The carbon, water and energy balances of two lodgepole pine stands recovering from mountain pine beetle attack in British Columbia

by

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Abstract

Over the past decade British Columbia (BC) has experienced the largest mountain pine beetle (MPB) outbreak on record. This study used the eddy covariance (EC) technique to examine the impact of the MPB outbreak on the net ecosystem production (NEP) and evapotranspiration ($E$) of two lodgepole pine stands in the central interior of BC from 2007 to 2010. MPB-06, an 85-year-old stand, and MPB-03, a 110-year-old stand, were first attacked by the beetle in 2006 and 2003, respectively. EC measurements were also made in two harvested stands, one in 2005 and one in 1997 (CC-05 and CC-97, respectively) during the 2007 growing season.

Annual NEP increased from -81 to 64 g carbon (C) m$^{-2}$ from 2007 to 2010 at MPB-06 due to an increase in gross ecosystem photosynthesis ($P_g$). At MPB-03, annual NEP also varied with $P_g$, ranging from -57 g C m$^{-2}$ in 2007 to 6 g C m$^{-2}$ in 2009. Annual ecosystem respiration ($R_e$) did not vary greatly over the four years at both sites. At MPB-03, $P_g$ was reduced by drought in 2009 and 2010. The increase in $P_g$ at both sites was due to an increase in the photosynthetic capacity of the surviving trees and vegetation, as shown by foliar net-assimilation measurements. Light response analysis indicated that daytime $R_e$ values derived using nighttime NEP data were likely realistic estimates of the actual respiratory fluxes. NEP measurements at CC-97 and CC-05, showed that these stands are likely to remain C sources for as many as 10 years following harvesting. There was little interannual variation in $E$ at both sites as the surviving trees and vegetation compensated for reductions in $E$ due to the death of the overstory. Root-zone drainage was much greater at MPB-03 than at MPB-06, due to larger $P$ at MPB-03. Growing season water deficit showed both stands to be water limited in spite of the high proportion of dead pine trees. Results from this study showed the importance of the remaining healthy trees and vegetation in the recovery of these stands from MPB attack.
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<td>LAI</td>
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<td>mountain pine beetle</td>
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<td>W m⁻²</td>
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<td>mm d⁻¹</td>
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<td>µmol m⁻² s⁻¹</td>
<td>ecosystem photosynthetic capacity</td>
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| Pᵣgₙₐₓ N         | µmol m⁻² s⁻¹ | ecosystem photosynthetic capacity, from Pᵣg
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<td>- All units of respiration are in ( \mu\text{mol m}^{-2}\text{s}^{-1} ) or ( \text{g C m}^{-2}\text{time}^{-1} )</td>
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<td>hours</td>
<td>$t$ is the time of day (PST)</td>
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<tr>
<td>$U$</td>
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<td>$u_*$</td>
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<td>$\lambda E_{eq}$</td>
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<td>phase angle of the diurnal course of $T_a$</td>
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<tr>
<td>$\theta$</td>
<td>m$^3$ m$^{-5}$</td>
<td>soil fine fraction (soil particle size &lt; 2 mm)</td>
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<tr>
<td>$\sigma_L$</td>
<td>g m$^{-2}$</td>
<td>specific leaf mass</td>
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$^8$“time” indicates the use of seconds, hours, days and years.
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1. Introduction

Anthropogenic emissions have increased atmospheric carbon dioxide (CO₂) concentrations from the pre-industrial level of 260 ppm to 387 ppm by the end of 2009 (Canadell et al. 2007, Friedlingstein et al. 2010). In 2009, total CO₂ emissions from fossil fuel burning and cement production were 8.40 Pg C, a decrease of 1.3 % from 2008 due to the global economic crises; however, with economic recovery, emissions are projected to increase by more than 3% in 2010 (Friedlingstein et al. 2010). Friedlingstein et al. (2010) also report that land-use change (LUC) accounts for additional emissions of ~0.90 Pg C. This is of major concern since modeling with and without greenhouse gas (GHG) forcing clearly indicates that the increase in the atmospheric concentration of CO₂ and other GHGs, such as methane and nitrous oxide, is very likely causing global climate warming (Grace 2004, IPCC 2007). Between 2000 and 2008, the terrestrial biosphere absorbed 29% of the annual anthropogenic CO₂ emissions resulting from fossil fuel burning, cement production and LUC, with the oceans absorbing a further 26%, although the year-to-year variability in the fraction absorbed was high (Le Quéré et al. 2009). Despite this uptake by the biosphere, the rate of increase in the atmospheric CO₂ concentration continues to rise, averaging 1.93 ppm year⁻¹ from 2000-2006 (Canadell et al. 2007), and the fraction of annual emissions remaining in the atmosphere increased 0.3% year⁻¹, from 1959 to 2008 (Le Quéré et al. 2009). Since GHGs affect the global climate, the uptake and release of these gases by the terrestrial biosphere has a direct influence on climate change (Heinmann and Reichstein 2008). The connection between the terrestrial carbon (C) cycle and climate change suggests that if a significant portion of the C stored in the terrestrial biosphere were to be released to the atmosphere, there would likely be a significant impact on climate (Heinmann and Reichstein 2008).
The exchange of CO$_2$ between terrestrial ecosystems and the atmosphere occurs through two main processes; ecosystem uptake of atmospheric CO$_2$ is the result of gross ecosystem photosynthesis ($P_g$), while ecosystem respiration ($R_e$) results in the release of CO$_2$ to the atmosphere. $R_e$ is comprised of autotrophic respiration ($R_a$) from the foliage, stems, roots and mycorrhizae, and heterotrophic respiration ($R_h$) results from the microbial decomposition of above- and below-ground organic matter. The difference between the two (typically large) fluxes of $R_e$ and $P_g$ is the net ecosystem exchange (NEE), with a positive value indicating a gain of CO$_2$ by the atmosphere and a negative value indicating gain by the ecosystem. The eddy covariance (EC) technique has emerged as the preferred method for measuring NEE on land (Baldocchi 2003, 2008). The term net ecosystem production is defined by $\text{NEP} = -\text{NEE}$, with a positive value indicating a net CO$_2$ uptake by the ecosystem (C sink) over a period of time (e.g., a year), while a negative NEP indicates a net CO$_2$ release (C source) to the atmosphere (i.e., $\text{NEP} = P_g - R_e$).

Both within Canada and globally, networks, such as the Fluxnet Canada Research Network (FCRN), now known as Canadian Carbon Program (CCP), Ameriflux and CarboEurope, under the umbrella of FLUXNET, a global network of EC sites, have been established to monitor C balances in various ecological regions. FLUXNET includes more than 500 EC sites from many regional networks operating on a long-term basis (Fig. 1-1).
In Canada, EC measurements made in the boreal forest have shown annual C balances of stands to vary widely, with stand composition, climate and disturbance all having an influence (e.g., Barr et al. 2007, Bergeron et al. 2007, Mkhabela et al. 2009). Disturbances, such as forest fires, insect attacks and harvesting, can result in some of the largest year-to-year variability in NEP and shift forests from acting as C sinks to sources (Amiro et al. 2010). Modelling studies have estimated that, primarily due to disturbance, Canada’s forests recently switched from being a C sink, during the mid- to late-1990s, to being a C source during the last 10 years (Chen et al. 2000, Bond-Lamberty et al. 2007, Kurz et al. 2008). While the impact of forest fires and harvesting on NEP has received considerable attention in the past decade (Amiro et al. 2003, Humphreys et al. 2005, Amiro et al. 2006), insect attacks have only recently begun to be studied (Cook et al. 2008; Clark et al. 2010).

The current mountain pine beetle (MPB) (*Dendroctonus ponderosae*) outbreak in British Columbia (BC), which began in 2001-2002, is unprecedented in terms of tree mortality and area
affected. A 2009 aerial survey reported just under 9 million ha of forests showing beetle impact, down from the peak infestation of 10 million ha in 2007 (Westfall and Ebata 2009) (Fig. 1.2). The main host of the beetle is lodgepole pine (*Pinus contorta* var. *latifolia*), which is found throughout the interior of BC. The magnitude of the current outbreak is primarily due to the combination of an abundance of mature lodgepole pine and increasing wintertime minimum temperatures over the past several years (Safranyik and Wilson 2006). Although the beetles prefer mature lodgepole pine (~60-160 years old), they can inhabit virtually all *Pinus* spp. in western North America (Taylor *et al.* 2006). The beetles colonize through pheromone-mediated mass attacks which overwhelm the host’s defences (Aukema *et al.* 2006). After eggs laid by the female beetles hatch under the bark, the larvae feed on the phloem, cutting off the tree’s transport of photosynthate (Taylor *et al.* 2006). The beetles also introduce a blue-stain fungus into the tree which clogs the xylem, reducing the tree’s capacity to transport water and nutrients from the soil (Gorte 2008). Generally, in the first year of MPB attack, the needles of attacked trees remain green (green attack stage). However, following the first winter of attack, the needles turn red on trees that have been killed (red attack stage) and one or two years later the needles fall, giving the trees a grey appearance (grey attack stage).
The effects of MPB attacks on forest C cycling are not well understood. However, they have the potential to influence NEP, through their impact on $P_g$ and $R_e$. Following MPB attack, the reduction in healthy leaf area associated with tree mortality would likely lead to a decline in $P_g$, while the increase in dead organic matter (needles, branches, stems and roots) would be expected to lead to an eventual increase in $R_h$. While no previous measurements of NEP have been made in MPB attacked stands, a study by Kurz et al. (2008), using the Carbon Budget
Model of the Canadian Forest Sector (CBM-CFS3), predicted the cumulative impact of the BC MPB outbreak from 2000-2020 to be a net loss 270 Tg C over 374,000 km$^2$ of forest, with the impact peaking in 2009 with a net biome production (NBP, defined as NEP plus the impacts of disturbance) of -53 g C m$^{-2}$. Coops and Wulder (2010) made MODIS-based estimates of $P_g$ over the entire BC MPB infestation area, from 2002 to 2005, and reported a decreased of 10-20% from pre-outbreak levels, with more severely attacked stands having a greater reduction. While both of the preceding studies provide insight as to the impacts of the MPB attack on the C balance of these stands, the EC technique has the advantage of making continuous measurements of NEP at the stand level, with fluxes calculated every half-hour. This allows the C balance to be determined over a range of time scales, from half-hourly to annual. When these fluxes are combined with half-hourly climate measurements, empirical models of the response of NEP to climate variation can be developed (Barr et al. 2004). EC measurements are also essential for validating process models and remote sensing algorithms.

