change in energy storage in the air column and biomass per unit ground area (Brown et al., 2013). The slope of the regression line remained constant at 0.80 during the two years of measurements.

3　Results

3.1　Climate data

The climate at the site is characterized by cold winters and short warm summers with moderate annual precipitation (P) typical for the Sub-Boreal Spruce zone. Historical mean annual air temperature (T_a) measured at the Prince George Airport is 4 °C for 1971–2000 (Environment Canada, 2012). Measurements at MPB-09 showed that 2010 was a warmer and drier year with a mean annual T_a of 4.9 °C compared to 3.0 °C in 2011 (Fig. 2; Table 2). Growing season rainfall in 2010 was 120 mm less than in 2011. During the dry summer of 2010, volumetric soil water content (θ) at the 3 cm depth decreased to its lowest value of $0.26\,\mathrm{m^3\,m^{-3}}$ on 21 August, with only 16 mm of rainfall during the previous 55 days (Fig. 3). The corresponding soil water matric potential of $-200\,\mathrm{kPa}$ suggests that soil water was available to plants at $\theta > 0.26\,\mathrm{m^3\,m^{-3}}$. In contrast, 156 mm of rain fell during the same period in the following year during which θ remained at an average value of $0.55\,\mathrm{m^3\,m^{-3}}$. An extended dry period in 2010 was also observed at two lodgepole pine stands nearby (Brown et al., 2012). Annual P at MPB-09 increased from 506 mm in 2010 to 864 mm in 2011. The coldest wintertime temperatures observed at the site during the two years of study were -30 °C on 23 November 2010 and -33 °C

Table 2. Mean annual and growing season climate conditions at MPB-09.

	2010	2011
T_a (26 m) (°C)	4.9 (12.7)[a]	3.0 (11.6)
T_s (3 cm) (°C)	6.1 (12.0)	5.3 (10.9)
P (mm)	506 (225)	864 (343)
θ ($\mathrm{m^3\,m^{-3}}$) (3 cm depth)	0.49 (0.44)	0.55 (0.55)
Q ($\mathrm{\mu mol\,m^{-2}\,s^{-1}}$)[b]	245 (406)	224 (345)
Growing season length[c] (days)	158	146

[a] Growing season values are in parentheses.
[b] 24 h average.
[c] Growing season length defined as days when daily mean $T_\mathrm{a} > 0$ °C and $T_\mathrm{s} > 1$ °C.
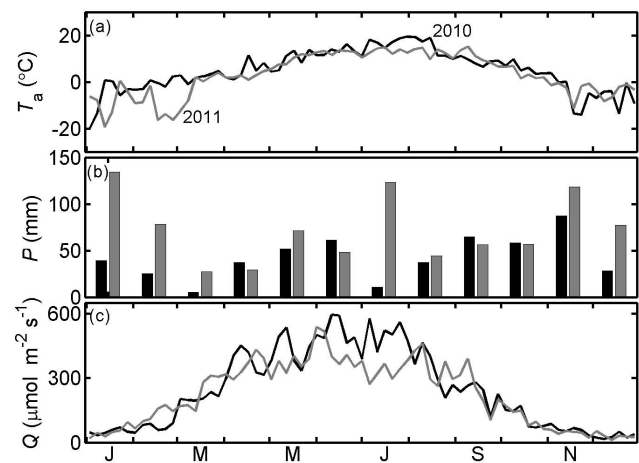

