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Agricultural and Forest Meteorology 150 (2010) 254–264

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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# Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia

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ARTICLE INFO

*Article history:*
Received 29 June 2009
Received in revised form 7 November 2009
Accepted 10 November 2009

*Keywords:*
Mountain pine beetle
Eddy covariance
Net ecosystem production
Disturbance
Harvesting
Respiration
Photosynthesis

ABSTRACT

British Columbia (BC), Canada is experiencing a severe mountain pine beetle (MPB) (*Dendroctonus ponderosae*) epidemic extending over an area of 135,000 km$^2$. The widespread mortality of lodgepole pine (*Pinus contorta* var. *latifolia*) caused by the beetle has significant implications for BC's timber supply and Canada's carbon (C) budget. This study used the eddy-covariance technique to examine how the beetle is impacting the net ecosystem production (NEP) of two attacked lodgepole pine-dominated stands in the central interior of BC. MPB-06 is an 83-year-old stand that was first attacked in 2006. At the start of 2007 roughly 60% of the canopy had been attacked and by October 2008 only 21% of the trees remained healthy. MPB-03, a 110-year-old stand, had >95% pine canopy mortality as a result of a 2003 beetle attack, and also differed from MPB-06 in that it had a more developed secondary structure (consisting of tree seedlings and saplings and sub-canopy and canopy trees) that survived the beetle attack. Eddy-covariance measurements were also conducted in two stands near MPB-06 harvested in 2005 and 1997 (CC-05 and CC-97) for approximately three-week periods each during the 2007 growing season. MPB-06 had an annual NEP of −82 and −33 g C m$^{-2}$, while MPB-03 had an NEP of −56 and 4 g C m$^{-2}$ in 2007 and 2008, respectively. In the 2007 and 2008 growing seasons (May–September), MPB-06 was a sink of 12 and 52 g C m$^{-2}$, while MPB-03 was a sink of 17 and 68 g C m$^{-2}$, respectively. The productivity at MPB-06 resulted from an increase in photosynthesis by the remaining healthy trees and understory vegetation, while at MPB-03 the secondary structure and understory vegetation showed a strong capacity to sequester C due to an opening up of the stand as a result of canopy mortality. Average daily values of NEP during the measurement periods at CC-97 and CC-05 were −0.37 and −0.87 g C m$^{-2}$, respectively, showing that even 10 years following harvesting, these stands are likely to remain growing season C sources. That MPB-06 and MPB-03 were growing season C sinks suggests that deferring the harvest of stands with significant levels of secondary structure could prevent MPB-attacked forested areas from becoming C sources over extended periods.

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## 1. Introduction

The current British Columbia (BC) outbreak of mountain pine beetle (*Dendroctonus ponderosae*) (MPB), which began in the late 1990s, had killed a total of 710 million m$^3$ of lodgepole pine (*Pinus contorta* var. *latifolia*) by the end of 2007, and is predicted to kill ~76% of the mature pine volume in the province by 2015 (Walton et al., 2008). Lodgepole pine accounts for almost 30% of the timber volume in the timber harvesting land base of BC and the pine-dominated stands located in the Sub-Boreal Spruce biogeoclimatic zone account for approximately 70% of BC's timber production (Meidinger and Pojar, 1991). The current MPB outbreak is believed to have peaked in 2005 with a volume of ~141 million m$^3$ of merchantable pine killed that year on the timber harvesting land base (Walton et al., 2008). This compares with the average annual allowable cut of approximately 68 million m$^3$ (British Columbia Ministry of Forests and Range, 2006), between 1995 and 2005, from all provincial timber supply areas in BC. Although such epidemics have occurred in the past, none have been this large in areal extent or in duration. The size of the current epidemic is primarily due to the combination of an abundance of mature lodgepole pine and rising wintertime minimum temperatures for

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doi:10.1016/j.agrformet.2009.11.008

the past several years (Safranyik and Wilson, 2006). Despite the fact that large areas have been affected by the epidemic and that the carbon (C) balance of Canadian forests is driven by disturbance (Kurz and Apps, 1999; Amiro et al., 2006), there is a dearth of measurements examining the influence of insect attacks on C-cycling in forests, and there are few known empirical studies examining net ecosystem $CO_2$ exchange measurements.

Net ecosystem production (NEP) is a direct measure of the degree to which an ecosystem is a source (NEP $< 0$) of, or a sink (NEP $> 0$) for atmospheric C over the time period of interest and is defined as the difference between gross ecosystem photosynthesis ($P_g$) (also known as gross primary production) and ecosystem respiration ($R_e$). A beetle epidemic could affect stand NEP in several different ways. First, $P_g$ would be expected to be dramatically reduced with the increasing severity of attack due to the death of canopy trees. This would be accompanied by a corresponding decrease in autotrophic respiration ($R_a$), i.e., the release of $CO_2$ from the metabolic activity in roots, boles and leaves. The decline in $P_g$ could be reduced by increased growth of secondary structure (consisting of tree seedlings and saplings, sub-canopy and canopy trees that survive a beetle attack; Coates et al., 2006), if present, and shrubs and herbs. An increase in decomposable biomass, mainly in the form of fallen needles, dead roots, standing and fallen dead wood would be expected to lead to a large increase in heterotrophic respiration ($R_h$) or C released due to microbial decomposition. A study conducted in Oregon found that lodgepole pine killed by MPB began falling 3 and 5 years after death in thinned and unthinned stands, respectively (Mitchell and Preisler, 1998) and that 50% of the attacked trees had fallen within 9 years in unthinned stands. A substantial increase in $R_h$ would be expected once dead standing biomass begins to fall and decompose (Amiro et al., 2006).

The MPB is native to BC, and while epidemics are often associated with lodgepole pine, the beetles can inhabit virtually all *Pinus* spp. in western North America (Taylor et al., 2006). The beetles colonize via pheromone-mediated mass attacks which effectively overwhelm a tree's ability to defend itself (Aukema et al., 2006). When eggs laid by the female beetles under the bark hatch, the larvae feed on the phloem, cutting off the tree's nutrient supply (Taylor et al., 2006). The beetles also introduce a blue-stain fungus into the tree which clogs the xylem, thereby reducing the tree's capacity to transport water (Gorte and Ramseur, 2008).

There are three stages to a MPB attack. The green-attack stage describes the first year of attack, during which time a tree's foliage remains green. During the second year of attack, the red-attack stage, the foliage senesces and turns red. Following the second year, the tree enters the grey-attack stage and the needles turn brown and begin to fall.

Kurz et al. (2008) recently used the Canadian Forest Service C accounting model CBM-CFS3 to predict that the cumulative impact of the beetle outbreak in BC, between 2000 and 2020, will result in a net loss of 270 Mt C extending over an area of 374,000 km$^2$. This averaged to a net biome production (NBP) (defined as the NEP of stands in the region with the inclusion of the effects of disturbance) of $-42 \pm 21$ g C m$^{-2}$ year$^{-1}$ over the 20-year period. The same study predicted that the impact of the beetle (excluding the effect of additional harvesting in response to the attack) would peak in 2009 with an NBP of $-53$ g C m$^{-2}$ year$^{-1}$, with NBP slowly recovering thereafter. However, in 2020 the total area would still remain a net C source. The results presented here are the first measurements of NEP in MPB-attacked stands and thus will help determine ecophysiological responses at the stand level as well as provide empirical data for evaluating forest disturbance C models. To this end, this study had the following four objectives: (1) to measure the annual NEP in a stand without a well-developed secondary structure in the early to middle stages of attack, and in a stand with significant secondary structure in the middle to late stages of attack, (2) to determine the impact of beetle attack on $P_g$ and $R_e$, (3) to determine the effects of the beetle on the photosynthetic characteristics of these stands, and (4) to evaluate the impact of salvage harvesting on the NEP of these stands.