In addition to the potential impacts on the C balance, there is much concern over how the beetle outbreak will impact the hydrology of the affected stands, with predictions of an increase in water yield, peak flow and base flow (BC Ministry of Environment 2008; Rex and Dubé 2009). Higher water yield would likely lead to increases in the occurrence of flooding and changes in fish habitat and watershed nutrient status. A hydrological study by Potts (1984), on a watershed in Montana where 35% of the timber had been killed by the MPB, found a 15% increase in the annual water yield, a 10% increase in low flows and an increase in peak runoff in the first five years following attack. A change in water yield could partly occur through a decrease in canopy interception rates because after attack, forest canopies open up due to needle loss and eventual tree fall. Thus, beetle-attacked stands become similar to harvested stands,
which have greater winter snow accumulation and higher melt rates than unharvested stands (Winkler et al. 2010).

Evapotranspiration ($E$), which is comprised of evaporation from the soil surface and wet vegetation, and transpiration from vegetation, is likely to be affected by beetle attack too, but little is known about such impacts because existing water balance studies have tended to focus on water yields, rather than $E$ specifically. A significant decrease in $E$ due to a reduction in live leaf area associated with tree mortality can be expected to lead to higher water tables and water yields. The impact on $E$ is likely to depend on the fraction of trees killed by the beetle, and the presence of secondary structure (living tree seedlings and saplings, sub-canopy and canopy trees that survive the attack), and the amount of shrub and herb vegetation. If only a small fraction of trees are killed, then $E$ might not change greatly; however, if an entire stand without secondary structure is killed, then a large reduction in $E$ can be expected to occur. As Hélie et al. (2005) note, the large variability in BC precipitation and temperature regimes and vegetation types make it difficult to predict whether post-outbreak changes in transpiration would be large or small.

In order to improve our understanding of the effects of insect attacks on forest C and water cycling, this thesis examines the impact of the MPB on the C, water and energy balances of two lodgepole pine stands in the northern interior of BC. The first stand is located at Kennedy Siding (MPB-06), about 35 km southeast of the town of Mackenzie (Fig.1.3). This approximately 80-year-old stand contained few non-lodgepole pine trees and was first attacked by the beetle during the summer of 2006, shortly before EC measurements began in late July. The second stand is located adjacent to Crooked River Provincial Park (MPB-03), about 70 km north of Prince George, and approximately 100 km south of MPB-06. MPB-03 is approximately 110 years old and was first attacked in 2003. When EC measurements began in March 2007, it
had > 95% pine canopy mortality. The overstory of MPB-03 was comprised of about 92% lodgepole pine and 8% subalpine fir (*Abies lasiocarpa*), and had a developed secondary structure consisting of lodgepole pine, subalpine fir and white hybrid spruce (*Picea glauca*) sub-canopy trees, saplings, and seedlings.

![Map showing the locations of MPB-06 and MPB-03.](image)

Figure 1.3. The locations of MPB-06 and MPB-03.

In Chapter 2, NEP from the first two years of measurements is examined. Chapter 2 has been published as: Brown M, Black TA, Nesic Z, Foord VN, Spittlehouse DL, Fredeen AL, Grant NJ, Burton PJ, and Trofymow JA. 2010. Impact of mountain pine beetle attack on the net ecosystem production of lodgepole pine stands in British Columbia. Agricultural and Forest Meteorology, 150: 254-264. 2007 and 2008 were the first and second year after the beetle attack at MPB-06, and were the fourth and fifth years after attack at MPB-03. Monthly diurnal NEP
over the two years is examined and annual totals of NEP, $P_g$ and $R_e$ are presented. A comparison of NEP measurements made in the two beetle-attacked stands and two harvested stands in the 2007 growing season provides insight into the contrasting management strategies of clearcut harvesting versus allowing stands to naturally regenerate.

Chapter 3 presents an analysis of $E$ in MPB-06 and MPB-03 from 2007 to 2009. The canopy characteristics, consisting of canopy conductance ($g_c$), Priestley-Taylor $\alpha$ and the decoupling coefficient $\Omega$ are presented and $E$ is modelled. The water deficit and drainage of water from the root zone of the two stands are compared and discussed in relation to the beetle attack.

Chapter 4 examines the C balance of both stands from 2007 to 2010, focusing on changes in $P_g$ and $R_e$ over a longer period than in Chapter 2. The response of $R_e$ values derived from nighttime and daytime NEP data to $T_s$ are compared, and a light response analysis of NEP and $P_g$ provides insight into the recovery of the stands. Foliar CO$_2$ exchange measurements of various stand components are reported and compared to stand level $P_g$. Finally, the water use efficiency (WUE) of both sites is analysed.

Chapter 5 summarizes the major conclusions of this study, discusses how these findings relate to other research on the effects of MPB attack on forest C cycling and identifies areas for future research.

A number of appendices are also presented which include $E$ data from MPB-06 in 2006 and from the two harvested sites in 2007, the flux footprints from the two sites and the design of the EC and climate measurement systems, photographs of the two canopies in each of the four years of the study, the EC data logger code, and the Matlab program used to calculate the CO$_2$ and water vapour fluxes.
2. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia

2.1 Introduction

The current British Columbia (BC) outbreak of mountain pine beetle (*Dendroctonus ponderosae*) (MPB), which began in the late 1990’s, 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$^3$ (BC 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 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 no known empirical studies examining net ecosystem CO₂ 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 CO₂ 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 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 km². 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 ± 21 g C m⁻² yr⁻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 yr⁻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.
2.2 Methods

2.2.1 Site locations

NEP measurements were made at two locations in the northern interior of BC (Fig. 2.1; Table 2-1). This region is located in the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar 1991) and both stands were dominated by lodgepole pine (*Pinus 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 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 2-2). MPB-03 was first attacked in 2003 and when NEP measurements began in 2007 the site was >95% in the red-attack and gray-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.

Figure 2.1. 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>
<thead>
<tr>
<th></th>
<th>MPB-06</th>
<th>MPB-03</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand age (yr)</td>
<td>~80</td>
<td>~110</td>
</tr>
<tr>
<td>Tower location</td>
<td>55°06’42.8”N</td>
<td>54° 28’24.8”N</td>
</tr>
<tr>
<td></td>
<td>122°50’28.5”W</td>
<td>122° 42’48.4”W</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>750</td>
<td>710</td>
</tr>
<tr>
<td>Canopy height (m)</td>
<td>~15</td>
<td>~17</td>
</tr>
<tr>
<td>Stand density (height &gt; 10 m)</td>
<td>1275 (204¹)</td>
<td>558 (123)</td>
</tr>
<tr>
<td>Stand basal area m²/ha (height &gt;10m)</td>
<td>Live: 11.8 – 19.2</td>
<td>Live: 0.7 – 3.2</td>
</tr>
<tr>
<td></td>
<td>Dead: 0.2 – 0.9</td>
<td>Dead: 8.1 – 14.7</td>
</tr>
<tr>
<td>Seedling/sapling density</td>
<td>Pinus contorta: 7470</td>
<td>Pinus contorta: 2800</td>
</tr>
<tr>
<td></td>
<td>Abies lasiocarpa: 100</td>
<td>Abies lasiocarpa: 2300</td>
</tr>
<tr>
<td></td>
<td>Picea glauca: 110</td>
<td>Picea glauca: 190</td>
</tr>
<tr>
<td>LAI (overstory)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2007</td>
<td>1.4</td>
<td>0.9</td>
</tr>
<tr>
<td>2008</td>
<td>1.3</td>
<td>0.8</td>
</tr>
<tr>
<td>% MPB attacked when tower established</td>
<td>&lt;5</td>
<td>&gt;90</td>
</tr>
<tr>
<td>Litter-fibric-humus C content (kg m⁻²)</td>
<td>1.10– 3.78</td>
<td>1.88 – 2.81</td>
</tr>
<tr>
<td>Mineral soil C content (0-55 cm) (kg m⁻²)</td>
<td>1.76 – 3.15</td>
<td>1.21 – 2.76</td>
</tr>
<tr>
<td>Fine soil bulk density (kg m⁻³)</td>
<td>1180 (220)</td>
<td>1160 (323)</td>
</tr>
<tr>
<td>Soil texture</td>
<td>Gravelly sandy loam</td>
<td>Gravelly sandy loam</td>
</tr>
<tr>
<td>Soil coarse fragments (% by volume &gt; 2 mm)</td>
<td>34 (11)</td>
<td>70 (7)</td>
</tr>
</tbody>
</table>

¹ Standard deviation in brackets.
Table 2-2. Stand MPB attack status at MPB-06.

<table>
<thead>
<tr>
<th></th>
<th>August 2006</th>
<th>June 2007&lt;sup&gt;1&lt;/sup&gt;</th>
<th>October 2007&lt;sup&gt;1&lt;/sup&gt;</th>
<th>August 2008&lt;sup&gt;2&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-attacked (%)</td>
<td>50</td>
<td>43</td>
<td>28</td>
<td>21</td>
</tr>
<tr>
<td>Green-attacked (%)</td>
<td>50</td>
<td>10</td>
<td>19</td>
<td>5</td>
</tr>
<tr>
<td>Red-/grey-attacked (%)</td>
<td>-</td>
<td>47</td>
<td>53</td>
<td>73</td>
</tr>
</tbody>
</table>

<sup>1</sup>Hilker <i>et al.</i> (2008)

<sup>2</sup>Means of values from this study and of Seip and Jones (2008).

### 2.2.2 Flux, climate and ecophysiological measurements

A thirty-two-meter-tall scaffold flux tower (~2.1 m long x ~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<sub>2</sub> 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 turbulent fluctuations of CO<sub>2</sub> and H<sub>2</sub>O were measured using an open-path infrared gas analyzer (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 3 100-W solar panels.
(CTI-130, Carmanah Technologies Corp., Victoria, BC) with an 800-Ah battery unit consisting of 8 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 m 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 m and 1500 m during the daytime and nighttime 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., $F_c = \rho_a \bar{w}'s_c'$, 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 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 (model CS616, CSI) at 0-10 cm and 30-50 cm at MPB-06 and (model EC-5, Decagon Devices Inc, Pullman, Washington) at 10 cm, 20 cm 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 CO₂ 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 minutes of sampling. Measurements were made between 10:00 and 16:00h PST on August 21-23 2006 in ambient light conditions. All three days were generally sunny with maximum downwelling PAR reaching 1800 µmol m⁻² s⁻¹. Net assimilation (Aᵅ) and stomatal conductance (gₛ) 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 4 representative needles (intact to the branchlet) were placed in the LED light source chamber. In both systems a CO₂ concentration and air flow rate were maintained for 3 min at 400 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 $A_n$ and $g_s$. Area-based estimates of $A_n$ 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 x 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. (2008). 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).
2.2.3 *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 degree 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 modeled 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 degree 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.
2.2.4 **Flux quality control and data analysis**

Flux quality control procedures included rejection of data when a 30-minute period had more than 30% of an individual trace with an instrument diagnostic warning flag that indicated a bad measurement, and setting minimum (300 µmol mol\(^{-1}\)) and maximum (1000 µmol 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 \(u^* (u^*_{th})\) 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 common-place in EC studies (Gu *et al.* 2005), the threshold was within ±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 extrapolates 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 the time-varying parameters from the empirical relationships described above, was not applied during the winter (when $T_s$ was $<1 \, ^\circ C$). In the moving window approach, the parameter is 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

$$\text{NEP} = \frac{\alpha Q A_{\text{max}}}{\alpha Q + A_{\text{max}}} - R_d$$

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

2.2.5 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.