Fig. 2. Climate data at MPB-09 for 2010 and 2011 with **(a)** 5-day averaged air temperature (T_a), **(b)** monthly total precipitation (P) and **(c)** 5-day averaged downwelling PAR (Q).
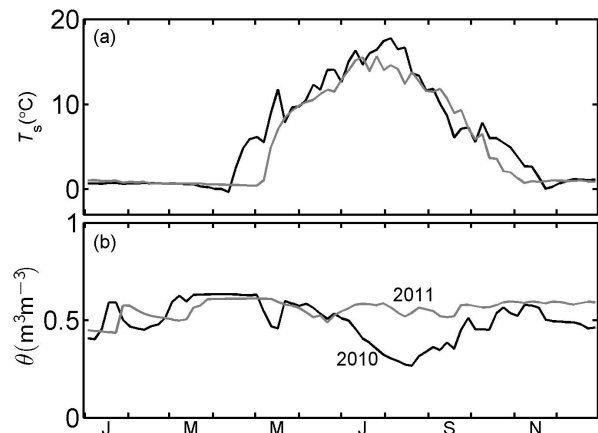
Fig. 3. Interannual variability in **(a)** 5-day averaged soil temperature (T_s) and **(b)** volumetric soil water content (θ) at the 3 cm depth at MPB-09 for 2010 and 2011.

on 19 February 2011. During both years, snowfall began in mid-November and a 1 m-deep snow layer persisted for 4–5 months during the winter. During this time, a minimum T_s of $-0.5\,^\circ\mathrm{C}$ was observed near the soil surface at the 3 cm depth. Snowmelt was complete on 2 April 2010 and 27 April 2011, and was followed by an increase in T_s in the upper 20 cm of the soil profile. The growing season length (daily mean $T_a > 0\,^\circ\mathrm{C}$ and daily mean T_s at the 3 cm depth $> 1\,^\circ\mathrm{C}$) lasted almost two weeks longer in 2010 than in 2011.

3.2 Seasonal and diurnal variation in NEP

Monthly C exchange varied between the two years and their seasons (Fig. 4). NEP was greater during the spring of 2010 than in 2011. In 2010, the monthly total NEP was $8.6\,\mathrm{g\,C\,m^{-2}}$ in April and $3.7\,\mathrm{g\,C\,m^{-2}}$ in May, whereas in 2011 it was $4.8\,\mathrm{g\,C\,m^{-2}}$ and $4.0\,\mathrm{g\,C\,m^{-2}}$ in the two months respectively. In 2010, the earlier onset of spring with higher T_a and T_s compared to 2011, led to a greater C uptake during the daytime, which more than compensated for the high C losses during the nighttime in April and May. In both years, the highest NEP was in June, with monthly total values of 25.1 and $42.9\,\mathrm{g\,C\,m^{-2}}$ in 2010 and 2011, respectively. Monthly total NEP in June 2011 was almost twice the value of June 2010, due to much higher daytime values in 2011, while nighttime values remained the same. The greater C uptake during the daytime in 2011 was due to a higher GEP as a result of increasing vegetation growth, perhaps in response to more light penetration through the canopy and reduced competition for nutrients and water following the lodgepole pine removal. Nighttime C loss reached its highest values in July of both years with minimum NEP values of $-5.7\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in 2010 and $-8.2\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in 2011 (Fig. 4d). During the second half of the growing season monthly NEP declined in both years and became negative in August 2010 but remained positive in August 2011 (Fig. 4e). This shows that while R_e dominated in August 2010, GEP dominated in August 2011. By September, CO_2 respired during the nighttime exceeded photosynthetic uptake during the daytime leading to a negative monthly NEP in both years.

3.3 Annual NEP, GEP and R_e

The annual courses of the 5-day averages of NEP, GEP and R_e, along with E are shown in Fig. 5. In both 2010 and 2011, NEP was generally positive during the growing season with a greater CO_2 uptake in 2011. NEP reached its lowest value of $-1.9\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ in October 2010 and September 2011. In July, GEP reached its highest value of $6.7\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ in 2010 and $9.4\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ in 2011. The highest value of R_e was also observed in July, increasing from $6.0\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ in 2010 to $8.4\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ in 2011. During the wintertime when R_e dominated the forest C balance, the average values of NEP in 2010 and
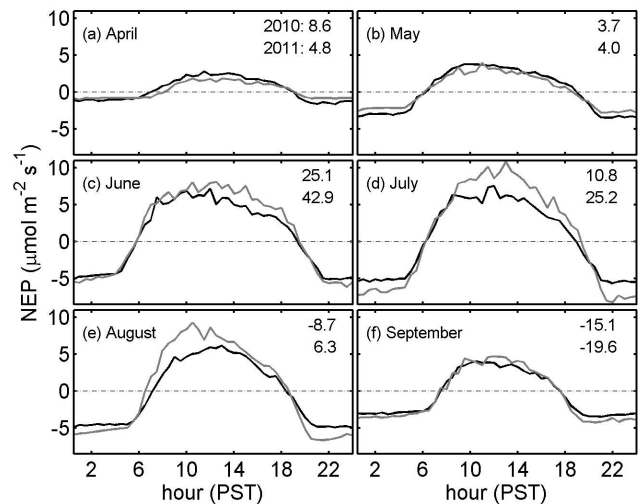