## 2. Methods

### 2.1. Site locations

NEP measurements were made at two locations in the northern interior of BC (Fig. 1; Table 1). This region is located in the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar, 1991) and both stands were dominated by lodgepole pine (*P. contorta* Dougl. Ex Loud. var. *latifolia* Engelm.). The first stand is located approximately 35 km southeast of the town of Mackenzie at Kennedy Siding (MPB-06). This stand contained few non-pine trees, with the understory consisting mainly of pine seedlings, scattered shrubs and a ground cover of moss, lichen and dwarf shrub species. The second stand is located adjacent to Crooked River Provincial Park (MPB-03), approximately 70 km north of Prince George, BC and approximately 100 km south of MPB-06. In addition to overstory lodgepole pine and ground cover dominated

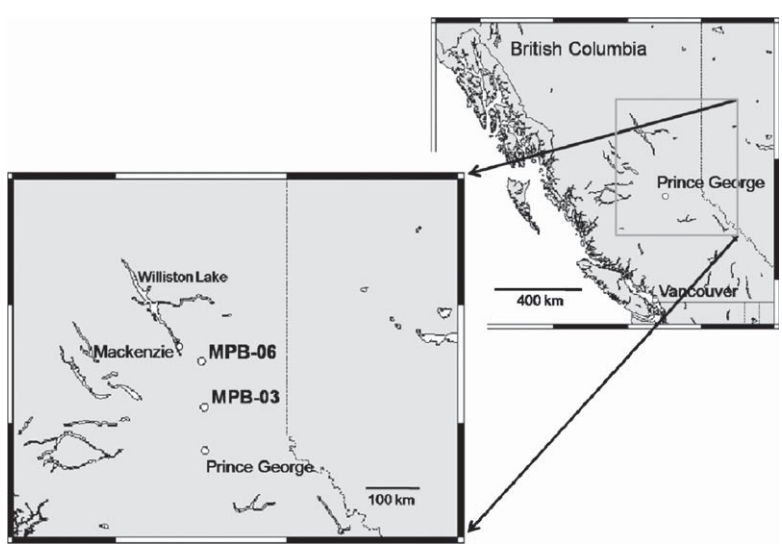


**Fig. 1.** The locations of MPB-06 and MPB-03. CC-05 and CC-97 are located approximately 1 km E and 2 km SW, respectively, of the MPB-06 flux tower.

**Table 1**
Stand characteristics at MPB-06 and MPB-03.

| | MPB-06 | MPB-03 |
|---|---|---|
| Stand age (year) | ~80 | ~110 |
| Tower location | 55°06′42.8″N<br>122°50′28.5″W | 54° 28′24.8″N<br>122° 42′48.4″W |
| Elevation (m) | 750 | 710 |
| Canopy height (m) | ~15 | ~17 |
| Stand density (height > 10 m) (stems $ha^{-1}$) | 1275 (204[a]) | 558 (123) |
| Stand basal area $m^2 ha^{-1}$ (height >10 m) | Live: 11.8–19.2<br>Dead: 0.2–0.9 | Live: 0.7–3.2<br>Dead: 8.1–14.7 |
| Seedling/sapling density (stems $ha^{-1}$) | *Pinus contorta*: 7470<br>*Abies lasiocarpa*: 100<br>*Picea glauca*: 110 | *Pinus contorta*: 2800<br>*Abies lasiocarpa*: 2300<br>*Picea glauca*: 190 |
| Understory vegetation | *Alnus tenuifolia*, *Salix* spp.,<br>*Vaccinium* spp. | *Salix* spp., *Amelanchier alnifolia*,<br>*Vaccinium* spp., *Arctostaphylos uva-ursi* |
| LAI (overstory) | | |
| 2007 | 1.4 | 0.9 |
| 2008 | 1.3 | 0.8 |
| % MPB-attacked when tower established | <5 | >90 |
| Litter-fibric-humus C content (kg $m^{-2}$) | 1.10–3.78 | 1.88–2.81 |
| Mineral soil C content (0–55 cm) (kg $m^{-2}$) | 1.76–3.15 | 1.21–2.76 |
| Fine soil bulk density (kg $m^{-3}$) | 1180 (220) | 1160 (323) |
| Soil texture | Gravelly sandy loam | Gravelly sandy loam |
| Soil coarse fragments (% by volume > 2 mm) | 34 (11) | 70 (7) |

[a] Standard deviation in brackets.

by mosses, lichens and dwarf shrubs, MPB-03 had a developed secondary structure consisting of saplings of subalpine fir (*Abies lasiocarpa*) and white spruce (*Picea glauca*) and seedlings of all three tree species plus deciduous shrubs. Stand, understory, and soil characteristics were determined on three National Forest Inventory style ground plots (NFI, 2004) at each site located 120° apart and 50 m from each tower. The first major MPB attack at MPB-06 occurred during the summer of 2006. By May 2007 the majority of the canopy had been attacked (Table 2). MPB-03 was first attacked in 2003 and when NEP measurements began in 2007 the site was >95% in the red-attack and grey-attack stages. NEP measurements were also made in two harvested stands during the summer of 2007. They (CC-05 and CC-97) are located approximately 1 km E and 2 km SW, respectively, of the MPB-06 flux tower. CC-97 is a 10-year-old clearcut, which was left to naturally regenerate. The site is characterized by a large number of lodgepole pine seedlings (1200 stems $ha^{-1}$) with the soil surface covered by a mix of lichens and moss (Seip and Jones, 2007). CC-05 is a site that was salvage logged following MPB attack and planted in 2006 with a mixture of lodgepole pine and hybrid white spruce seedlings. The ground cover is similar to that of CC-97 except with a lower abundance of lichen (Seip and Jones, 2007). Prior to harvest, both sites were dominated by lodgepole pine. All four sites are flat and on coarse textured gravelly soils of glacio-fluvial origin.

### 2.2. Flux, climate and ecophysiological measurements

A thirty-two-meter-tall scaffold flux tower (~2.1 m long × ~1.5 m wide) was established at each of MPB-06 and MPB-03 in July 2006 and March 2007, respectively. Flux and climate measurements began on 18 July 2006 and 20 March 2007 at the respective sites. Both sites were generally located on horizontal ground with a homogeneous fetch greater than 1 km in all directions. NEP was measured directly using the eddy-covariance (EC) method, which has become the standard technique to measure net ecosystem $CO_2$ exchange (Baldocchi, 2003). A 3-dimensional ultrasonic anemometer (model CSAT3, Campbell Scientific Inc. (CSI), Logan, Utah) was used to measure the three components of the wind vector, and air temperature, and turbulent fluctuations of $CO_2$ and $H_2O$ were measured using an open-path infrared gas analyser (IRGA) (model LI-7500, LI-COR, Inc., Lincoln, Nebraska). Signals were measured with a data logger (CSI, model CR1000) with a synchronous-device-for-measurement (SDM) connection. High frequency (10 Hz) data were stored on a compact flash card that was replaced every 2–4 weeks. Half-hourly covariances and other statistics were calculated on the data logger and transmitted with climate data daily by cell phone to the laboratory. The system was powered using three 100-W solar panels (CTI-130, Carmanah Technologies Corp., Victoria, BC) with an 800-Ah battery unit consisting of eight absorbent glass mat batteries (EX-1000, Carmanah Technologies Corp.). During the winter the sampling rate was reduced to 5 Hz to conserve power. At both sites, instrumentation was mounted at the height of 26 m, which was ~8 and ~6 m above the top of the canopy at MPB-06 and MPB-03, respectively. These heights resulted in growing season upwind distances from the flux tower to the 80% cumulative flux contour being typically 400 and 1500 m during the daytime and nighttime, respectively, at both sites. Fluxes of $CO_2$ ($F_c$) were calculated as the covariance of the $CO_2$ mixing ratio ($s_c$) and vertical velocity ($w$), i.e., $F_c = \rho_a \overline{w's_c'}$, where $\rho_a$ is the density of dry air, the overbar denotes half-hourly averaging and the primes indicate fluctuations from the average. High frequency signals were not detrended. Three coordinate rotations were applied to the high frequency wind data to make $\bar{v} = \bar{w} = 0$ (Tanner and Thurtell, 1969). Net ecosystem exchange (NEE) was calculated as the sum of $F_c$ and the rate of change of $CO_2$ storage in the air column beneath the EC instrumentation. The storage term was calculated from the difference between $\bar{s}_c$ measured at the 26-m

**Table 2**
Stand MPB attack status at MPB-06.

| | August 2006 | June 2007[a] | October 2007[a] | August 2008[b] |
|---|---|---|---|---|
| Non-attacked (%) | 50 | 43 | 28 | 21 |
| Green-attacked (%) | 50 | 10 | 19 | 5 |
| Red-/grey-attacked (%) | – | 47 | 53 | 73 |

[a] Hilker et al. (2009).
[b] Means of values from this study and of Seip and Jones (2007).

height in the previous and following half hours applied to the air column beneath the EC sensors (see Morgenstern et al., 2004). NEP was calculated as NEP = −NEE.