2.3 Results

2.3.1 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. 2.2). Snowfall during the 2006-2007 winter at MPB-06 was estimated to be 354 mm (liquid water equivalent) and total annual precipitation (1 Nov 2006 to 31 Oct 2007 rain 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 ($\theta$) for the 0-10 cm depth, 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 in 2008. The much higher precipitation 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 $\theta$ (10 cm depth) 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).
2.3.2 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. $A_n$ 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 $A_n$ and $g_s$ between pairs of green-attacked and non-attacked trees (Table 2-3) ($A_n$ 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. 2.3a). 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 21:00h PST) average NEP was 2.36 and 1.90 µmol m$^{-2}$ s$^{-1}$ in 2006 and 2007, respectively. Light response analysis shows that $A_{\text{max}}$, $\alpha$ and $R_d$ were all greater in 2006 than 2007 (Fig. 2.3b).
Table 2-3. Comparison of daily values of net assimilation ($A_n$) and stomatal conductance ($g_s$) of pairs of non-attacked (NA) and green-attacked (GA) trees at MPB-06.

<table>
<thead>
<tr>
<th>Date</th>
<th>$A_n$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$)</th>
<th>$g_s$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NA</td>
<td>GA</td>
</tr>
<tr>
<td></td>
<td>Ambient$^2$</td>
<td>LED$^3$</td>
</tr>
<tr>
<td>Aug 21</td>
<td>3</td>
<td>3.05 (1.08)$^4$</td>
</tr>
<tr>
<td>Aug 22</td>
<td>11</td>
<td>4.01 (0.93)</td>
</tr>
<tr>
<td>Aug 23</td>
<td>10</td>
<td>3.58 (1.52)</td>
</tr>
<tr>
<td>All 24</td>
<td>24</td>
<td>3.21 (1.18)</td>
</tr>
</tbody>
</table>

$^1$ Daily averages of measurements made between 10:30 – 15:00h PST.
$^2$ Measurements were made using a conifer chamber under ambient light.
$^3$ Measurements were made using an LED light source chamber.
$^4$ Standard deviation.
Figure 2.3. (a). Ensemble-average diurnal course of measured NEP measurements made between July 29 and August 20 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 \((A_{\text{max}})\), quantum yield \((\alpha)\) and daytime respiration \((R_d)\), were 9.8 \(\mu\text{mol \, m}^{-2} \, \text{s}^{-1}\), 0.05 and 3.93 \(\mu\text{mol \, m}^{-2} \, \text{s}^{-1}\) for 2006 and 8.6 \(\mu\text{mol \, m}^{-2} \, \text{s}^{-1}\), 0.01 and 1.7 \(\mu\text{mol \, m}^{-2} \, \text{s}^{-1}\) for 2007.

### 2.3.3 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. 2.4 for MPB-06 and Fig. 2.5 for MPB-03. For January to March and November to December, average NEP values for 2007 and 2008 were -0.52 and -0.42 \(\mu\text{mol \, m}^{-2} \, \text{s}^{-1}\) at MPB-06 and -0.41 and -0.35 \(\mu\text{mol \, m}^{-2} \, \text{s}^{-1}\) at MPB-03, respectively. These wintertime rates of C loss were similar to the value of \(~0.45 \mu\text{mol \, m}^{-2} \, \text{s}^{-1}\) 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. 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 - 3.5 µmol m$^{-2}$ s$^{-1}$ in July and August 2007 and 2008.
Figure 2.4. The diurnal patterns of monthly ensemble-averaged half-hour values of NEP for MPB-06 for 2007 and 2008. Values in panels are NEP in g C m$^{-2}$ per month or for November to March.
Figure 2.5. Same as Fig. 2.4, except for MPB-03.

Growing season monthly maximum values of \( A_{\text{max}} \), \( \alpha \) and \( R_d \) for MPB-06 and MPB-03 are shown in Figs. 2.6 and 2.7, respectively. At both sites values of all three parameters were generally higher in 2008. At MPB-06, \( A_{\text{max}} \) 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, \( A_{\text{max}} \) 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, (equation 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.

![Figure 2.6. Maximum assimilation rate ($A_{\text{max}}$), quantum yield ($\alpha$) and daytime respiration ($R_{\text{d}}$) for MPB-06 from May to September 2007 and 2008. From May to September 2007 and 2008, the $r^2$ of equation 1 was between 0.3 - 0.5.](image)

Figure 2.6. Maximum assimilation rate ($A_{\text{max}}$), quantum yield ($\alpha$) and daytime respiration ($R_{\text{d}}$) for MPB-06 from May to September 2007 and 2008. From May to September 2007 and 2008, the $r^2$ of equation 1 was between 0.3 - 0.5.
Figure 2.7. Same as Fig. 2.6, except for MPB-03. From May to September 2007 and 2008, the $r^2$ of equation 1 was between 0.1 - 0.3.

2.3.4 Comparison of cumulative half-hourly annual NEP, $P_g$ and $R_e$

Cumulative NEP, $P_g$ and $R_e$ are shown in Figs. 2.8 and 2.9. Annual NEP was -82 and -33 g C m$^{-2}$ at MPB-06 in 2007 and 2008 (Fig. 2.8). $P_g$ increased from 440 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 $T_a > 5^\circ$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. 2.9), while both $P_e$ 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 clear C sources, are shown in Table 2-4.

![Diagram of net ecosystem production (NEP), ecosystem respiration ($R_e$), and gross ecosystem photosynthesis ($P_g$) at MPB-06 for 2007 and 2008.](image)

Figure 2.8. (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.
Figure 2.9. Same as Fig. 2.8, except for MPB-03.
Table 2-4. Annual totals and estimated uncertainties of net ecosystem production (NEP), ecosystem respiration ($R_e$) and gross ecosystem photosynthesis ($P_g$) (g C m$^{-2}$).

<table>
<thead>
<tr>
<th></th>
<th>MPB-06 2007</th>
<th>2008</th>
<th>MPB-03 2007</th>
<th>2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEP</td>
<td>-82 (-53, -93)$^1$</td>
<td>-33 (-17, -61)</td>
<td>-56 (-6, -69)</td>
<td>4 (53,-15)</td>
</tr>
<tr>
<td>$R_e$</td>
<td>521 (552, 507)</td>
<td>555 (579, 532)</td>
<td>469 (514, 444)</td>
<td>518 (553, 492)</td>
</tr>
<tr>
<td>$P_g$</td>
<td>440 (480, 430)</td>
<td>522 (539,491)</td>
<td>432 (469, 419)</td>
<td>522 (567, 509)</td>
</tr>
</tbody>
</table>

$^1$Upper and lower 95% confidence intervals. See Methods section for details. Confidence intervals at MPB-03 in 2007 were calculated using NEP measurements from the 2008 winter (soil temperature <1 °C).

### 2.3.5 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. 2.10a). 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 to 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$^{-2}$ (Fig. 2.10b).
Figure 2.10. 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.

2.4 Discussion

2.4.1 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, many of the attacked trees at MPB-06 had died, resulting in a 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.

### 2.4.2 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 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 for 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 et al. (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 sub-alpine-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 out of the understory deciduous component occurred in June at MPB-03, a rapid increase in the photosynthetic response to $Q$ was observed. The high $A_{\text{max}}$ 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.

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$^{-2}$ yr$^{-1}$ 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 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*
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 trees survive 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\(^{-2}\) yr\(^{-1}\) in 2004 and 2005) (Mkhabela et al. 2009), than that observed in this study.

### 2.4.3 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. 2010; 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\(^{-2}\) y\(^{-1}\) 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.

2.5 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 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 areas from becoming C sources over extended periods.
3. Evapotranspiration and canopy characteristics of two lodgepole pine stands following mountain pine beetle attack in British Columbia

3.1 Introduction

In British Columbia (BC), the mountain pine beetle (MPB) (*Dendroctonus ponderosae*) had impacted an area just under 9 million ha in 2009 (Westfall and Ebata 2009). The beetle is native to BC forests and while there have been many outbreaks in the past, none has been as severe in duration or areal extent as the current one. The primary host for the MPB is lodgepole pine (*Pinus contorta* var. *latifolia*), which the beetles colonize via pheromone-mediated mass attacks (Aukema *et al.* 2006). Once 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 2008). There are three stages to a MPB attack. The green attack stage occurs in the first several months after a tree has been attacked, during which time the needles remain green. The red attack stage follows the first winter after the initial attack when the tree has been killed and the needles turn red. Finally, the tree enters the grey attack stage one or two years later when the needles begin to fall.

There is currently much concern over how the outbreak will impact the hydrology of the affected stands, with many believing it will result in increased water yields, higher peak flows and higher base flows and that it could take 30 or more years before the hydrology returns to pre-attack levels (Rex and Dubé 2009; British Columbia Ministry of Environment 2008). Higher water yields would likely lead to increases in the occurrence of flooding as well as changes in
fish habitat and watershed nutrient status. Potts (1984) conducted a hydrological study on a
watershed in Montana where 35% of the timber had been killed by the MPB, and found a 15% increase in the annual water yield, a 10% increase in low flows and an increase in peak runoff in the first five years following attack.

A change in water yields could occur through a decrease in canopy interception rates. Following attack, forests canopies open up because tree mortality leads to needle loss and then tree fall. Reduced interception allows more precipitation to reach the forest floor (Hélie et al. 2005). It is well documented that harvested stands have greater spring snow accumulation and higher melt rates than unharvested stands (Winkler et al. 2010). In the interior of BC, where snow accumulation and snow melt dominate the hydrology, this effect of reduced interception could be substantial.

Evapotranspiration ($E$) is likely to be affected by beetle attack, however little is known as existing water balance studies have tended to focus on water yields, rather than $E$ specifically. A significant decrease in $E$ due to tree mortality would lead to higher water tables and water yields. The impact on $E$ is likely to depend on the fraction of trees killed by the beetle, and the presence of secondary structure (tree seedlings and saplings, sub-canopy and canopy trees that survive the attack). If a small fraction of trees are killed then $E$ might not change greatly, however, if an entire stand without a secondary structure is killed then a large reduction in $E$ could be expected. Hélie et al. (2005) note that in BC the large variability in precipitation regimes, vegetation types and temperatures make it difficult to predict whether changes in transpiration would be large or small.