Fig. 4. Ensemble-averaged diurnal net ecosystem production (NEP) during the growing season of 2010 (black lines) and 2011 (grey lines) showing **(a)** April **(b)** May **(c)** June **(d)** July **(e)** August and **(f)** September. Monthly NEP values for the two years shown in the panels are in $\mathrm{g\,C\,m^{-2}\,month^{-1}}$.
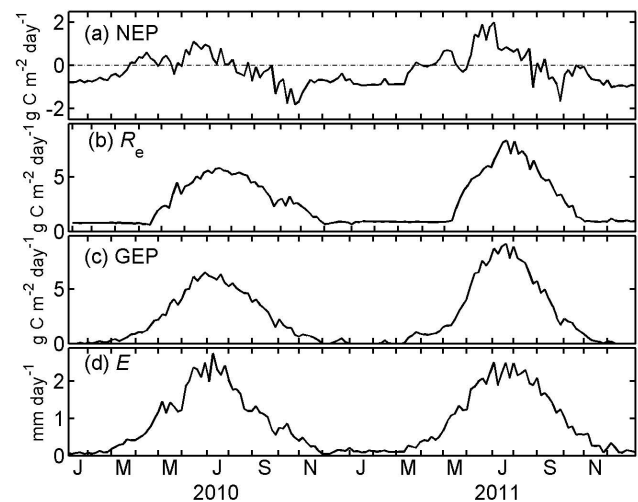

Fig. 5. 5-day averaged **(a)** net ecosystem production (NEP), **(b)** ecosystem respiration (R_e) **(c)** gross ecosystem photosynthesis (GEP) and **(d)** evapotranspiration (E) in 2010 and 2011.

2011 were $-0.57\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ and $-0.76\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$, respectively.

Annual NEP increased from $-108\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2010 to $-57\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2011 (Fig. 6; Table 3). The stand remained an annual C source in both years, but the C loss was lower in the second year. GEP increased from $812\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2010 to $954\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2011. This increase was greater than that of R_e, which was from $920\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2010 to $1011\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2011. The proportionally greater increase in GEP in relation to that of R_e, in the second year after harvesting explains the

Table 3. Annual totals of net ecosystem production (NEP), gross ecosystem photosynthesis (GEP), ecosystem respiration (R_e) in and evapotranspiration (E) at MPB-09*. Values in parentheses show the lower and upper 95 % confidence intervals for the annual totals derived from the Monte Carlo simulation (see Sect. 2.3.2 for details).

	NEP $(\mathrm{g\,C\,m^{-2}\,yr^{-1}})$	GEP $(\mathrm{g\,C\,m^{-2}\,yr^{-1}})$	R_e $(\mathrm{g\,C\,m^{-2}\,yr^{-1}})$	E (mm)
2010	−108 (−120, −98)	812 (798, 823)	920 (908, 929)	316
2011	−57 (−72, −45)	954 (932, 971)	1011 (987, 1040)	332