Measurements of climate variables were also made continuously at both sites. These included: above-canopy upwelling and downwelling shortwave and longwave radiation (model CNR1, Kipp and Zonen B.V., Delft, The Netherlands) and above-canopy upwelling and downwelling, and below-canopy downwelling photosynthetically active radiation (PAR) (model LI-190AS, LI-COR Inc.), precipitation at canopy height (tipping bucket rain gauges, model TE525WS-L, CSI at MPB-03 and model 2501, Sierra Misco, Berkeley, CA at MPB-06), wind speed at the 25 m height (model 05103 R.M. Young Inc., Traverse City, MI), air temperature and relative humidity at 6 m (model HMP45C, Vaisala Oyj, Helsinki, Finland), soil temperature (chromel-constantan 30 gauge thermocouple wire, Omega Engineering Stamford, Connecticut) at depths of 5, 10, 20 and 50 cm, soil heat flux (3 heat-flux plates model HP01, Hukseflux Delft, The Netherlands) at a depth of 5 cm and water content reflectometer, (model CS616, CSI) at 0–10 and 30–50 cm at MPB-06 and soil moisture sensor, (model EC-5, Decagon Devices Inc, Pullman, Washington) at 10, 20 and 50 cm at MPB-03. Meteorological measurements were made every second, and 30-min average values calculated. Measurements of diffuse PAR (model BF3, Delta-T Devices Inc., Cambridge, UK) were made at a weather station in the CC-97 clearcut located ~1.5 km east of the MPB-06 tower during the 2007 summer. Snow-pack depth was also measured at the clearcut weather station using an acoustic distance sensor (model SR50M, CSI) and precipitation calculated from these data and manual measurements of liquid water equivalent.

Leaf area index (LAI) was calculated for the canopies at both sites using a LI-COR Plant Canopy Analyzer (model LAI-2000, LI-COR Inc.) as well as a TRAC (Tracing Radiation and Architecture of Canopies) instrument (Third Wave Engineering, Nepean, Ontario, Canada) and hemispherical photography (Egginton et al., 2008).

To determine the influence the beetle had on the tree's ability to photosynthesize at an early stage of attack, foliar $CO_2$ exchange measurements were made on 24 pairs of green-attacked and non-attacked trees of similar size and age, located within 3 m of each other over three days at MPB-06. Shoots were clipped from the lower branches of the canopy at a height of approximately 6 m using a pruning pole and measured within 5 min of sampling. Measurements were made between 10:00 and 16:00 h PST on 21–23 August 2006 in ambient light conditions. All three days were generally sunny with maximum downwelling PAR reaching 1800 (mol $m^{-2}$ $s^{-1}$. Net assimilation ($A_{net}$) and stomatal conductance ($g_s$) measurements were made using two portable photosynthesis measurement systems (model LI-6400, LI-COR Inc.), following the approach of Pypker and Fredeen (2002). One system used a clear acrylic conifer chamber (model 6400-05, LI-COR Inc.), while the other used a closed opaque chamber (model 6400-02B, LI-COR Inc.) with a red/blue LED light source. Shoots were placed in the conifer chamber under ambient light conditions, while four representative needles (intact to the branchlet) were placed in the LED light source chamber. In both systems a $CO_2$ concentration and air flow rate were maintained for 3 min at 380 ppmv and 500 μmol $s^{-1}$ (300 mL $min^{-1}$), respectively. Air temperature, atmospheric water vapour pressure deficit and PAR were continuously recorded during each measurement along with $A_{net}$ and $g_s$. Area-based estimates of $A_{net}$ were calculated after determining half the total leaf area, using the volumetric displacement technique, for each branchlet or leaf sampled and leaf area to dry leaf biomass ratios (specific leaf area, SLA) were determined.

In order to assess the rate of advance of the beetle attack, tree health status inventories at MPB-06 were conducted in August 2006 and August 2008. The attack status of individual trees was determined along two 350 m long transects × 2 m wide. Green attack was identified by the presence of beetle core holes, while red-attack was identified by foliage colour, and grey attack by the transition to brown colour. Inventories were also conducted in June and October 2007 by Hilker et al. (2009). In addition, independent tree health assessments were also made annually in August by biologists evaluating woodland caribou to partial retention logging of MPB-attacked stands (Seip and Jones, 2007).

### 2.3. Wintertime fluxes

Recently, the observation of wintertime $CO_2$ uptake has led researchers to question the reliability of the LI-7500 IRGA in cold air conditions (Grelle and Burba, 2007; Burba et al., 2008). Comparisons using closed-path analysers suggest the problem is due to heat generated by the open-path analyser in cold conditions leading to a sensible heat flux inside the open-path array which affects the $CO_2$ density (Burba et al., 2008; Bonneville et al., 2008). To assess the reliability of our wintertime fluxes, we first classified MPB-06 NEP as wintertime data when soil temperature at the 5 cm depth ($T_s$) was <1 °C and the air temperature at 26 m ($T_a$) was <5 °C. Of these data, in 2007, 32% showed negative NEE ($CO_2$ uptake) and were discarded. When separated into daytime and nighttime data, negative fluxes accounted 54% of the daytime data but only 19% of the nighttime data. This agrees with the findings of Lafleur and Humphreys (2008) who observed wintertime $CO_2$ uptake occurred 49% and 22% of the time during the daytime and nighttime, respectively. Burba et al. (2006) conducted experiments on the open-path wintertime $CO_2$ uptake phenomenon and reported that the problem is more serious during the daytime due to the absorption of solar radiation by the LI-7500, which further heats the instrument surface. They found that temperatures inside the open-path array were correlated with wind speed such that at higher wind speeds, heat produced by the instrument was more effectively removed from the open-path array so the difference between air temperature and surface temperature of the instrument was reduced. They found that for all air temperatures, winds exceeding 6–8 m $s^{-1}$ reduced the surface temperature of the detector housing of the LI-7500 to less than 1 °C above ambient. Thus we examined the effect of wind speed on our 2007 wintertime data at MPB-06 by plotting the fraction of negative NEE values against wind speed. The fraction of negative values decreased with increasing wind speed, with the largest reduction (from 0.28 to 0.18) occurring as wind speed increased from 3 to 4 m $s^{-1}$. Consequently, we discarded all daytime winter data when wind speed was <4 m $s^{-1}$, which removed a further 67% of these values, leaving 98 daytime winter values. During the nighttime, the fraction of negative values was relatively constant at ~0.12 regardless of wind speed, thus we did not discard any nighttime data based on wind speed. For the nighttime, there were 844 remaining acceptable wintertime values. In total, 56% of wintertime fluxes were accepted, leaving a total of 942 acceptable half-hour fluxes during the wintertime. The same screening procedure was applied to 2008 wintertime data.

At MPB-03, data collection did not begin until 22 March 2007, so we filled 1 January to 22 March 2007 with values modelled using the parameters from the 2008 empirical logistic relationship between NEE and $T_s$ (see below for more details) and 2008 half-hourly $T_s$ data. It is not expected that the wintertime $T_s$ would vary much between years. In fact, between January and March for 2008 and 2009, $T_s$ was always within a 0.5 °C range, slightly above 0 °C. At the Prince George airport, located ~80 km from MPB-03, wintertime snowfall was similar between years with an accumulation of 2.4 and 2.1 m in 2007 and 2008, respectively. Following the method of analysis of wintertime NEE data at MPB-06, we removed all negative NEE values and daytime data when the wind speed was < 4 m $s^{-1}$ at MPB-03.

By removing only wintertime negative NEE measurements it is possible that a bias towards greater $CO_2$ loss was introduced because at these small rates of respiration instrumentation random noise could result in occasional small negative $CO_2$ fluxes. Alternatively, wintertime respiration might have been greater than the measurements suggest because heating in the open-path array might have had the effect of lowering measured $F_c$ from its actual value.

### 2.4. Flux quality control and data analysis

Flux quality control procedures included rejection of data when a 30-min period had more than 30% of an individual trace with an instrument diagnostic warning flag that indicated a bad measurement, and setting minimum (300 $\mu$mol mol$^{-1}$) and maximum (1000 $\mu$mol mol$^{-1}$) bounds on $CO_2$ concentrations as measured by the open-path IRGA. Wind rose analysis showed that the predominant wind direction at MPB-03 was from the west to southwest but during the winter there was also strong flow from the north-east. At MPB-06 the predominant wind direction during the growing season was from the west to southwest. Fluxes were not rejected on the basis of wind direction since the fetch was greater than 1 km in all directions around the tower. Wind through the tower and sonic occurred seldomly and when it did there was no detectable effect.