Studies have found that trees that survive beetle attack can flourish in the following few years as a result of reduced competition for nutrients, water and light (Waring and Pitman 1985).
Similarly, if secondary structure is present, the death of the canopy can lead to a rapid increase in understory tree and vegetation growth. This could mitigate the expected reduction in $E$ due to the death of attacked trees. In a thinning experiment in Alberta, Reid et al. (2006) found that by the end of the first growing season of thinning, where the stand density was reduced by ~90%, there was a dramatic increase in total sap flow and transpiration per unit leaf area by lodgepole pine trees in thinned stands to rates more than double that of trees in un-thinned stands. Average daily sap flow over the growing season was 2.7 L for trees in stands thinned 5 years earlier, 1.9 L for trees in the stands thinned the same year (2002) and 1.3 L for the trees in the un-thinned stands.

This study used the eddy-covariance (EC) technique to measure water vapour exchange above two MPB attacked stands in central BC to determine how $E$ has been affected by the beetle and how it and associated canopy characteristics changed during the first 5 years of recovery.

### 3.2 Methods

#### 3.2.1 Site description

The measurements were made in two stands located in the northern interior of BC, in the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar 1991). Both stands were dominated by lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.). The first stand (MPB-06) is located at Kennedy Siding, approximately 35 km southeast of the town of Mackenzie. This stand was first attacked by the beetle late in the summer of 2006. The progression of the attack is shown in Table 3-1. This stand contained few non-pine trees, and the understory consisted mainly of pine seedlings, scattered shrubs and a ground cover of moss and lichen. The second stand (MPB-03) was located adjacent to Crooked River Provincial Park, approximately 70 km
north of Prince George, BC and approximately 100 km south of MPB-06. In addition to an overstory comprised of about 92% lodgepole pine and 8% subalpine fir (Abies lasiocarpa) and ground cover dominated by mosses, lichens and dwarf shrubs, MPB-03 had a developed secondary structure consisting of sub-canopy trees and saplings of lodgepole pine, subalpine fir and white spruce (Picea glauca) and seedlings of all three tree species plus deciduous shrubs. MPB-03 was first attacked in 2003 and when net ecosystem production (NEP) measurements began in 2007 the site was >95% in the red-attack and gray-attack stages. Both sites were flat and on coarse textured gravelly soils of glacio-fluvial origin. The fine soil bulk density measured approximately 1180 and 1160 kg m$^{-3}$ and coarse fragment contents (volume >2mm) were 34 and 70 % at MPB-06 and MPB-03, respectively. In 2007, the stand density was ~1235 and ~560 and stand basal area is 12.0-20.1 m$^{2}$ ha$^{-1}$ and 8.8-17.9 m$^{2}$ ha$^{-1}$ (live and dead trees with height > 10 m) at MPB-06 and MPB-03, respectively. LAI decreased at both sites from 1.4 and 0.9 in 2007 to 1.3 and 0.6 in 2009 at MPB-06 and MPB-03, respectively. Live LAI at MPB-06, as determined by canopy photo analysis, was 0.42, 0.31, and 0.30 in 2007, 2008 and 2009, respectively.
Table 3-1. Stand mountain pine beetle attack status at MPB-06.

<table>
<thead>
<tr>
<th></th>
<th>August 2006</th>
<th>June 2007(^1)</th>
<th>October 2007(^1)</th>
<th>August 2008(^2)</th>
<th>August 2009(^3)</th>
<th>August 2010(^4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-attacked (%)</td>
<td>50</td>
<td>43</td>
<td>28</td>
<td>21</td>
<td>23</td>
<td>16</td>
</tr>
<tr>
<td>Green-attacked (%)</td>
<td>50</td>
<td>10</td>
<td>19</td>
<td>5</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Red-/grey-attacked (%)</td>
<td>-</td>
<td>47</td>
<td>53</td>
<td>73</td>
<td>75</td>
<td>82</td>
</tr>
</tbody>
</table>

\(^1\) Hilker et al. (2008)
\(^2\) Means of values from this study and of Seip and Jones (2007).
\(^3\) Means of values from this study and of Dale Seip (personal communication).
\(^4\) Means of values from photo analysis (Spittlehouse et al. 2010) and of Dale Seip (personal communication).

3.2.2 Flux, climate and ecophysiological measurements

A 32-m-tall scaffold flux tower (~2.1 m long x ~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. Fluxes of CO\(_2\) \((F_c)\), sensible \((H)\) and latent heat \((\lambda E)\) were measured directly using the EC technique. 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 turbulent fluctuations of CO\(_2\) and H\(_2\)O concentration were measured using an open-path infrared gas analyzer (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. At both sites, EC sensors were mounted at the height of 26 m, which was ~8 m and ~6 m above the top of the canopy at MPB-06 and MPB-03, respectively. Following Webb et al. (1980), \(F_c\) and \(\lambda E\) were calculated as the product of the dry air density and the covariance of the CO\(_2\) and water vapour.
mixing ratios, respectively, and vertical velocity measured at 10 Hz. Further details of the measurements system and the data processing procedure are provided in Chapter 2.

Climate variables measured included above-canopy (30-m height) upwelling and downwelling shortwave and longwave radiation (model CNR1, Kipp and Zonen B.V., Delft, The Netherlands) (at 30-m height) and above-canopy upwelling and downwelling, and below-canopy (3-m height) 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 (model 05103 R.M. Young Inc., Traverse City, MI), air temperature and relative humidity (model HMP45C, Vaisala Oyj, Helsinki, Finland) at the 25-m height, 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 (model CS616, CSI) at the 0-10 cm and 30-50 cm depths at MPB-06 and (model EC-5, Decagon Devices Inc, Pullman, Washington) at the 10-cm, 20-cm and 50-cm depths at MPB-03. Meteorological measurements were made every second, and 30-min average values were calculated. Snow-pack depth was also measured at a clearcut weather station located ~1 km from MPB-06, 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). Live LAI at MPB-06 was determined by canopy photo analysis. Photographs of the forest canopy were taken each year in 8 directions.
from the tower. The images were adjusted to ensure the same area of the canopy was analysed each year and the fraction of green leaf area was determined by overlaying a 240-point grid on each image and counting the number of grid points on green forest canopy. Each year, live LAI was determined as the LAI measured in 2006 adjusted by the fraction of green canopy from the photographic analysis.

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 x 2 m wide transects. Green attack was identified by the presence of beetle entry holes in the bark, while red attack was identified by foliage colour and grey attack by the predominant loss of foliage. Inventories were also conducted in June and October 2007 by Hilker et al. (2008). In addition, independent tree health assessments were also made annually in August by biologists evaluating woodland caribou response to partial retention logging of MPB attacked stands (Seip and Jones 2007).

3.2.3 Flux quality control and data analysis

A 32-m-tall scaffold flux tower (~2.1 m long x ~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. Fluxes of CO₂ (Fc), sensible (H) and latent heat (λE) were measured directly using the EC technique. 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 turbulent fluctuations of CO₂ and H₂O concentration were measured using an open-path infrared gas analyzer (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. At both sites, EC sensors were mounted at the height of 26 m, which was ~8 m and ~6 m above the top of the canopy at MPB-06 and MPB-03, respectively. Following Webb et al. (1980), $F_c$ and $\lambda E$ were calculated as the product of the dry air density and the covariance of the $CO_2$ and water vapour mixing ratios, respectively, measured at 10 Hz. Further details of the measurements system and the data processing procedure are provided in Chapter 2.

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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). Live LAI at MPB-06 was determined by canopy photo analysis. Photographs of the forest canopy were taken each year in 8 directions from the tower. The images were adjusted to ensure the same area of the canopy was analysed each year and the fraction of green leaf area was determined by overlaying a 240-point grid on each image and counting the number of grid points on green forest canopy. Each year, live LAI was determined as the LAI measured in 2006 adjusted by the fraction of green canopy from the photographic analysis.

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3.2.4 Canopy characteristics

In order to investigate the processes controlling $E$, we calculated canopy conductance ($g_c$), the Priestley-Taylor $\alpha$ (Priestley-Taylor 1972) and decoupling coefficient ($\Omega$) (McNaughton and Jarvis 1983). The combination of the stomatal conductance and leaf area of the trees and
understory vegetation (including the moss layer), collectively referred to here as \( g_c \), was calculated by rearranging the Penman-Monteith equation (Monteith and Unsworth 2008) as

\[
\frac{1}{g_c} = \frac{\rho c_p D}{\gamma \lambda E} + \frac{1}{g_a} \left[ \frac{s}{\gamma} \left( \frac{R_a}{\lambda E} - 1 \right) - 1 \right]
\]

(1)

where \( s \) is the change in saturation vapour pressure with temperature (kPa K\(^{-1}\)); \( R_a \) is the available energy flux, \( R_n - G - S_t \), in which \( R_n \) is the net radiation, \( G \) (W m\(^{-2}\)) is soil (surface) heat flux (W m\(^{-2}\)), and \( S_t \) is the rate of change in energy storage (per unit ground area) in the air and biomass between the EC sensors and the ground surface (W m\(^{-2}\)) (calculation of \( S_t \) is described below); \( \rho \) is the air density (kg m\(^{-3}\)); \( c_p \) is the specific heat of air (J kg\(^{-1}\) K\(^{-1}\)); \( \gamma \) is the psychrometric constant (kPa K\(^{-1}\)); \( D \) the vapour pressure deficit (kPa) and \( g_a \) is the aerodynamic conductance (mm s\(^{-1}\)) for heat and mass transfer as described in Jassal et al. (2009):

\[
g_a = u_s \left( \frac{u}{u_s} + \frac{2}{k} \left( \frac{\psi_m - \psi_h}{k} \right) \right)^{-1}
\]

(2)

where \( k \) is the von Karman constant (0.40) and \( \psi_m \) and \( \psi_h \) are the integral diabatic correction factors for momentum and sensible heat transfer, respectively (Jassal et al. 2009). The coefficient 2 is recommended for all vegetated surfaces by Garratt (1978). Using 1 as the coefficient resulted in \( g_a \) values generally 2-3 times greater than when using 2; however, there was not a significant change in \( g_c \). Typically, the second term on the right hand side of Eq. 1 accounted for < 20% of the calculated value of \( g_c \).

The Priestley–Taylor \( \alpha \) was calculated as \( \alpha = \lambda E / \lambda E_{\text{eq}} \), where \( \lambda E_{\text{eq}} \) is the equilibrium latent heat flux, calculated as \( \lambda E_{\text{eq}} = s / (s + \gamma) R_a \). The decoupling coefficient \( \Omega \) is effective for describing how well \( D \) at the leaf surface is coupled to \( D \) of the atmosphere (Jarvis and McNaughton 1986):
\[ \Omega = \frac{s / \gamma + 1}{s / \gamma + 1 + g_a / g_c} \]  

(3)

in which \( \Omega \) approaches 0 when the canopy is well-coupled to the atmosphere as \( g_a/g_c \) increases \((E \text{ driven by } D)\), and approaches 1 when the canopy is decoupled from the atmosphere as \( g_a/g_c \) decreases, in which case \( E \) is controlled by \( R_a \).

In order to determine the physiological controls of \( E \), only values of \( g_c \), \( \alpha \) and \( \Omega \) were used for analysis when the foliage was dry. Thus data measured 3 hours before or after a rainfall event were discarded.