* Recent analysis indicates that in 2012, annual totals of NEP, GEP and R_e at MPB-09 were −52, 922 and 974 $\mathrm{g\,C\,m^{-2}}$, respectively.
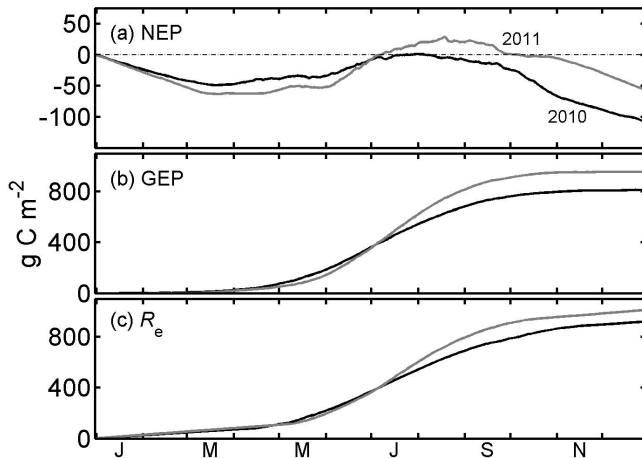

Fig. 6. Cumulative annual **(a)** net ecosystem production (NEP), **(b)** gross ecosystem photosynthesis (GEP) and **(c)** ecosystem respiration (R_e) in 2010 and 2011.

Fig. 7. Relationship between nighttime ecosystem respiration (R_e) with friction velocity threshold ($u_{*\mathrm{th}}$) applied ($u_{*\mathrm{th}} = 0.2\,\mathrm{m\,s^{-1}}$) and 3 cm soil temperature (T_s) in 2010 and 2011. Each data point is an average of 10 half-hour values. The equation parameters are given in Table 4.

significant increase of NEP despite the shorter growing season length in 2011. The 95 % confidence intervals on the annual totals of NEP, GEP and R_e indicate that the annual values were significantly different in the two years and that the stand was clearly a C source in 2010 and 2011 (Table 3). Furthermore, the 20 % random error associated with each half-hour measurement of NEP resulted in an uncertainty of less than 3 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in both years.

3.4 Environmental controls on R_e and GEP

The relationship between nighttime R_e and T_s at the 3 cm depth was described using the logistic model (Eq. 2; Fig. 7). At lower T_s, R_e showed a similar response in both years. For $T_s > 10\,^\circ\mathrm{C}$, the increase of R_e was greater in 2011. T_s explained 58 % of the variance in R_e in 2010 and 48 % in 2011. The relationship between temperature-normalized R_e and θ at the 3 cm depth was found to be very weak ($r^2 = 0.0036$) indicating that the difference in response at higher temperatures could not be explained by differences in soil moisture between the two years. For $T_s > 10\,^\circ\mathrm{C}$, higher values of R_e in 2011 were likely due to higher autotrophic respiration (R_a) associated with higher GEP in that year.
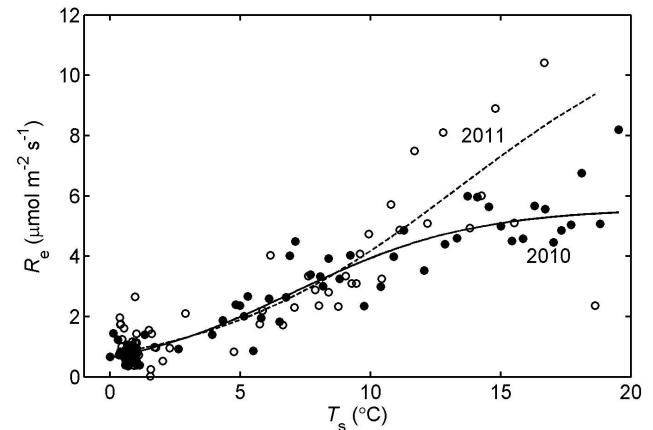
The relationship between GEP and Q was modeled using the rectangular hyperbolic light response function, i.e. the Michaelis–Menten relationship (Eq. 3). The photosynthetic capacity ($A_{\max}$) increased by 26 % from 12.1 $\mathrm{\mu mol\,m^{-2}\,s^{-1}}$ in 2010 to 15.2 $\mathrm{\mu mol\,m^{-2}\,s^{-1}}$ in 2011 (Fig. 8; Table 4). Moreover, quantum yield (α) increased from 0.044 $\mathrm{mol\,C\,mol^{-1}}$ photons in 2010 to 0.066 $\mathrm{mol\,C\,mol^{-1}}$ photons in 2011.