EC measurements made during the night provide a direct measure of $R_e$ (van Gorsel et al., 2008). At both sites, only nighttime EC data when friction velocity ($u_*$) was greater than the threshold $u_*$ ($u_*$) of 0.30 m s$^{-1}$ were considered for analysis to ensure sufficient turbulent mixing (Baldocchi, 2003). Selection of $u_{*th}$ was achieved by plotting half-hourly $CO_2$ flux (both annually, and for the growing season and the rest of the year) against $u_*$ and determining the value for which a further increase in $u_*$ no longer led to an increase in the flux (Massman and Lee, 2002). Although $u_{*th}$ was not clearly defined, which, unfortunately, is commonplace in EC studies (Gu et al., 2005), the threshold was within $\pm$0.05 m s$^{-1}$ of 0.30 m s$^{-1}$. Daytime $R_e$ was estimated using the standard algorithm established by the Fluxnet Canada Research Network (FCRN) of the Canadian Carbon Program (Barr et al., 2004) which assumes an empirical logistic relationship between nighttime $R_e$ ($u_* > u_{*th}$) and $T_s$ (the $r^2$ was 0.44 for MPB-06 in 2007 and 0.50 and 0.42 for MPB-06 and MPB-03 in 2008, respectively) and is applied to daytime (see Humphreys et al., 2005). $P_g$ was calculated as daytime NEP + daytime $R_e$. Gaps in the daytime NEP data were filled with the difference between modelled $P_g$ and $R_e$. $P_g$ was also modelled using the FCRN standard algorithm, which assumes a rectangular hyperbolic relationship between $P_g$ and incident PAR (the $r^2$ for MPB-06 and MPB-03 was 0.18 and 0.13 for 2007, and 0.51 and 0.42 for 2008, respectively). The gap-filling procedure used was altered from that described in Barr et al. (2004) in that the moving window, which estimates the seasonal variation of time-varying parameters from the empirical relationships described above, was not applied during the winter (when $T_s$ was <1 °C). In the moving window approach, the parameter are calculated as the slope of the linear regression between estimates of $R_e$ (and $P_g$) obtained from the annual relationships, and $R_e$ (and $P_g$) from the measurements. The window is 100 data points wide and is moved in an increment of 20 points at a time. Ideally, each window would cover a period of a few days. However, during the winter at these sites, when NEE measurements were sparse due to the screening procedure, a single 100 point window was found to span weeks or 2–3 months. Over such time spans climatic variability, such as changes in $T_a$, could result in variations in $R_e$ even though $T_s$ varied little.

EC data were assessed for energy balance closure, although an energy balance correction was not applied. Half-hourly measurements of net radiation flux, surface soil heat flux, sensible and latent heat flux were used together with estimates of changes in air-column sensible and latent heat and biomass heat storage (Humphreys et al., 2003). Daytime energy balance closure during the 2007 growing season was 79% and 88% at MPB-06 and MPB-03, respectively.

To determine the photosynthetic and respiratory characteristics of the two ecosystems, the following Michaelis–Menten light response (rectangular hyperbolic relationship) was used

$$NEP = \frac{\alpha Q A_{max}}{\alpha Q + A_{max}} - R_d \quad (1)$$

where $\alpha$ is the quantum yield, $A_{max}$ is ecosystem photosynthetic capacity, $R_d$ is the daytime $R_e$ and $Q$ is the incident PAR (Griffis et al., 2003). This analysis was done on a monthly basis using daytime data for $Q > 5$ $\mu$mol m$^{-2}$ s$^{-1}$.

### 2.5. Uncertainty analysis

Uncertainties associated with annual totals of NEP, $P_g$ and $R_e$ were determined using the following two techniques. Random error was assessed using propagation of errors following Morgenstern et al. (2004), which assigned a 20% random error to each half-hourly value of NEP. The uncertainty due to the gap-filling algorithms was estimated using Monte Carlo simulation following the procedure of Krishnan et al. (2006) which generated gaps in measured NEP (i.e., not gap-filled) ranging from a half-hour to 10 days using a uniformly distributed random number generator, 1000 times. For each time, the relationships between $R_e$ and $T_s$, and $P_g$ and $Q$ were then determined using the algorithms described above. Modelled values were used to gap-fill the original dataset. The annual values of NEP, $R_e$ and $P_g$ were then sorted to determine the 95% confidence interval.

## 3. Results

### 3.1. Seasonal weather

Mean annual $T_a$ at both sites was approximately 3.0 °C in 2007 and 2008. Growing season (May–September) $T_a$ in the study region is typically cool with an average daily (24 h) $T_a$ of 12 °C (1971–2000 normal from the Mackenzie Airport, Environment Canada). At MPB-06, the mean growing season $T_a$ was 11.8 and 12.4 °C in 2007 and 2008, respectively. Growing season rainfall was 246 mm in 2007 and 250 mm in 2008 (Fig. 2). Snowfall during the 2006–2007 winter at MPB-06 was estimated to be 354 mm (liquid water equivalent) and total annual precipitation (1 November 2006 to 31 October 2007 hydrologic year) was approximately 732 mm. Snowfall during the 2007–2008 winter was estimated to be 339 mm and total annual precipitation was approximately 608 mm. Average soil fine-fraction (soil particles <2 mm) volumetric water content for the 0–30 cm depth ($\theta$), varied from 0.09 to 0.16 m$^3$ m$^{-3}$ at MPB-06 during the growing season of the two years. Field capacity (−0.1 MPa) and wilting point (−1.5 MPa) $\theta$ values for the soils at the two sites were estimated to be approximately 0.17 and 0.05 m$^3$ m$^{-3}$, respectively (Campbell and Norman, 1998). At MPB-03, mean growing season $T_a$ was 12.7 °C during both 2007 and 2008, while growing season rainfall was 576 mm in 2007 and 620 mm in 2008. The much higher rainfall total at MPB-03 compared to MPB-06 is likely due to a higher occurrence of convective showers and storms at MPB-03. Growing season $\theta$ at MPB-03 varied from 0.13 to 0.20 m$^3$ m$^{-3}$ over the two years. Wintertime $T_s$ at both sites never dropped below −0.5 °C, likely a result of the heavy snowfalls in late-October and November, which would have insulated the soil surface before the soil could freeze (Monson et al., 2006).

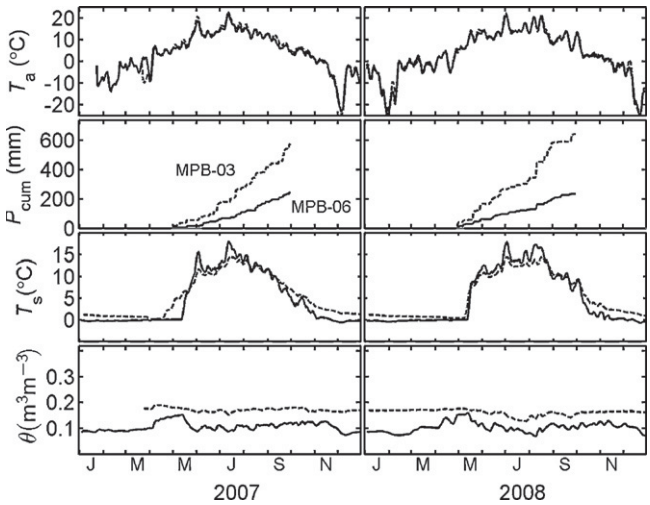


**Fig. 2.** Air temperature ($T_s$), cumulative precipitation ($P_{cum}$), soil temperature ($T_s$), soil water content ($\theta$), wind speed ($u$) and PAR ($Q$) at MPB-06 and MPB-03 for 2007 and 2008. For $P_{cum}$ only the growing season (May–September) values are shown. At MPB-06 total annual precipitation was estimated to be 732 and 608 mm in 2007 and 2008, respectively.