To estimate potential evapotranspiration \((E_{\text{pot}})\), the Priestley-Taylor (1972) equation was used:

\[ E_{\text{pot}} = \alpha_{\text{max}} E_{eq} \]  

(4)

where \( E_{eq} \) is the equilibrium evapotranspiration rate. \( \alpha_{\text{max}} \) was calculated as

\[ \alpha_{\text{max}} = 1/(a + bD) \]  

(5)

This parameterization of \( \alpha_{\text{max}} \) was used because maximum values of \( E/E_{eq} \) were found to increase as \( D \) decreased (see Results).

### 3.2.5 Energy balance closure

Eddy covariance data were assessed for energy balance closure (i.e., confirmation that \( R_a = \lambda E + H \)). Half-hourly measurements of \( R_m, G, H \) and \( \lambda E \) were used together with estimates of \( S_t \). The rate of change in energy storage \((S_t)\) is comprised of changes in sensible \((S_H)\) and latent heat storage \((S_{\lambda E})\) in the air column, and heat storage in the tree boles \((S_b)\), branches and foliage \((S_{br\_fol})\), and the rate of energy consumption by photosynthesis \((S_p)\). Heat storage in the tree boles was calculated following Lee and Black (1993) as, \( S_b = 2.5 A_T a \cos(\omega t - \varphi + \pi/4) \). The
coefficient 2.5, was selected because the bole volume of the stand is 0.70 that of the Douglas-fir stand studied by Lee and Black (1993) for which a coefficient of 3.57 was used, $A_{Ta}$ ($^\circ$C) and $\varphi$ are the amplitude and phase angle of the diurnal course of $T_a$, $\omega$ is the diurnal angular frequency (radians hour$^{-1}$) and $t$ is the time of day (PST). The rate of energy consumption by photosynthesis was calculated as $S_p = -F_c C$, where $F_c$ is ($\mu$mol m$^{-2}$ s$^{-1}$) positive upward and $C$ is the photosynthetic energy conversion factor (0.469 J $\mu$mol$^{-1}$). Heat storage in branches and foliage was calculated as $S_{br_fol} = LAI \sigma_L c_L (\Delta T_L / \Delta t)/(1 - W_w)$, where $\sigma_L$ is the specific leaf weight (mass of dry leaves per metre square of leaf), $W_w$ is the water content on a wet mass basis (~0.40), $c_L$ is the leaf specific heat (calculated using this wet mass fraction), and $\Delta T_L / \Delta t$ is the average rate of leaf temperature change ($^\circ$C s$^{-1}$) over a half-hour. Sensible heat and latent heat storage were calculated as $S_H = \rho c_p z_m \Delta T_L / \Delta t$, and $S_{\lambda E} = (\rho c_p / \gamma) z_m \Delta e_a / \Delta t$, where $\Delta e_a / \Delta t$ is the average rate of change in vapour pressure over a half-hour and $z_m$ is the measurement height. The calculations of $S_H$ and $S_{\lambda E}$ assume the changes in leaf temperature and vapour pressure are similar at all heights up to 26 m, where air temperature and humidity were measured which might cause a slight overestimation in these terms. However, these stands are quite open so the overestimation should be minimal.

The relationships between half-hourly values of $H + \lambda E$ and $R_a$ are shown in Fig. 3.1 and Table 3-2. The slopes for both sites were always $>0.89$ on an annual basis, and $>0.92$ for the growing season data. The coefficient of determination, $r^2$ was higher at MPB-03, with the lowest $r^2$ occurring in 2009 at MPB-06. When $R_a$ was $> 500$ W m$^{-2}$, $\lambda E + H$ tended to underestimate $R_a$. This was more so the case at MPB-06, especially in 2009 where $\lambda E + H$ underestimated $R_a$ by up to 40% at these high values of $R_a$. 

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Figure 3.1. Energy balance closure at the two sites as shown by the relationships between half-hourly values of latent and sensible heat \((\lambda E + H)\) and available radiation \((R_a)\) for the 2007, 2008 and 2009 growing seasons. Data points are bin averages of 10 values starting from the smallest value. Individual linear orthogonal regression lines are shown for the three years. Statistics for the linear regression are shown in Table 3-2.
Table 3-2. Linear orthogonal regression parameters between half-hourly latent and sensible heat ($\lambda E + H$) and available energy ($R_a$).

<table>
<thead>
<tr>
<th></th>
<th>MPB-06 2007</th>
<th>2008</th>
<th>2009</th>
<th>MPB-03 2007</th>
<th>2008</th>
<th>2009</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>0.90</td>
<td>0.92</td>
<td>0.92</td>
<td>1.00</td>
<td>0.96</td>
<td>0.95</td>
</tr>
<tr>
<td>Intercept</td>
<td>-3.89</td>
<td>-2.52</td>
<td>2.86</td>
<td>-14.53</td>
<td>-7.01</td>
<td>-9.88</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.75</td>
<td>0.79</td>
<td>0.73</td>
<td>0.81</td>
<td>0.83</td>
<td>0.83</td>
</tr>
<tr>
<td>Growing Season (1 May-30 September)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>0.97</td>
<td>0.95</td>
<td>0.97</td>
<td>1.03</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Intercept</td>
<td>-3.33</td>
<td>-1.33</td>
<td>3.75</td>
<td>-11.27</td>
<td>-4.29</td>
<td>-4.68</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.74</td>
<td>0.79</td>
<td>0.75</td>
<td>0.84</td>
<td>0.83</td>
<td>0.84</td>
</tr>
</tbody>
</table>

Wilson et al. (2002) evaluated energy balance closure at 22 eddy-covariance sites, ranging from Mediterranean to arctic ecosystems, and found an average lack of closure of about 20%. A lack of closure can stem from errors associated with either or both the EC and the available energy flux. Wilson et al. (2002) concluded that although it was not possible to evaluate all possible sources of error, there seemed to be a connection between the lack of closure and fluxes of CO$_2$. At boreal aspen (Populus tremuloides), black spruce (Picea mariana) and jack pine (Pinus banksiana) stands in Saskatchewan, Canada, Barr et al. (2006) reported $H + \lambda E$ to underestimate $R_a$ by 11, 15 and 14%, respectively, resulting in closure values slightly greater than those reported here. The very flat terrain on which these stands are located is likely a major contributing factor to the relatively good closure determined for these sites as such terrain minimizes the likelihood of horizontal advective loss of scalars. As well, the homogeneity of these stands increases the likelihood that the net radiometer and soil heat flux plates are
measuring a flux representative of the larger footprint measured by the EC system (Wilson et al. 2002).

3.3 Results

3.3.1 Climate

5-day averages of climate variables from 2007 – 2009 are shown in Fig. 3.2, and average growing season (1 May – 30 September) climate values are presented in Table 3-3. 2009 was the warmest, driest and sunniest of the three years. The low growing season rainfall in 2009 resulted in the lowest volumetric water content of the soil fine fraction (soil particles < 2 mm) ($\theta$) (0 – 10 cm depth at MPB-06 and 10 cm depth at MPB-03) values observed. At MPB-06, total annual snowfall liquid water equivalent was 330, 305 and 384 mm and total annual precipitation was 730, 589 and 681 mm in 2007, 2008 and 2009, respectively. At MPB-06, snowmelt was completed (as indicated by abrupt increases in soil temperature and heat flux) on 15 May in 2007 and 2008 and on 7 May in 2009; at MPB-03 snowmelt was completed on 20 April in 2007, 15 May in 2008 and 7 May in 2009. During 2009 there was a hot and dry period which began on 17 July and lasted until 10 August. During this time MPB-06 received only 6 mm of rainfall and MPB-03 received none. Conditions were especially warm from 21 July to 2 August with maximum daily $T_a$ always being > 25 °C and $D$ consistently reaching values > 2.5 kPa, peaking at 3.65 kPa on 27 July. At MPB-06, $\theta$ dropped steadily from mid-July 2009, reached a low of 0.04 m$^3$ m$^{-3}$ in early August and did not recover until early September. At MPB-03, $\theta$ reached a low of 0.12 m$^3$ m$^{-3}$ on 9 August and fluctuated with rainfall thereafter until reaching more seasonably normal values in early September. Further details of the mean annual climate are provided in Chapter 2.
Figure 3.2. 5-day average values of photosynthetically active radiation (\(Q\)), precipitation (\(P\)), vapour pressure deficit (\(D\)), air temperature (\(T_a\)) and soil fine fraction volumetric water content (\(\theta\)). Values of \(D\) are calculated from daytime values (\(Q > 0\)) and values of \(P\) are only for the growing season.

Table 3-3. Average values of climate variables for the growing season (1 May – 30 September).

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (26 m height) (° C)</td>
<td>11.8</td>
<td>12.4</td>
<td>12.9</td>
<td>12.7</td>
<td>12.7</td>
<td>14.0</td>
</tr>
<tr>
<td>Soil temperature (5-cm depth) (° C)</td>
<td>10.4</td>
<td>11.1</td>
<td>11.9</td>
<td>10.3</td>
<td>10.3</td>
<td>10.8</td>
</tr>
<tr>
<td>Rainfall (mm)</td>
<td>246</td>
<td>250</td>
<td>177</td>
<td>576</td>
<td>620</td>
<td>477</td>
</tr>
<tr>
<td>(\theta) (m(^3) m(^{-3})) (0-30-cm depth)</td>
<td>0.11</td>
<td>0.11</td>
<td>0.08</td>
<td>0.17</td>
<td>0.16</td>
<td>0.15</td>
</tr>
<tr>
<td>(Q) ((\mu)mol m(^{-2}) s(^{-1}))</td>
<td>396</td>
<td>396</td>
<td>418</td>
<td>413</td>
<td>410</td>
<td>442</td>
</tr>
<tr>
<td>(D)(^1) (kPa)</td>
<td>0.80</td>
<td>0.83</td>
<td>0.94</td>
<td>0.86</td>
<td>0.84</td>
<td>1.04</td>
</tr>
<tr>
<td>GSL(^2) (days)</td>
<td>136</td>
<td>141</td>
<td>134</td>
<td>147</td>
<td>160</td>
<td>155</td>
</tr>
<tr>
<td>(R_n)(^3) (GJ m(^{-2}))</td>
<td>1.49</td>
<td>1.57</td>
<td>1.57</td>
<td>1.70</td>
<td>1.63</td>
<td>1.72</td>
</tr>
</tbody>
</table>

\(^1\) Daytime average values.
\(^2\) Growing season length (half-hourly values of air temperature and soil temperature were > 0 and 1°C, respectively).
\(^3\) Growing season total.