3.5 Evapotranspiration

The seasonal course of E at MPB-09 followed more or less that of GEP (Fig. 5d). The maximum 5-day average E occurred at the beginning of July and was 2.8 $\mathrm{mm\,day^{-1}}$ in 2010 and 2.6 $\mathrm{mm\,day^{-1}}$ in 2011. E was generally higher during the first part of the 2010 than in the following year, but declined in late summer (July to September) due to reduced rainfall. Annual E at MPB-09 was 316 mm in 2010 and 332 mm in 2011 (Table 3). Brown et al. (2012) obtained a similar annual value (284 mm) for 2010 in an unharvested MPB-attacked stand with significant secondary structure located 30 km north of MPB-09. A highly significant

Table 4. Parameters for the relationships of nighttime respiration (R_e) to soil temperature at the 3 cm depth (T_s) using the logistic equation, and the relationships of gross ecosystem photosynthesis (GEP) to downwelling PAR (Q) using the Michaelis–Menten function.
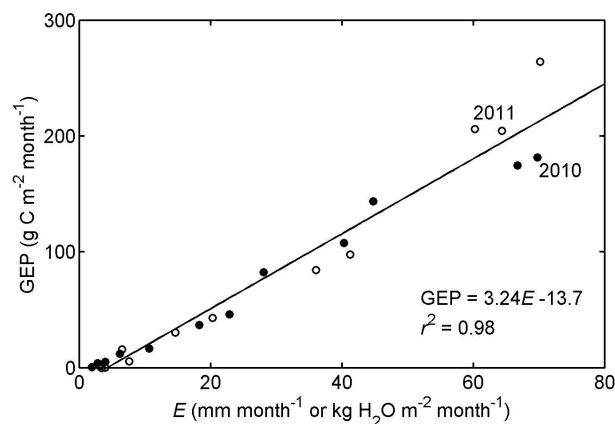
Year	Nighttime R_e and T_s				GEP and Q		
	r_1 (μmol m^{-2} s^{-1})	r_2 (°C^{-1})	r_3 (°C)	r^2	α (mol mol^{-1} photons)	A_{max} (μmol m^{-2} s^{-1})	r^2
2010	5.55	0.30	6.92	0.58	0.044	12.1	0.26
2011	12.73	0.21	13.50	0.48	0.066	15.2	0.26
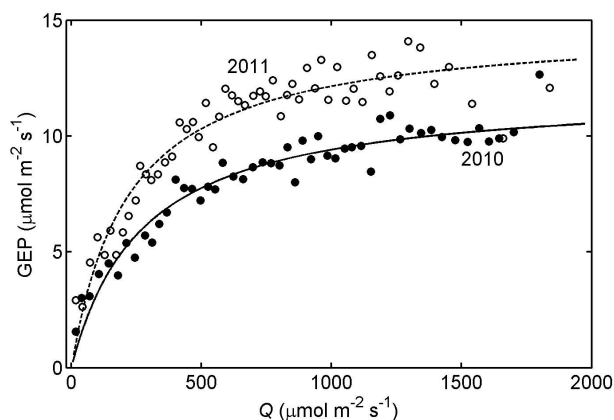
Fig. 8. Light-response curve showing gross ecosystem photosynthesis (GEP) plotted against downwelling PAR (Q) for 2010 and 2011. Each data point is an average of 50 half-hour values. The equation parameters are given in Table 4.