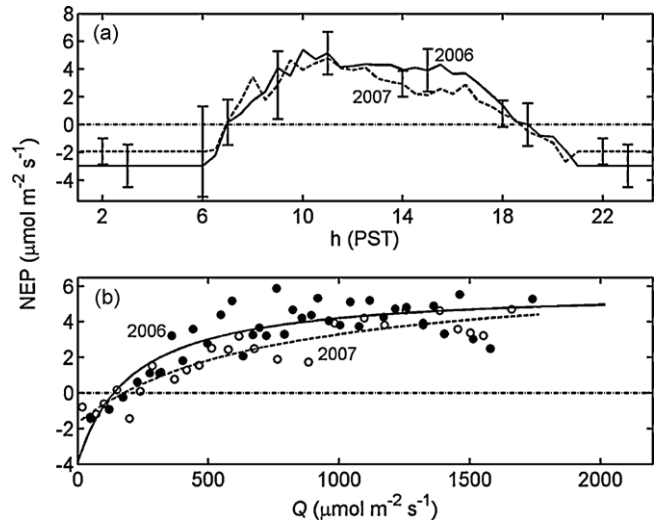


**Fig. 3.** (a) Ensemble-average diurnal course of measured NEP measurements made between 29 July and 20 August, 2006 and 2007 at MPB-06. All half-hourly nighttime measurements were averaged to a single nighttime value for both years (see text). Vertical bars are standard deviations. (b) Light-response ($Q$) analysis for MPB-06 daytime NEP measurements made during the same period. Maximum assimilation rate ($A_{max}$), quantum yield ($\alpha$) and daytime respiration ($R_d$), were 9.8 μmol m$^{-2}$ s$^{-1}$, 0.05 and 3.93 μmol m$^{-2}$ s$^{-1}$ for 2006 and 8.6 μmol m$^{-2}$ s$^{-1}$, 0.01 and 1.7 μmol m$^{-2}$ s$^{-1}$ for 2007.

### 3.2. Comparison of NEP in attacked and non-attacked trees and stands

Although MPB-06 was still green and appeared healthy during July and August 2006, ~50% of the trees had been attacked by late-July. The average bole diameter at 1.3 m above the ground of attacked lodgepole pine trees was 14.3 cm, while that of non-attacked trees was 8.0 cm, showing the preference of the beetle for larger trees. $A_{net}$ and $g_s$ measurements were made to determine the effect of the beetle attack on photosynthesis at this early stage of attack. A two-way analysis of variance showed that there was a slight but insignificant difference at the 95% confidence level in $A_{net}$ and $g_s$ between pairs of green-attacked and non-attacked trees (Table 3) ($A_{net}$ and $g_s$ values were approximately 25% and 15% higher respectively, for the LED light source measurements). As a result, we treated NEP measurements made between 29 July and 20 August 2006, as a healthy control period to compare with measurements made during the same interval in 2007, when approximately 50% of the trees had been killed. The climate during the comparison periods was similar, with average $T_a$, $T_s$ and daytime PAR being 13.4 °C, 12.7 °C and 670 μmol m$^{-2}$ s$^{-1}$ in 2006 and 12.8 °C, 12.5 °C and 600 μmol m$^{-2}$ s$^{-1}$ in 2007. However, 2006 was a relatively dry summer and as a result average $\theta$ was only 0.06 m$^3$ m$^{-3}$ compared to 0.10 m$^3$ m$^{-3}$ in 2007.

Measured values of NEP over the comparison interval in both years were used to create an ensemble-average diurnal course of NEP (Fig. 3a). All half-hourly nighttime measurements were averaged to a single nighttime value. For the 22-day comparison period, NEP was 18 g C m$^{-2}$ in 2006 compared to 23 g C m$^{-2}$ in 2007. Average nighttime NEP was less (more negative) in 2006 (−2.98 μmol m$^{-2}$ s$^{-1}$) than 2007 (−1.95 μmol m$^{-2}$ s$^{-1}$) and during the daytime (between 6:00 and 21:00 h PST) average NEP was 2.36 and 1.90 μmol m$^{-2}$ s$^{-1}$ in 2006 and 2007, respectively. Light-response analysis shows that $A_{max}$, $\alpha$ and $R_d$ were all greater in 2006 than 2007 (Fig. 3b).

### 3.3. Diurnal courses of monthly ensemble-averaged NEP in beetle-attacked stands

The diurnal courses of monthly ensemble-averaged half-hour values of NEP are compared in Fig. 4 for MPB-06 and Fig. 5 for MPB-03. For January to March and November to December, average NEP values for 2007 and 2008 were −0.52 and −0.42 μmol m$^{-2}$ s$^{-1}$ at MPB-06 and −0.41 and −0.35 μmol m$^{-2}$ s$^{-1}$ at MPB-03, respectively. These wintertime rates of C loss were similar to the value of ~0.45 μmol m$^{-2}$ s$^{-1}$ measured during February in a boreal aspen stand in Saskatchewan, Canada (Black et al., 1996) where, like these sites, $T_s$ remained at about −0.5 °C, despite the low values of $T_a$. Despite the widespread mortality caused by the beetle, total NEP during the growing season (May–September) was positive at both sites in both years (12 and 52 g C m$^{-2}$ at MPB-06 and 17 and 68 g C m$^{-2}$ at MPB-03 in 2007 and 2008, respectively). At MPB-06, daytime maximum half-hourly NEP values were significantly higher in June and July 2008, reaching 5 μmol m$^{-2}$ s$^{-1}$ in July.

**Table 3**
Comparison of daily values of net assimilation ($A_{net}$) and stomatal conductance ($g_s$) of pairs of non-attacked (NA) and green-attacked (GA) trees at MPB-06[a].

| Date 2006 | $n$ | $A_{net}$ (μmol $CO_2$ m$^{-2}$ s$^{-1}$) | | | | $g_s$ (mol $H_2O$ m$^{-2}$ s$^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | NA | | GA | | NA | | GA | |
| | | Ambient[b] | LED[c] | Ambient | LED | Ambient | LED | Ambient | LED |
| August 21 | 3 | 3.05 (1.08)[d] | 2.48 (1.49) | 3.17 (1.55) | 2.55 (1.52) | 0.019 (0.005) | 0.008 (0.006) | 0.011 (0.005) | 0.011 (0.007) |
| August 22 | 11 | 4.01 (0.93) | 5.02 (1.57) | 2.85 (1.49) | 4.23 (2.46) | 0.016 (0.013) | 0.022 (0.010) | 0.012 (0.014) | 0.020 (0.013) |
| August 23 | 10 | 3.58 (1.52) | 3.94 (1.25) | 2.88 (2.53) | 2.72 (2.55) | 0.016 (0.016) | 0.016 (0.008) | 0.012 (0.019) | 0.012 (0.013) |
| All | 24 | 3.21 (1.18) | 4.49 (1.47) | 2.97 (1.85) | 3.39 (2.44) | 0.016 (0.013) | 0.018 (0.009) | 0.011 (0.015) | 0.015 (0.013) |

[a] Daily averages of measurements made between 10:30 and 15:00 h PST.
[b] Measurements were made using a conifer chamber under ambient light.
[c] Measurements were made using an LED light source chamber.
[d] Standard deviation.

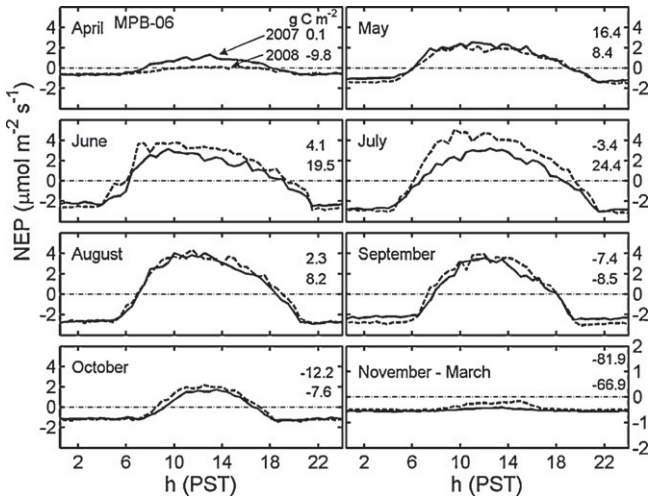


**Fig. 4.** The diurnal patterns of monthly ensemble-averaged half-hour values of NEP for (a) MPB-06 for 2007 and 2008. Values in panels are NEP in g C m$^{-2}$ per month or for November–March.