### 3.3.2 Diurnal energy balance

The ensemble-averaged diurnal energy balance for July, the month \(R_n\) tends to peak, is shown in Fig. 3.3 for 2008. For this month, the slope of the relationship between \(H + \lambda E\) and \(R_n\) was 1.01 and 0.97 with intercepts of 2.0 and -12.5 W m\(^{-2}\) for MPB-06 and MPB-03, respectively. During July, the Bowen ratio (\(\beta\)) was approximately 2.0 at MPB-06 and 1.7 at MPB-03. Sensible heat was virtually the same at both sites, reaching a mid-day high of 270 to 280 W m\(^{-2}\) while maximum daytime \(\lambda E\) was 130 and 145 W m\(^{-2}\) at MPB-06 and MPB-03, respectively. During the nighttime, mean \(R_n\) was -53 and -58 W m\(^{-2}\), \(H\) was -12 and -9 W m\(^{-2}\) and \(\lambda E\) was 7 and 4 W m\(^{-2}\) at MPB-06 and MPB-03, respectively. The sum of \(G + S_t\) reached a high of 75 and 35 W m\(^{-2}\) and a low of -40 and -25 W m\(^{-2}\), at MPB-06 and MPB-03, respectively.
Figure 3.3. Ensemble averaged net radiation ($R_n$), sensible ($H$) and latent ($\lambda E$) heat fluxes, and ground heat flux ($G$) + total energy storage change ($S_t$) for July 2008 for MPB-06 and MPB-03. Bars are standard deviations.

3.3.3 Seasonal energy balance

At MPB-06, daily (24-h) averages of $R_n$ varied from a maximum of ~150 W m$^{-2}$ during the growing season to a low of ~20 W m$^{-2}$ during the winter (Fig. 3.4). Daily averages of $H$ peaked between May and June at 84, 92 and 94 W m$^{-2}$ in 2007, 2008 and 2009, and $\lambda E$ in July at ~45 W m$^{-2}$ in all three years. At MPB-03, which is more southerly, values were greater, with $R_n$ peaking between June and July at 160-190 W m$^{-2}$. Maximum daily averages of $H$ increased during the three years from 93 W m$^{-2}$ in 2007, to 100 W m$^{-2}$ in 2009, and $\lambda E$ reached a maximum of ~55 W m$^{-2}$ in July of all three years. During the winter, $H$ and $\lambda E$ averaged ~5 and ~7 W m$^{-2}$.
respectively, at both sites. Monthly values of $H$ followed $R_n$ very closely, increasing rapidly between March and May as the days became longer, during which time $\lambda E$ remained low. Although these stands are technically classified as sub-boreal forests, the relatively low $\lambda E$ values during the spring are typical of boreal coniferous systems as $T_a$ is still cool, $D$ is low and cold soils limit water uptake by the trees (Arain et al. 2003). Latent heat, was slightly positive during the winter due to sublimation and at times $\lambda E$ was greater (~10 W m$^{-2}$) when $T_a$ warmed up for short periods. At MPB-06, over the three years monthly $\beta$ ranged from a winter low of ~-1.5 to a high of 5 – 7 in April. As $\lambda E$ increased, $\beta$ gradually declined throughout the growing season from ~2.5 in June to just over 1.0 in September. At MPB-03, average $\beta$ in winter was ~0.6 and it declined from 4.4 – 5.0 in April to 1.7 – 2.1 in June and ~1.5 in September.

Throughout the year 24-h $G + S_i$ was small, as is common for coniferous forests (Baldocchi et al. 1997; Arain et al. 2003). Maximum and minimum monthly $G + S_i$ values occurred in May and September/October and were ~10 and ~-10 W m$^{-2}$ at MPB-06 and ~6 and ~-4 W m$^{-2}$ at MPB-03, respectively. Minimum $G$ (i.e., greatest loss of soil heat) occurred in the fall because the soils were still warm at depth and there was not yet a snow layer to insulate the soil surface. During the winter, when the snow was deep, there was a small heat loss from the ground of ~-1 and ~-3 W m$^{-2}$ at MPB-06 and MPB-03, respectively.
Figure 3.4. Monthly average net radiation ($R_n$), sensible ($H$) and latent ($\lambda E$) heat flux, and ground heat flux ($G$) + total energy storage change ($S_t$) (2007 to 2009) at MPB-06 and MPB-03.

3.3.4 Evapotranspiration

5-day average values and annual totals of $E$ are shown in Fig. 3.5. There was little annual variation at either site, with $E$ varying by less than 10 mm y$^{-1}$ at MPB-06 and by just over 20 mm y$^{-1}$ at MPB-03 over the three years. Growing season averages of $E$ at MPB-06 and MPB-03 were, respectively, 1.12 and 1.48 mm day$^{-1}$ in 2007, 1.14 and 1.54 mm day$^{-1}$ in 2008, and 1.21 and 1.46 mm day$^{-1}$ in 2009. Maximum daily values of $E$, which occurred in late July, were ~2.5 and ~3.0 mm day$^{-1}$ at MPB-06 and MPB-03, respectively. The highest values tended to occur in the hours and days following rainfall. During the winter, $E$ was approximately 0.2 mm day$^{-1}$ at both sites.
and increased rapidly following snow melt in May. These wintertime values of $E$ are similar to the values of $0.1 – 0.25 \text{ mm day}^{-1}$ from a black spruce stand reported by Arain et al. (2003).

Figure 3.5. 5-day averages of evapotranspiration ($E$) from 2007 to 2009. Values are annual totals of $E$ (mm).

3.3.5 **Canopy conductance, Priestley-Taylor $\alpha$ and $\Omega$**

The annual means of daytime $g_c$ under dry foliage conditions ($T_a > 0 \ ^\circ\text{C}$) were 3.25, 3.35 and 2.89 mm s$^{-1}$ at MPB-06 and 3.92, 4.24 and 3.38 mm s$^{-1}$ at MPB-03 in 2007, 2008 and 2009, respectively. The lowest values occurred in 2009, the driest of the three years, and the highest occurred in 2008, the wettest year. Monthly mean values of daytime $g_c$ varied from 1 to 6 mm s$^{-1}$ and 2 to 6 mm s$^{-1}$ (Fig. 3.6) with daytime means being as high as 6.5 and 7.4 mm s$^{-1}$ at MPB-06 and 5.5 and 6.2 mm s$^{-1}$ at MPB-03.
and MPB-03, respectively. Values of $g_c$ were relatively low in April and May, when snow was still on the ground for much of the time, and rose steadily until reaching maximum values in September and October when $D$ and $R_n$ were in rapid decline due to shorter day lengths and lower solar elevation. At MPB-03, there was more variation in growing season $g_c$ than at MPB-06, especially in 2008 when June $g_c$ was quite high, and in 2009 when there was a sharp reduction in August. At MPB-06, monthly $g_c$ values were highest during the latter half of the growing season in 2007. Monthly $g_a$ values were between 100 and 150 mm s$^{-1}$ at MPB-06 and between 110 and 160 mm s$^{-1}$ at MPB-03. Values were highest in April and May and reached a minimum in September.

Over the three growing seasons, $\alpha$ averaged 0.53 and 0.51 at MPB-06 and MPB-03, respectively, showing these sites to be water stressed, since $\alpha$ is much less than unity (when $\lambda E = \lambda E_{eq}$). Like $g_c$, $\alpha$ increased steadily throughout the growing season, until reaching a maximum in September and October (Fig. 3.6). At MPB-03, there was a significant drop in $\alpha$ in August 2009 during the dry period. There was very little change in monthly values of $\Omega$ over the three years, with the exception of August 2008 when there was an abrupt drop. Monthly $\Omega$ increased from April to September and ranged from 0.04 to 0.2 at both sites, although values were slightly higher at MPB-03. These low $\Omega$ indicate that both these stands are strongly coupled to the atmosphere.
Figure 3.6. Monthly growing season averages of daytime dry foliage canopy conductance ($g_c$), aerodynamic conductance ($g_a$), Priestly-Taylor $\alpha$ and decoupling coefficient $\Omega$.

Diurnal ensemble average $g_c$ for July over the three years is shown in Fig. 3.7. Following sunrise, $g_c$ rose quickly to reach the highest levels of the day by mid-morning, during which time $D$ was still low, allowing the stomata to open and maximize photosynthetic uptake while minimizing water loss through transpiration. In the morning the vegetation also tends to be less water stressed due to overnight xylem recharge (Lambers et al. 1998). Following the morning maxima, $g_c$ gradually declined during the afternoon as $D$ increased. In the late-afternoon downwelling PAR ($Q$) decreased quickly, resulting in low $g_c$. Although the diurnal pattern was
similar in all years, July $g_c$ was lowest in 2009, probably due to the drier conditions at both sites that year.

Figure 3.7. Diurnal ensemble average canopy conductance ($g_c$) for July.

3.3.6 Climatic controls on $g_c$

Since $g_c$ is known to strongly respond to $D$, we attempted to model half hourly $g_c$ for the period of 15 May to 30 September using the following equation.

$$g_{c\text{mod}} = \frac{1}{c + dD}$$

(6)

where $c$ and $d$ are empirically determined parameters. The first half of May was excluded from the analysis because snow was still present on the ground, causing $E$ to be significantly lower than after the snow had melted. When $g_c$ was calculated from (Eq. 6), modelled $g_c$ ($g_{c\text{mod}}$)
consistently underestimated $g_c$, especially during the middle hours of the day when $D$ was high. When plotted against $D$ at low, medium and high $Q$ levels the response of $g_c$ to $D$ was found to vary, with a higher $g_c$ for a given $D$ at higher $Q$ levels (Fig. 3.8). Thus a $Q$ function was added so that:

$$g_{cmod} = [1/(c + dD)](e + fQ)$$

(7)

This resulted in $g_{cmod}$ accounting for approximately 47 and 49% of the variation in $g_c$ at MPB-06 and MPB-03, respectively (Fig. 3.9; Table 3-4), with $g_{cmod}$ underestimating $g_c$ at higher values.
Figure 3.8. The response of dry foliage canopy conductance ($g_c$), to vapour pressure deficit ($D$) at different levels of photosynthetically active radiation ($Q$) at MPB-06 in July 2008. Data points are the averages of bins of 10 values of $g_c$ starting at the smallest values of $D$. Curves are fits to Eq. (6) with the following values of $c$ and $d$: 0.032 and 0.483 for $Q < 500 \, \mu\text{mol m}^{-2} \text{s}^{-1}$, 0.0003 and 0.358 for $500 < Q < 1000 \, \mu\text{mol m}^{-2} \text{s}^{-1}$ and -0.006 and 0.261 for $Q > 1000 \, \mu\text{mol m}^{-2} \text{s}^{-1}$. 
Table 3-4. Parameters in Eq. 7 and cumulative totals of evapotranspiration ($E$) and $E$ modelled ($E_{mod}$) for daytime only for 15 May and 30 September.