Fig. 9. Relationship between monthly mean gross ecosystem photosynthesis (GEP) and evapotranspiration (E) at MPB-09 in 2010 and 2011. The line and equation is the linear regression relationship for all points.

linear correlation ($r^2 = 0.98$, $p < 0.001$) was found between monthly mean values of GEP and E for both years with a mean monthly water use efficiency (WUE = GEP/E) of 3.24 g C kg^{-1} H$_2$O (Fig. 9). However, growing season average WUE in 2010 of 2.77 g C kg^{-1} H$_2$O was lower than the value of 3.15 g C kg^{-1} H$_2$O in 2011. The lower value in 2010 may be due to the higher contribution of soil evaporation in 2010 caused by sparse groundcover following the harvesting disturbance.

3.6 Comparison of NEP following partial and clear-cut harvesting

During the period between June and September 2010, the clear-cut (MPB-09C) was a C source with monthly total NEP values ranging from -15 g C m^{-2} month^{-1} in June to -50 g C m^{-2} month^{-1} in September (Fig. 10). In comparison, the partially harvested stand (MPB-09) was a C sink in June and July and a weak source in August and September of 2010. For all 4 months, MPB-09C was a large C source of 103 g C m^{-2}, while MPB-09 was a weak C sink of 9 g C m^{-2} over the same time period of 2010 and of 47 g C m^{-2} in 2011 (Table 5). Furthermore, GEP and R_e totals were 294 g C m^{-2} and 397 g C m^{-2} for MPB-09C and 530 g C m^{-2} and 521 g C m^{-2} for MPB-09, respectively. Av-

erage daily (24 h) NEP at MPB-09C was -1.0 g C m^{-2}. In comparison, measurements made in a nearby 2-year-old clear-cut and a 10-year-old clear-cut in July and August of 2007 showed the average daily NEP to be -0.87 and -0.37 g C m^{-2}, respectively (Brown et al., 2010).

4 Discussion

4.1 NEP of the partially harvested stand

In the first two years after partial harvesting the MPB-attacked stand, MPB-09 was a C sink during the growing season, but the high R_e during winter months caused it to be an annual C source in both years. The annual NEP increased from -108 g C m^{-2} in 2010 to -57 g C m^{-2} in 2011. Both GEP and R_e increased in the second year after harvesting but the increase of GEP was greater, resulting in a higher C uptake by the stand compared to the previous year. The cooler and wetter conditions in 2011 may have provided favorable conditions for plant growth, enhancing recovery of the residual stand. Although the growing season lasted two weeks longer in 2010, the greater C uptake during the midsummer of 2011 played a more important role in determining the annual NEP at MPB-09. High C losses observed in
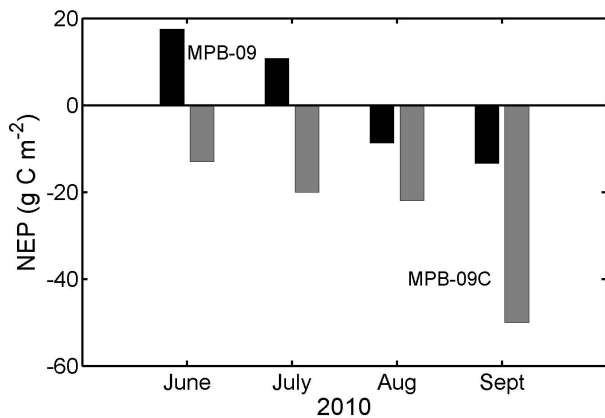
Fig. 10. Monthly total net ecosystem production (NEP) from 10 June to 22 September of 2010 for MPB-09 and MPB-09C.

Table 5. Net ecosystem production (NEP), gross ecosystem photosynthesis (GEP) and ecosystem respiration (R_e) totals for the clear-cut (MPB-09C) and the partially harvested stand (MPB-09) during the summer (10 June–22 September) of 2010 and 2011*. Values in parentheses show the lower and upper 95 % confidence intervals for the growing season totals derived from Monte Carlo simulation.

	NEP (g C m^{-2})	GEP (g C m^{-2})	R_e (g C m^{-2})
MPB-09C 2010	−103 (−131, −78)	294 (254, 341)	397 (388, 521)
MPB-09 2010	9	530	521
MPB-09 2011	47	712	665

* Recent analysis indicates that 2012 growing season NEP, GEP and R_e values for MPB-09 were 74, 700 and 626 g C m^{-2}, respectively.