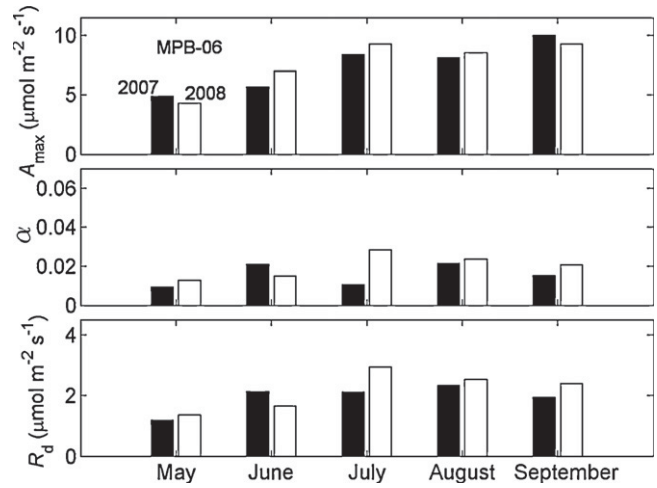


**Fig. 6.** Maximum assimilation rate ($A_{max}$), quantum yield ($\alpha$) and daytime respiration ($R_d$) for MPB-06 from May to September 2007 and 2008. From May to September 2007 and 2008, the $r^2$ of Eq. (1) was between 0.3 and 0.5.

During the other growing season months, NEP was more similar between years. During the nighttime, C losses reached a maximum in July when half-hourly values of ~3 μmol m$^{-2}$ s$^{-1}$ were observed. At MPB-03, daytime half-hourly values of NEP were significantly higher in 2008, reaching a maximum of ~6 μmol m$^{-2}$ s$^{-1}$ in July, August and September. The highest nighttime half-hourly C losses were between 3 and 3.5 μmol m$^{-2}$ s$^{-1}$ in July and August 2007 and 2008.

Growing season monthly maximum values of $A_{max}$, $\alpha$ and $R_d$ for MPB-06 and MPB-03 are shown in Figs. 6 and 7, respectively. At both sites values of all three parameters were generally higher in 2008. At MPB-06, $A_{max}$ increased from 4–5 μmol m$^{-2}$ s$^{-1}$ in May to 9–10 μmol m$^{-2}$ s$^{-1}$ in September, while $\alpha$ and $R_d$ tended to be highest in July and August. At MPB-03, $A_{max}$ in 2007 reached its maximum value in July, while in 2008 the maximum was in September. In both years $\alpha$ and $R_d$ were highest in June and July. Using the Michaelis–Menten light-response relationship (Eq. (1)), we found that $Q$ explained between 26% and 48% of the variation in half-hourly NEP values at MPB-06, and between 20% and 32% at MPB-03. During May 2007 and 2008 at MPB-03, $Q$ only accounted for 11% and 3% of the variation in NEP.

### 3.4. Comparison of cumulative half-hourly annual NEP, $P_g$ and $R_e$

Cumulative NEP, $P_g$ and $R_e$ are shown in Figs. 8 and 9. Annual NEP was −82 and −33 g C m$^{-2}$ at MPB-06 in 2007 and 2008 (Fig. 8). $P_g$ increased from 439 g C m$^{-2}$ in 2007 to 522 g C m$^{-2}$ in 2008, indicating that the smaller fraction of healthy trees in 2008 was able to sequester more C than the larger fraction in 2007, although the growing season conditions (daytime $T_a > 5$ °C) lasted a week longer in 2008. Annual $R_e$ was significantly greater in 2008 (555 g C m$^{-2}$) than in 2007 (521 g C m$^{-2}$). At MPB-03, NEP increased from −56 g C m$^{-2}$ in 2007 to 4 g C m$^{-2}$ in 2008 (Fig. 9), while both $P_g$ and $R_e$ increased significantly from 432 and 469 g C m$^{-2}$ in 2007 to 522 and 518 g C m$^{-2}$ in 2008, respectively. Growing season conditions lasted 16 days longer at MPB-03 in 2008. Over both years at MPB-06 and MPB-03, the 20% random error assigned to each half-hour resulted in an annual NEP error of <3 g C m$^{-2}$ year$^{-1}$. The uncertainties associated with the gap-filling relationships, which indicate that in all but one of the measurement years these sites were clearly C sources, are shown in Table 4.

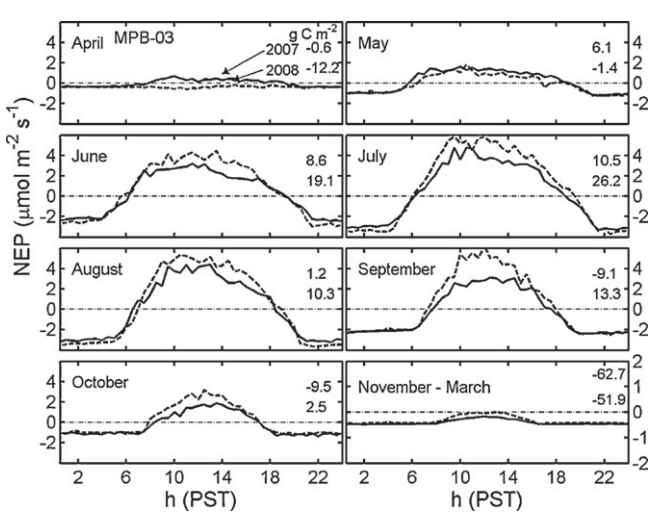


**Fig. 5.** Same as Fig. 4, except for MPB-03.

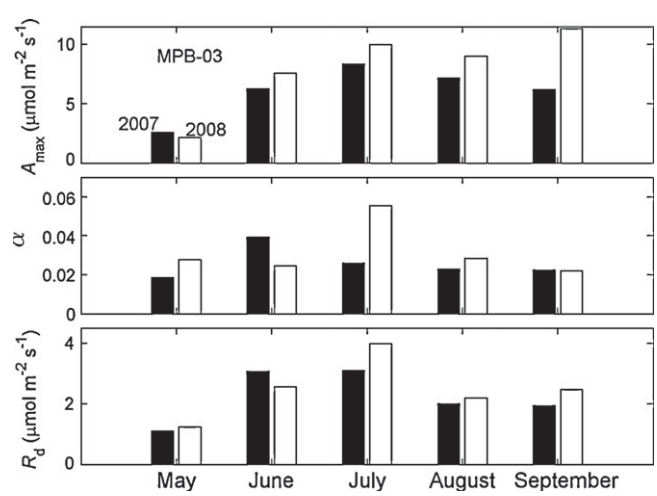


**Fig. 7.** Same as Fig. 6, except for MPB-03. From May to September 2007 and 2008, the $r^2$ of Eq. (1) was between 0.1 and 0.3.

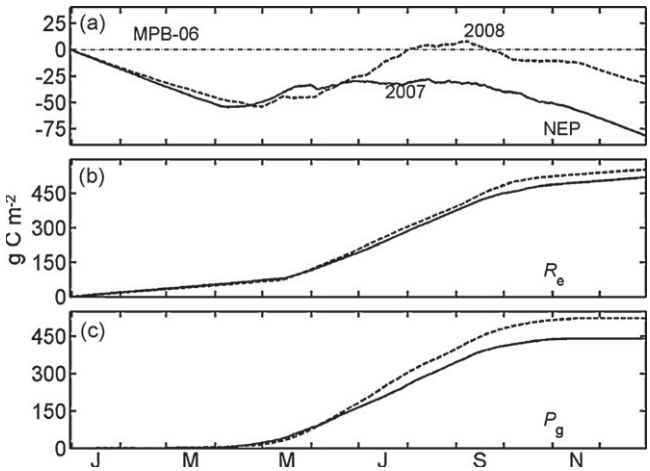


**Fig. 8.** (a) Cumulative net ecosystem production (NEP), (b) ecosystem respiration ($R_e$) and (c) gross ecosystem photosynthesis ($P_g$) at MPB-06 for 2007 and 2008.

### 3.5. NEP during the growing season at the harvested sites

During the daytime, half-hourly NEP reached a maximum of 1.7 μmol m$^{-2}$ s$^{-1}$ at CC-97, but was only briefly positive at CC-05 during mid-day hours (Fig. 10). Average daily (24-h) NEP during the 29 June–23 July 2007 measurement period at CC-97 was −0.37 ± 0.20 g C m$^{-2}$, while during this same period, MPB-06 had a near neutral daily NEP of −0.07 ± 0.35 g C m$^{-2}$. During the 24 July–16 August 2007 measurement period at CC-05, average daily NEP was −0.87 ± 0.13 g C m$^{-2}$, while average daily NEP at MPB-06 was 0.40 ± 0.41 g C m$^{-2}$.