<table>
<thead>
<tr>
<th></th>
<th>MPB-06</th>
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<th>MPB-03</th>
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<tr>
<td></td>
<td>2007</td>
<td>2008</td>
<td>2009</td>
<td>2007</td>
</tr>
<tr>
<td>$c$</td>
<td>0.0090</td>
<td>0.0013</td>
<td>0.0127</td>
<td>0.0162</td>
</tr>
<tr>
<td>$d$</td>
<td>0.1212</td>
<td>0.1023</td>
<td>0.1084</td>
<td>0.096</td>
</tr>
<tr>
<td>$e$</td>
<td>0.2373</td>
<td>0.1112</td>
<td>0.1873</td>
<td>0.1615</td>
</tr>
<tr>
<td>$f$</td>
<td>$1.981 \times 10^{-4}$</td>
<td>$2.356 \times 10^{-4}$</td>
<td>$2.264 \times 10^{-4}$</td>
<td>$3.488 \times 10^{-4}$</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.44</td>
<td>0.51</td>
<td>0.45</td>
<td>0.46</td>
</tr>
<tr>
<td>$E$ (mm)$^1$</td>
<td>164</td>
<td>169</td>
<td>180</td>
<td>213</td>
</tr>
<tr>
<td>$E_{mod}$ (mm)$^1$</td>
<td>165</td>
<td>157</td>
<td>167</td>
<td>201</td>
</tr>
</tbody>
</table>

$^1$ Total of daytime values only.
Figure 3.9. Relationship between canopy conductance \( (g_c) \) calculated from measurements (Eq. 1) and that modelled \( (g_{c\text{mod}}) \) (Eq. 7) at MPB-03 between 1 June and 30 September 2008. The solid line represents the regression: \( g_{c\text{mod}} = 1.50g_c -2.47 \). \( Q. r^2 = 0.44, \) RMSE = 2.46. The dotted line is the 1:1 line.

Daytime means of dry foliage \( g_c \) also responded to daily mean \( \theta \). At both sites the relationship was strongest in 2007 when \( \theta \) was slightly higher than the other two years (Fig. 3.10). We added a \( \theta \) function to Eq.7 to see if the coefficient of variation between \( g_{c\text{mod}} \) and \( g_c \) would improve, but since the improvement was < 2% the function was not included in the model.
We then used the Penman-Monteith equation with $g_{c_{\text{mod}}}$ (Eq. 7) and $g_a$ (Eq. 2) to obtain modelled $E$ ($E_{\text{mod}}$). Cumulative totals of half-hourly 15 May – 30 September $E$ and $E_{\text{mod}}$ agreed with each other to within 10% (Table 3-4).

To examine the diurnal variation in $g_c$ and $E$, as well as to assess the accuracy of $g_{c_{\text{mod}}}$, half-hourly values of $R_n$, $D$, $g_c$, $g_{c_{\text{mod}}}$, $E$ and $E_{\text{mod}}$ are shown in Fig. 3.10, for the period between 21 and 25 July 2008. During this period, $R_n$ peaked at ~650 W m$^{-2}$ around midday and fell to ~100 W m$^{-2}$ at night. At both sites, $D$ increased steadily over the five days from a daytime maximum of 1.2 kPa on 21 July to 2.9 kPa on 25 July. The diurnal variation in $D$ lagged that of $R_n$ by 2-3 h, with values being relatively low in the morning and highest in the late afternoon when $R_n$ had already begun to decline. Canopy conductance was much higher at the beginning of the period when $D$ was low, especially during the morning hours. There was a pronounced decrease in $g_c$ over the five days as $D$ steadily rose, but the diurnal trend remained the same. Modelled canopy conductance followed $g_c$ quite closely during most of the measurement period, with the exception of 21 and 22 July, 2008, at MPB-06 when $g_c$ was quite erratic and $g_{c_{\text{mod}}}$ did not reach the maximum levels. During the same 5 days at MPB-03, $g_{c_{\text{mod}}}$ was often higher than $g_c$, with the exception of 21 July when there was good agreement. Evapotranspiration increased rapidly in the morning, reached maximum values around mid-day and decreased in the afternoon when $D$ was high. During the early morning when $g_c$ was high, $E$ was still low due to low $Q$ and $D$ but during the afternoon $E$ closely followed $g_c$. Not surprisingly, like $g_{c_{\text{mod}}}$, $E_{\text{mod}}$ followed $E$ more closely at MPB-06, than at MPB-03 where $E_{\text{mod}}$ overestimated $E$. 
Figure 3.10. Net radiation ($R_n$), water vapour deficit ($D$), measured and modelled canopy conductance ($g_c$ and $g_{cmod}$) and measured and modelled evapotranspiration ($E$ and $E_{mod}$) at a) MPB-06 and b) MPB-03. Grey lines are modelled values.

### 3.3.7 Water balance and deficit

The daily change in root zone soil water storage ($\Delta S$) and daily $P - E$ are compared in Fig. 3.11 and Table 3-5. The analysis period was from 1 June, following snow melt and drainage, to 30 September. In 2007 and 2008 at MPB-06, $P$ exceeded $E$ by < 100 mm, generating a small water surplus, whereas in 2009 $E$ was greater than $P$ during much of the growing season. At MPB-03 the water surplus was much larger, as $P$ exceeded $E$ by over 200 mm in every year. Cumulative $\Delta S$ was calculated as the sum of the daily changes in soil water storage ($S$) (i.e., $\Sigma \Delta S$) to the soil depth of 60 cm since 1 June. At both sites during much of the growing season there was a general decline in $S$ with recharge occurring in August and September. The decline in $S$ was greater at MPB-06 than MPB-03, due to the lower $P$. At MPB-03, there was a small increase in $S$ throughout the 2007 growing season due to a more even rainfall distribution in that year. At both sites, the greatest decline in $S$ occurred in 2009, with a maximum decrease of 46 mm reached at MPB-06; however, both sites recovered by October. Cumulative root zone drainage ($D_r$) from the 60-cm soil depth was calculated as $\Sigma (P - E - \Delta S)$. Drainage totals were much greater at MPB-03 (200-300 mm) than at MPB-06, where growing season $D_r$ was never greater than ~60 mm.
Figure 3.11. Water balance. Precipitation ($P$) - evapotranspiration ($E$) (upper panels) and daily change in root zone soil water storage ($\Delta S$) (lower panels) from 1 June to 30 September.

Table 3-5. Cumulative daily totals of precipitation ($P$), evapotranspiration ($E$), daily change in root zone soil water storage ($\Delta S$) and root zone drainage ($D_r$) from 1 June to 30 September. $D_r$ was calculated as $D_r = P - E - \Delta S$.

<table>
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<tr>
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<th>MPB-06</th>
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<tr>
<td></td>
<td>2007</td>
<td>2008</td>
<td>2009</td>
<td>2007</td>
<td>2008</td>
<td>2009</td>
</tr>
<tr>
<td>$P$</td>
<td>234</td>
<td>192</td>
<td>149</td>
<td>529</td>
<td>514</td>
<td>413</td>
</tr>
<tr>
<td>$E$</td>
<td>154</td>
<td>159</td>
<td>164</td>
<td>198</td>
<td>209</td>
<td>189</td>
</tr>
<tr>
<td>$\Delta S$</td>
<td>18</td>
<td>21</td>
<td>-14</td>
<td>18</td>
<td>-9</td>
<td>1</td>
</tr>
<tr>
<td>$D_r$</td>
<td>62</td>
<td>12</td>
<td>-1</td>
<td>313</td>
<td>314</td>
<td>223</td>
</tr>
</tbody>
</table>
When modelling daily values of $\alpha_{\text{max}}$ (Eq. 5) to calculate $E_{\text{pot}}$, only growing season data following snowmelt, from 15 May to 30 September, when $\theta$ was high ($\theta_{\text{threshold}} > 0.11$ and $> 0.16 \text{ m}^3 \text{ m}^{-3}$ at MPB-06 and MPB-03, respectively) were included for analysis for individual years. At both sites, the field capacity and wilting point $\theta$ values for the soil fine fraction (soil particles $<2$ mm) were estimated to be $0.17$ and $0.05 \text{ m}^3 \text{ m}^{-3}$. The use of a different threshold at the sites is likely a result of the large difference in precipitation between them. At MPB-06 in 2009, the threshold value was lowered to $0.10 \text{ m}^3 \text{ m}^{-3}$ to include more data. Because $\theta$ was usually less than these thresholds, with the exception of 2007 when steady rainfall throughout the growing season kept the soils relatively moist, data from all three years were also combined to establish the relationships in Eq. 5. Although year to year changes in the physiology of the stand were likely occurring as the recovery progressed, the small variance of $E$ over the three years suggested there would be little yearly variation in the response of $\alpha_{\text{max}}$ to $D$. The annual values of the parameters were similar to those obtained using the combined data (Table 3-6). The parameters derived from the model were then used to calculate daily $\alpha_{\text{max}}$ values for each year.

Table 3-6. Evapotranspiration ($E$), equilibrium $E$ ($E_{eq}$) and potential $E$ ($E_{pot}$) for 15 May – 30 September at MPB-06 and MPB-03. Also shown are the parameters and coefficients of variation for Eq. 5 and water deficit (WD) totals.
Over the course of the growing season, $\alpha_{\text{max}}$ calculated for each of the years (Eq. 5) ranged from a high of 1.0 and 1.1 to a low of 0.31 and 0.25 at MPB-06 and MPB-03, respectively (Fig. 3.12). Although $D$ explained only a small proportion of the variation in $\alpha_{\text{max}}$ (Table 3-6), generally high $\alpha_{\text{max}}$ occurred when $D$ was low (Fig. 3.13). The ratios of $E_{\text{pot}}$ to $E_{\text{eq}}$ for 15 May – 30 September, for both sites were very similar (0.60-0.66 for MPB-06, and 0.63-0.65 for MPB-03). At MPB-06, the interannual variability in $E_{\text{pot}}$ was relatively small, with it being greatest in 2007 and smallest in 2008 (Table. 3-6). At MPB-03, the trend was different with $E_{\text{pot}}$ being highest in 2009 and lowest in 2007. The daily water deficit (WD = daily $E_{\text{pot}}$ – daily $E$) (Fig. 3.14) tended to be high at both sites in late May to early June as a result of $E_{\text{pot}}$ being elevated due to high $R_n$ and low $D$, and low $E$ due to cool air temperatures. Maximum daily WD was 1.5 mm at MPB-06 and 2.0 at MPB-03. At MPB-06, the cumulative WD was largest in 2007, while at MPB-03 it was largest in 2009 (Fig. 3.15; Table. 3-6). Using the value of $\alpha_{\text{max}}$ calculated by combining data from all three years resulted in similar values of WD for all years at both sites except for 2009 at MPB-03 when it was 40% lower.
Figure 3.12. Calculated daily values of maximum Priestley-Taylor $\alpha$ ($\alpha_{\text{max}}$) using Eq (5) from 15 May to 30 September at MPB-06 and MPB-03.
Figure 3.13. Relationship (Eq. 5) between daily values of daytime vapour pressure deficit ($D$) and daily Priestley-Taylor $\alpha$ at daytime soil water content $> 0.10 \text{ m}^3 \text{ m}^{-3}$ from 15 May to 30 September 2008 at MPB-03.
Figure 3.14. Daily water deficit (WD), calculated as daily potential evapotranspiration ($E_{pot}$) – daily evapotranspiration ($E$), from 15 May to 30 September at MPB-06 and MPB-03.
3.4 Discussion

3.4.1 Energy balance

The energy balance values presented here are typical of coniferous forests growing on well-drained sandy soils (Baldocchi et al. 2000). Although energy balance closure values are relatively high, complete closure was not achieved. Kidston et al. (2010) found, in a 14-m tall boreal jack pine stand, that a lack of complete closure can result from a loss of low-frequency covariance due to an insufficient averaging time. However, they pointed out that the use of
longer averaging times to capture the low-frequency covariance would likely result in a loss of the high-frequency covariance. $E$ values in this paper have not been “corrected” for lack of closure. Correction would have resulted in $< 15\%$ increase in $E$.