August and September coincided with warm soil conditions that would result in an increase in R_h from the decomposing coarse woody debris (Mkhabela et al., 2009; Barr et al., 2007).

The greatest C uptake at MPB-09 was in June when leaf emergence of the understory broadleaf vegetation occurred. This was also observed in an unharvested beetle-killed stand located approximately 30 km north of the study site (Brown et al., 2010). There, the majority (65–68 %) of GEP was found to have come from the understory non-tree species, indicating the importance of broadleaf residual vegetation in the C uptake of these disturbed sub-boreal forests (Bowler et al., 2012). The compensatory effects of the surviving vegetation following thinning is known to lead to vegetation shifts through less competition for resources such as light, nutrients and water (Campbell et al., 2009; Saunders et al., 2012; Vesala et al., 2005). By removing trees from a stand, the forest canopy opens up, allowing more light to penetrate through the canopy and increase the photosynthetic capacity of the underlying vegetation (Saunders et al., 2012). The significant contribution of understory CO_2 uptake was also found in a ponderosa pine (*Pinus ponderosa*) forest, showing a shift in species following thinning (Misson et al., 2005). The abundance of understory broadleaf vegetation at MPB-09 highlights its importance in determining the NEP of the partially harvested stand, such that the increase of shrub LAI compensates for the loss of tree LAI following the disturbance.

While no data are available prior to harvesting at this site, studies have consistently shown a reduction of GEP after forest thinning and clear-cutting due to the removal of aboveground biomass (Misson et al., 2005; Dore et al., 2010; Campbell et al., 2009; Giasson et al., 2006). Misson et al. (2005) found that forest thinning in a young ponderosa pine forest in the Sierra Nevada of California had a greater impact on GEP than R_e. Consequently the forest became a weak C source of 13 g C m^{-2} after thinning but shifted back

to a C sink after one year. At MPB-09, both GEP and R_e were higher in 2011 even though air temperature was above the historical average and incident PAR was greater in 2010. As shown by the light response curve, the photosynthetic capacity of the stand increased in the second year after harvesting. The observed increase of NEP could be attributed to stand regeneration as an increase in the understory vegetation was observed from 2010 to 2011.

There was virtually no relationship of R_e to θ at the 3 cm depth. The soil water matric potential during the dry period in the summer of 2010 was well above the permanent wilting point indicating that the trees weren't water stressed during low θ conditions in 2010. Dilustro et al. (2005) found that R_s and θ correlated significantly at sandy sites but not at clayey sites in managed mixed pine forests in southeastern Georgia, as the fine-textured soils buffer soil water effects on R_s due to a slow release of water. The increase in R_e observed at this site in the second year after the disturbance may have been due to an increase of R_a, as a result of increased GEP as the forest recovers (Jassal et al., 2007).

Evapotranspiration followed a similar pattern as GEP, increasing in the second year of harvesting. A higher photosynthetic uptake by the increasing biomass was likely associated with the increase in stomatal conductance and transpiration of the residual stand. WUE increased in 2011, possibly due to lower soil evaporation resulting from a greater groundcover in the second year after partial harvesting. It has been previously shown that recently disturbed forests increase their WUE as the stand recovers and closes its canopy, leading to more transpiration and photosynthesis from the leaves compared to evaporation from the ground (Mkhabela et al., 2009).

4.2 Comparison of NEP of the partially harvested stand and clear-cut

The clear-cut, MPB-09C, was a large C source, whereas MPB-09 was a weak C sink from June to September of