## 4. Discussion

### 4.1. $CO_2$ exchange in attacked and non-attacked trees

The non-significant difference in foliar $CO_2$ exchange rates between green-attacked and non-attacked trees suggests that during the first few weeks of attack, phloem and xylem flows had not yet been greatly affected. However, the coefficient of variation for LED and ambient light source measurements was approximately twice as high for green-attacked trees compared to non-attacked trees, which in combination with reduced (though not significantly) stomatal conductances, is likely an indication of incipient effects of beetle attack. By the 2007 growing season,

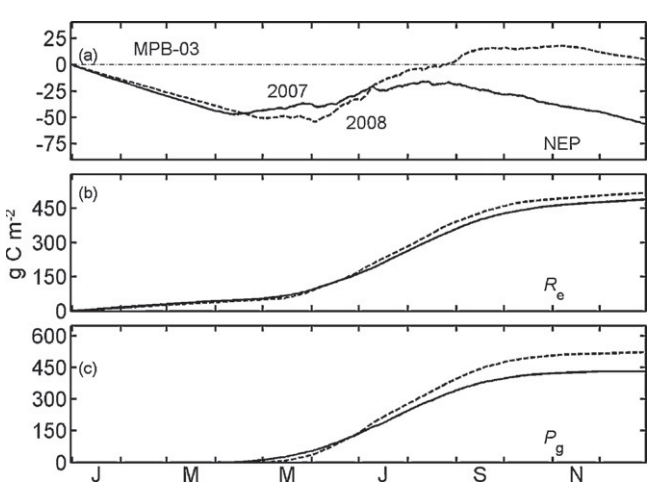


**Fig. 9.** Same as Fig. 8, except for MPB-03.

**Table 4**
Annual totals and estimated uncertainties of net ecosystem production (NEP), ecosystem respiration ($R_e$) and gross ecosystem photosynthesis ($P_g$) (g C m$^{-2}$).

| | MPB-06 | | MPB-03 | |
|---|---|---|---|---|
| | 2007 | 2008 | 2007 | 2008 |
| NEP | −82 (−53, −93)[a] | −33 (−17, −61) | −56 (−6, −69) | 4 (53, −15) |
| $R_e$ | 521 (552, 507) | 555 (579, 532) | 488 (514, 444) | 518 (553, 492) |
| $P_g$ | 439 (480, 430) | 522 (539,491) | 432 (469, 419) | 522 (567, 509) |

[a] Upper and lower 95% confidence intervals. See Section 2 for details. Confidence intervals at MPB-03 in 2007 were calculated using NEP measurements from the 2008 winter (soil temperature <1 °C).

many of the attacked trees at MPB-06 had died, resulting in reduced photosynthetic capacity compared to the comparison interval in 2006. However, total C sequestration was lower in 2006 than 2007 due to higher rates of respiration. The higher respiration in 2006 was likely due to the $R_a$ from the higher fraction of healthy trees. In addition, in 2006, $\theta$ values were close to the estimated wilting point, which might have been sufficiently low to inhibit $P_g$ (Lambers et al., 1998). Had $\theta$ values been more similar to those of 2007 it is likely $P_g$ would have been greater.

### 4.2. NEP in MPB-attacked stands

While both MPB-06 and MPB-03 were close to C neutral in April 2007, April 2008 was a month of C loss, probably due to cooler air temperatures, which inhibited photosynthesis. In both years at MPB-06 the snow melted by mid-May. At MPB-03, the snow melted by late April in 2007 and by mid-May in 2008. May 2007 was a relatively productive month at both sites, as a combination of abundant soil water from melting snow and warm air temperatures led to favourable conditions for photosynthesis. During this time below-ground $R_e$ was still limited by relatively cold soil conditions. Monson et al. (2005) reported that at a subalpine forest in Colorado, USA, the interannual variability in NEE (i.e., −NEP) over 5 years was mostly explained by variation in the length of the snowmelt period, having found that during the snowmelt period NEE was most negative in years when snowmelt occurred later in the spring. A later snowmelt can provide a constant supply of soil

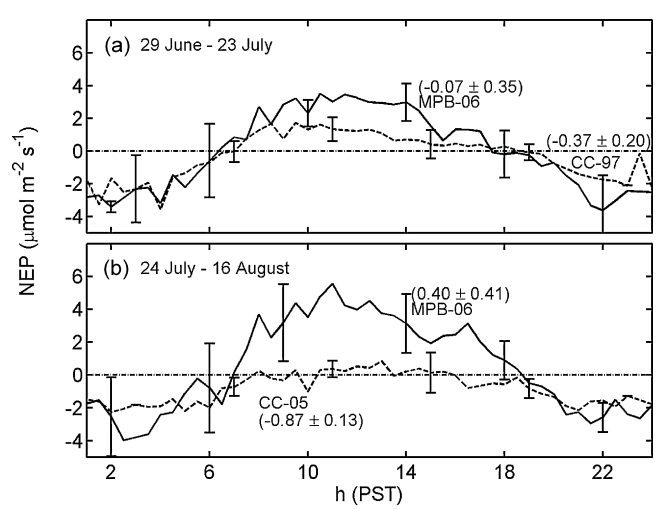


**Fig. 10.** Ensemble-average diurnal course of measured NEP in 2007 at (a) CC-97 and (b) CC-05, compared with measurements at MPB-06. Bars are standard deviations. Numbers in the brackets adjacent to the stand acronyms are average daily (24-h) NEP in g C m$^{-2}$ for the measurement period. Average 24-h canopy downwelling photosynthetically active radiation and air temperature were 460 and 405 μmol m$^{-2}$ s$^{-1}$ and 16 and 14 °C for 29 June–23 July and 24 July–16 August, respectively.

water when air temperatures are warmer than would have been the case if snowmelt had occurred earlier (Monson et al., 2005). Some recent studies have shown that air temperature plays the dominant role in determining photosynthetic recovery in coniferous forests (Tanja et al., 2003; Ensminger et al., 2004; Krishnan et al., 2008). Although $T_a$ was slightly higher at both sites in May 2008, there was a ~20% reduction in PAR, which likely partly accounts for the lower NEP observed in that month.

That MPB-06 was an annual C source shows that photosynthesis was greatly reduced due to the beetle epidemic. It was somewhat surprising that in 2008, MPB-06 was a greater growing season C sink than in 2007, despite a smaller percentage of healthy trees. The high productivity of the healthy 21% of trees in 2008 suggests those trees, along with shrubs and herbs, likely benefited from less competition for resources, such as soil water and nitrogen (Veblen et al., 1991). Berg et al. (2006) used dendrochronological techniques to conclude that in spruce-forests attacked by the spruce beetle (*Dendroctonus rufipennis*), non-attacked trees often rapidly increased their growth following attack, by similarly taking advantage of less competition for light, soil water and nutrients. The growing season C uptake at MPB-03 was likely a result of the high productivity of the secondary structure and shrubs and herbs, which remained healthy (and probably even experienced enhanced vigour) because the beetle attacks primarily mature lodgepole pine trees (Safranyik and Wilson, 2006). The greater C accumulation in 2008 compared to 2007 at MPB-03 was likely due to an increase in below-canopy light levels from an opening of the stand due to needle fall, as shown by hemispherical photography (Egginton et al., 2008). Shrubs and herbs would also be expected to benefit from higher below-canopy light levels and are capable of sequestering C at relatively high rates (Pypker and Fredeen, 2002).

In other studies, researchers have also observed an increase in the growth of surviving trees following beetle outbreaks, stand thinning and fire. For instance, Alfaro et al. (2004) used dendrochronology to determine that following three historical large-scale MPB outbreaks in south-central BC, surviving trees experienced extended periods of increased growth, averaging 14 years. Heath and Alfaro (1990) estimated the growth releases to have begun between 2 to 6 years following the start of a severe outbreak in central BC. Waring and Pitman (1985) reported that following MPB attack in Oregon, the growth efficiency (the increment in stem biomass per square meter of foliage) of surviving trees increased 2 and 3 years following attack and concluded that the major impact of the attack was the reduction in canopy leaf area which increased the available light and improved photosynthesis for the remaining live trees. Like Berg et al. (2006), Veblen et al. (1991) used dendrochronological methods and found that a spruce beetle outbreak in the 1940s in Colorado accelerated the growth of shade tolerant tree species (not attacked by the beetle), rather than leading to new seedling establishment, which resulted in a shift in stand structure from spruce to fir dominated forests. Growth rates remained high for >40 years and were greater for smaller sub-canopy trees than larger canopy trees. Yang (1998) measured foliar and stand growth in a 40-year-old lodgepole pine stand in Alberta, Canada and found that needle length and mass increased significantly 3 and 4 years after thinning while tree height, DBH and basal area increased 5 and 10 years following thinning. Smirnova et al. (2008) observed a growth release of surviving trees in jack pine (*Pinus banksiana*) stands in Quebec, which had experienced medium intensity fires. These studies suggest that at MPB-03 there could be a shift from a pre-beetle-attack lodgepole pine canopy to a post-beetle-attack subalpine fir dominated canopy as the latter comprises a significant portion of the secondary structure which is experiencing a rapid increase in growth following the attack.

The dissimilarity in response of stand level photosynthesis to $Q$ between sites is probably attributable to the differences in species composition. While MPB-06 is a uniform lodgepole pine canopy acclimated to full sunlight, which can be expected to respond to $Q$ in a relatively uniform manner, MPB-03 is composed of a mix of shade acclimated sub-canopy conifers, all responding uniquely to $Q$ (Lambers et al., 1998). Once the leaf emergence of the understory deciduous component occurred in June at MPB-03, a rapid increase in the photosynthetic response to $Q$ was observed. The high $A_{max}$ observed in September at both sites may be a result of the lower vapour pressure deficit than that observed during the mid-summer months when the trees limit water loss by lowering the stomatal conductance (Lambers et al., 1998).

There are few reported measurements of NEP in stands where insect attacks have occurred. In a Mediterranean forest in southern France, Allard et al. (2008) reported that a caterpillar attack decreased annual NEP compared to non-attack years. Similarly, Kirschbaum et al. (2007), in a modelling/EC study, reported that a psyllids (*Cardiaspina* spp.) attack in a *Eucalyptus delegatensis* forest, which led to a large unseasonable leaf-fall, had the effect of reducing $P_g$ and increasing C loss through respiration by insects and decomposition. Recently, Clarke et al. (2010) measured the effects of Gypsy moth attack on the NEE of oak-and pine-dominated stands in New Jersey.

For comparative purposes, it is useful to examine the results of studies of the effect of fire on forest C balance components. Amiro et al. (2006) found that a boreal mixed jack pine and black spruce (*Picea mariana*) stand that was severely burned in 1998 had an NEP of −87 and −132 g C m$^{-2}$ year$^{-1}$ in 2001 and 2002, respectively. When these measurements were made, the stand consisted of aspen saplings and shorter jack pine and black spruce seedlings, as well as ~18-m tall standing dead trees. The burnt site that was the focus of the Amiro et al. study shares characteristics similar to those of MPB-06 and MPB-03 in that they consisted of standing dead trees with decomposing dead roots below ground. Amiro et al. (2006) also measured an annual NEP of 68 g C m$^{-2}$ in 2002 in a boreal forest stand burned in 1989, which consisted of balsam poplar (*Populus balsamifera*), jack pine, trembling aspen (*Populus tremuloides*) and birch (*Betula papyrifera*), as well as dead snags of black spruce and jack pine. If left to naturally regenerate, it is possible that MPB-attacked stands without secondary structure might follow a similar path to recovery as burnt stands, as in both cases the trees have been killed but remain standing. They differ in that while most of the needles are consumed during a fire, they fall to the ground over a number of years following a beetle attack. In addition, much of the understory and upper soil organic layer are also consumed during a fire (Amiro et al., 2006), whereas these components are not directly affected by a beetle attack. In terms of C losses, while burnt stands experience a rapid and large loss of C as a direct result of fire, both beetle-attacked and burnt forests likely experience a prolonged elevated $R_h$ due to the decomposition of killed vegetation (Mkhabela et al., 2009). A significant difference is that while almost all trees are killed during severe crown fires, a portion of the tree survives a beetle attack, depending on the severity of attack and the stand composition. Thus, $P_g$ would likely be much greater following a beetle attack, due to the accelerated growth of the surviving vegetation. Indeed, the jack pine and black spruce stand burned in 1998 (mentioned above), had a much lower $P_g$ (271 and 319 g C m$^{-2}$ year$^{-1}$ in 2004 and 2005) (Mkhabela et al., 2009), than that observed in this study.

### 4.3. NEP of harvested sites

CC-05 was a relatively large C source during the 2007 growing season, as expected, given the site had been harvested just two years prior. However, CC-97, which had been regenerating for 10

years, was also still a growing season C source, which is significant, given that the site is composed of an abundance of actively photosynthesizing lodgepole pine saplings and that coarse woody debris left following harvesting had a decade to decompose. Since there is no significant photosynthetic uptake of C during the rest of the year, these measurements indicate that both these clearcut sites were annual C sources. There have been numerous other measurements of NEP made in early successional forests following clearcut harvesting (Zha et al., 2009; Kowalski et al., 2003; Pypker and Fredeen, 2002, 2003; Rannik et al., 2002). Stands varying in age from 1 to 10 years following clearcut harvest, in a variety of biogeoclimatic zones, have been observed to be annual C sources (Humphreys et al., 2005). For example, Humphreys et al. (2005) reported a harvested and then replanted coastal Douglas-fir (*Pseudotsuga menziesii*) stand to be an annual C source of 620, 520 and 600 g C $m^{-2}$ $year^{-1}$ in the first, second and third years following harvesting. A sub-boreal clearcut planted with white spruce and lodgepole pine had an average daily growing season NEP of 0.3 g C $m^{-2}$ $day^{-1}$ 5 years after harvesting but became a C source during the sixth year with an average daily growing season NEP of −0.9 g C $m^{-2}$ $day^{-1}$ (Pypker and Fredeen, 2002) illustrating the large interannual variation in NEP possible in recently harvested stands.

## 5. Conclusions

MPB-06 and MPB-03 were growing season C sinks and MPB-03 was a weak annual C sink in 2008, demonstrating the resiliency of sequestration in these stands to the beetle epidemic. The presence of secondary structure at MPB-03 likely accelerated the stand's return to C neutrality. In the MPB-06 stand, during the growing season the remaining live trees, along with shrubs, herbs and non-vascular plants provided a moderate level of C uptake, especially during the second year when below-canopy light and growth levels increased. Although needle fall and dead roots probably began to enhance heterotrophic respiration, we have yet to observe a large respiratory release from either site. Once a large portion of the dead trees fall, an increase in decomposition is likely, which could result in these sites becoming significantly larger C sources. Conversely, an increase in C uptake due to the rapid growth of secondary structure would likely offset some or all of those C losses. Thus, NEP measurements made over longer time scales are required to determine how these forests will continue to evolve. Additionally, the rapid warming of the northern interior of BC, which has enabled the current beetle epidemic to spread further north than during previous attacks (Safranyik and Wilson, 2006), is projected to intensify, likely leading to an increase in the prevalence of forest fires (Lemmen et al., 2008) and insect and disease epidemics (Taylor et al., 2006). Growing season NEP measurements in harvested stands show they can remain significant C sources for at least 10 years, which, when compared to MPB-06 and MPB-03 which were growing season C sinks, suggests that deferring the harvest of MPB-attacked stands with significant levels of secondary structure could prevent forested areas from becoming C sources over extended periods.

## Acknowledgements

This research was supported by grants from the Canadian Foundation for Climate and Atmospheric Science, the BC Forest Science Program, the BC Ministry of Forests and Range, and the Natural Science and Engineering Research Council of Canada (Discovery Grant to TAB). We greatly appreciate the technical assistance in the field provide by Dominic Lessard, Rick Ketler, Andrew Sauter, Andrew Hum, Rebecca Bowler, Sandra Allen, and Honey-Marie de la Giroday. Dale Seip, BC Ministry of Environment, has provided site information, advice and support throughout the project. Peter Jackson was extremely helpful in initiating the project and providing air photographs of the beetle-attacked stands in the study area. Jim Hesse, BC Parks, was very helpful in providing access to the MPB-03 site. We acknowledge the assistance of David Gaumont-Guay, Darin Brooks, Sandra Allen, Bob Hodgkinson, Maggie Marsland, Tim Brown and Grant Nishio in site selection. With support of the Canadian Forest Service, Terrestrial Ecosystem Services (under contract) measured the groundplots, Eric Bol prepared samples for lab analyses, and Colin Ferster prepared the data for compilation. Thanks also to Sam Davis, Keith Jones and Hans Beurskens at the BC Ministry of Forests and Range, Mackenzie District for assistance in accessing MPB-06 during winter.

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