2010. Since they both had the same site characteristics, such as vegetation, soil type, time of harvest and climate conditions, the results indicate that harvesting intensity has a major impact on the net CO_2 emissions from the forest. By retaining the healthy secondary structure, the GEP of the partially harvested stand was greater, resulting in C uptake during the growing season of 2010. Total C loss during the measurement period in the clear-cut was $103 \, \mathrm{g \, C \, m^{-2}}$ with an average daily loss of $1.0 \, \mathrm{g \, C \, m^{-2}}$. Since photosynthesis would be largely absent for the remainder of the year, MPB-09C was likely a large annual C source. Sub-boreal clear-cuts in the area that were replanted with lodgepole pine seedlings have been shown to still be summertime C sources of $0.37 \, \mathrm{g \, C \, m^{-2} \, day^{-1}}$ after 10 yr (Brown et al., 2010). Pypker and Fredeen (2002) found a 6-year-old clear-cut planted with hybrid white spruce seedlings to be an average daily C source of $0.9 \, \mathrm{g \, C \, m^{-2}}$ over the growing season. In this study, both GEP and R_e were greater at MPB-09 than at MPB-09C during the summertime.

There is limited research into the effects of management responses to insect outbreaks on the C balance of forests. This study shows that partial harvesting following an MPB attack reduces C losses as compared to clear-cut harvesting. Previous findings from a study at two beetle-killed lodgepole pine stands nearby that were left to recover naturally, found the stands to recover faster than previously hypothesized and becoming C neutral annually within 3 to 5 yr after attack (Brown et al., 2010; Brown et al., 2012). In 2010, MPB-09 was a greater C source than the unharvested beetle-killed stands, which at that point had reached the grey-attack stage, when the pine trees were dead and most of the needles had fallen. Furthermore, one year after partial harvesting, MPB-09 was losing more CO_2 annually than one year after the insect attack in one of the unharvested stands described in Brown et al. (2010). This suggests that for these sites the harvesting disturbance likely had a greater impact on NEP than the MPB attack itself.

Consequently, the choice of management strategy in response to MPB outbreak can have a major impact on NEP. The clear-cut, MPB-09C, was a much larger C source, indicating that partial harvesting is more favorable in reducing the CO_2 emissions of the stand. Since the healthy trees are retained, more aboveground biomass results in a higher photosynthetic capacity of the stand and a higher annual NEP compared to clear-cut harvesting. Windthrow can potentially affect the C balance of the residual stand after harvesting due to greater wind loads on retained trees. The risk of windthrow was initially thought to be significant in the case of MPB-09, however Nishio (2011) showed that one year after harvesting, windthrow at this site was only 9 %, indicating the trees were developing windfirm characteristics. This may in part be explained by the location of the stand downwind of an open area, which tends to have high wind speeds and may have resulted in the trees in the stand previously becoming windfirm (Nishio, 2011). Recent analysis of measurements

in 2012 indicate that the growing season C sink at MPB-09 increased to $74 \, \mathrm{g \, C \, m^{-2}}$ although annual NEP remained virtually the same as in 2011 (Tables 3 and 5). Our results suggest that if the residual forest continues its current rate of recovery, the stand would likely return to a C sink more quickly than clear-cuts in the area, which as indicated above, can remain a C source for at least 10 yr. The understory LAI would likely continue to increase until the tree canopy closes and less solar radiation reaches the forest floor, thus increasing the contribution of the tree canopy to CO_2 uptake relative to the understory.

5 Conclusions

This study examined the effects of partial and clear-cut harvesting on the C balance of a sub-boreal forest that was previously attacked by the MPB. Annual NEP at MPB-09 increased from the first to the second year after harvesting, with the stand remaining an annual C source in both years. The increase of GEP observed in 2011 was greater than the increase in R_e, indicating that the photosynthetic capacity of the forest played a major role in increasing annual NEP. The remaining healthy spruce and subalpine fir trees and understory vegetation in the partially harvested stand contributed to C uptake, which will likely enable the forest to return to C neutrality at a faster rate than clear-cuts. In the first two years after partial harvesting, MPB-09 was a growing-season C sink, which increased from 2010 to 2011. In contrast, the clear-cut, MPB-09C, was a large C source from June until September and likely an even larger C source annually. These results suggest that when considering forest management practices in response to the MPB outbreak, partial harvesting can result in greater NEP compared to clear-cut harvesting by retaining the healthy residual vegetation.

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