Surprisingly, the progression of the beetle attack did not appear to have an influence on the annual energy balance at either site, as $R_n$, $H$ and $\lambda E$ were similar in magnitude during all three years. In addition, fluxes were not significantly different at MPB-06 in August and September 2006 just after the stand was attacked. This shows that as these sites recover the amount of water being used in the flux of latent heat is rather constant. There were changes in the radiation distribution within the canopy. As the attacked trees died, the needles began to fall which resulted in an increase in the transmissivity of short and long-wave radiation through the canopy. At MPB-06, between 2007 (prior to any loss of needles) and 2009, direct and diffuse solar radiation transmissivity increased from 29 to 44$\%$ and from 41 to 51$\%$, respectively, while at MPB-03 solar radiation transmissivity increased from 48$\%$ in 2007 to 60$\%$ in 2009. Regarding albedo, there was a 16$\%$ decrease in the August value between 2007 and 2008 at MPB-06 (from 0.092 to 0.079), and while at MPB-03 the August value remained unchanged (0.074) over the three years (O’Halloran et al. 2010). Growing season albedo at MPB-06 was 0.10 in 2007 and 0.08 in 2008 and 2009, while at MPB-03 growing season albedo averaged 0.08 each year (2007 - 2009). During the winter, MPB-03 had higher albedo values than MPB-06 due to more needle-fall having occurred in the former, exposing more of the snow-covered ground surface (O’Halloran et al. 2010). Conversely, increased needle fall during the winter can lead to increased litter on the snow surface which can lower albedo (Winkler et al. 2010).

The energy balance at these sites could change dramatically when the dead trees fall in significant numbers. The winter albedo of both sites will likely increase, resulting in a reduction
in net radiation compared to the stands before attack (O’Halloran et al. 2010). Tree-fall is expected to become frequent about 5 years after attack (Mitchell and Preisler, 1998) and had already started at MPB-03 in 2008.

3.4.2 Evapotranspiration

The values of $E$ reported here are similar to those reported for other northern coniferous forests where the interannual variability in $E$ has also been quite low. Between 1998 and 2006 in a 90-year-old jack pine stand (OJP) in Saskatchewan, Canada, when annual $P$ was 472 mm, annual $E$ was also conservative, averaging 300 mm with a range of 62 mm (Zha et al. 2010). In a scots pine ($Pinus sylvestris$) forest in southern Finland where annual $P$ averaged 692 mm, EC measured annual $E$ averaged 295 mm, ranging from a low of 235 mm to a high of 356 mm over a 9 year period (Ilvesniemi et al. 2010). Baldocchi et al. (1997) reported daily $E$ from OJP to typically range between 0.5 and 2.5 mm day$^{-1}$ during the growing season and Kelliher et al. (1998) measured $E$ from a Siberian scots pine forest over 18 days during the growing season and found a maximum of 2.3 mm day$^{-1}$. Comparing jack pine with black spruce commonly found in the same area as pine, Brümmer et al. (2010) reported a range in $E$ from 221 and 288 mm in a dry year (2003) (when $P = 257$ and 315 mm year$^{-1}$) to 301 and 316 mm in wet years (2004 and 2006) ($P = 611$ and 618 mm year$^{-1}$) at OJP and a black spruce stand (SOBS) in Saskatchewan. Average annual $E$ was 280 and 308 mm year$^{-1}$ at black spruce stands in Manitoba and Quebec, where average annual $P$ was 493 and 917 mm year$^{-1}$ (Brümmer et al. 2010). Though these values tend to be slightly higher than at MPB-06, they are very similar to MPB-03.

Evapotranspiration has long been reported to be a conservative process with relatively small interannual variation (Roberts 1983), even as stands develop in leaf area and species.
composition (Phillips and Oren 2001; Oishi et al. 2010). As noted by Roberts (1983) and Kelliher et al. (1993), the understory, as well as evaporation from the soil, can play an important role in equalizing \( E \) from stands of varying leaf area. In these recovering stands the accelerated growth of the secondary structure and understory, including the moss and lichen layer, appears to compensate for the reduction in transpiration from tree death. Reid et al. (2006) found that lodgepole pine in stands thinned five years prior had higher sap flow rates and mean transpiration rates per unit leaf area than trees in un-thinned stands showing a sustained elevated productivity of trees in thinned stands. The lack of a reduction in \( E \) in response to the dry conditions in 2009 is a phenomenon that has also been observed in other studies. Oishi et al. (2010) found drought conditions in a oak-hickory (\textit{Quercus} – \textit{Carya}) forest in North Carolina, USA, did not reduce \( E \) significantly from non-drought years. The authors found that rainy days during drought free periods were characterized by low \( D \), which led to low \( E \), but during the drought periods \( D \) was high, leading to moderate levels of \( E \) despite the dry conditions. Similarly, in these MPB attacked stands, higher values of \( D \) during the 2009 growing season likely compensated for reductions in \( E \) due to water limitations and the observed stomatal closure, leading to annual totals of \( E \) similar to the previous non-drought years.

3.4.3 Canopy characteristics and controls

Decoupling coefficient, \( \Omega \), values at these sites were low, indicating a high degree of coupling to the \( D \) of the atmosphere. Low values of \( \Omega \) are typical of the relatively aerodynamically rough surfaces of coniferous forests (Jassal et al. 2010). For instance, Brümmer et al. (2010) reported \( \Omega \) to range between 0.11 and 0.19 at OJP, SOBS and at black spruce forests in Quebec and Manitoba. Values of \( g_a \) were also comparable to other conifer stands of these heights. The old
jack pine site (OJP) in Saskatchewan, with a canopy height of 13.5 m had typical growing season $g_a$ values of ~75 mm s$^{-1}$ (Baldocchi et al. 1997) and Kelliher et al. (1993) note that forests characteristically have a $g_a$ of about 200 mm s$^{-1}$. $E$ from aerodynamically rougher surfaces tends to be controlled by $D$ while $E$ from smoother vegetative surfaces is more controlled by $R_a$ (Jarvis and McNaughton 1986). The values of $\Omega$ reported here shows that $D$ plays a dominant role in controlling $E$ (Jarvis and McNaughton 1986).

Priestley-Taylor $\alpha$ values for these sites are similar to those reported in other studies in coniferous stands and much lower than those from well-watered vegetation with a closed canopy which tend to have an $\alpha$ near 1.26 (Jarvis and McNaughton 1986). OJP was found to have values of $\alpha$ of ~ 0.5 (Baldocchi et al. 1997) and SOBS values between 0.5 and 0.7 during the peak of the growing season (Arain et al. 2003). An aspen forest (SOA) (near OJP and SOBS) had a daytime mean $\alpha$ of 0.91 during the full leaf period (Blanken et al. 1998) and a Douglas-fir stand harvested in 1949 had a mean monthly $\alpha$ of 0.62 (Jassal et al. 2010).

The values of $g_c$ reported in these sub-boreal forest stands are similar to those from studies in the boreal forest. Baldocchi et al. (1997) reported daytime $g_c$ values for OJP to be typically < 3.8 mm s$^{-1}$ and concluded that those values were low as result of a stomatal closure due to low soil moisture, high $D$ and a low photosynthetic capacity of jack pine needles. Low $\theta$ can decrease $g_c$ via the release of the phytohormone, abscisic acid (ABA), from the roots which is then sensed by the stomata causing them to close (Lambers et al. 1998; Baldocchi et al. 1997). In the stands in this study, most years there was a positive linear relationship between daytime means of $g_c$ and $\theta$ (the $r^2$ was 0.36, 0.24 and 0.00 at MPB-06, and 0.26, 0.06 and 0.17 at MPB-03, in 2007, 2008 and 2009, respectively), although the relationship was strongest when $\theta$ was greater than ~0.08 m$^3$ m$^{-3}$ at MPB-06 and ~0.15 m$^3$ m$^{-3}$ at MPB-03. Below these levels, $g_c$ tended
to be low, and there was a lot of scatter in the relationship. Bernier et al. (2006) found that in Saskatchewan, relative soil water content explained approximately 46% of the variation in $E$ for SOA but only 10% for OJP due to very low values of $\theta$ in the latter. They concluded that the relationship between $g_c$ and $\theta$ is significantly affected by soil texture (i.e., the soil water retention curve) which determines the amount of water available to the trees. In the MPB attacked stands, the sandy and fast draining soils limited the growing season variation in $\theta$ (fine soil volumetric fraction); the total range in growing season $\theta$ (following snowmelt) over the three years was 0.08 m$^3$ m$^{-3}$ ($0.04 – 0.12$ m$^3$ m$^{-3}$) at MPB-06, and 0.04 m$^3$ m$^{-3}$ ($0.12 – 0.18$ m$^3$ m$^{-3}$) at MPB-03. It is also possible that the lack of a strong response of $g_c$ to $\theta$ indicates the trees are able to access water from deeper in the soil profile. However, since $g_c$ did not appear to plateau at the higher values of $\theta$, $\theta$ was likely almost always limiting $g_c$. Comparing with a conifer stand with relatively little soil water limitation, the SOBS stand in Saskatchewan had a typical growing-season mid-day $g_c$ of 5 – 10 mm s$^{-1}$ from 1999 to 2001 (Arain et al. 2003) indicating a higher $g_c$ under non-water limiting conditions.

Vapour pressure deficit and $Q$ were able to explain more than half of the variation in half hourly $g_c$. It was observed that at the highest values of $g_c$ ($~> 10$ mm s$^{-1}$; Fig. 3.9), $g_{cmod}$ consistently underestimated $g_c$, resulting in $E_{mod}$ underestimating $E$ when $E$ was highest. These high values of $g_c$ did not occur consistently under the same conditions of $D$ and $Q$ thus other factors also must have influenced $g_c$. These could include the varying response of the overstory, understory and moss and lichen layer to $D$ and $Q$, as well as the influence of the beetle attack. Nevertheless, when half-hourly values of $E$ and $E_{mod}$ were summed for 15 May – 30 September, the agreement was very good.
Like the growing season values of $g_c$, growing season measurements of conifer stomatal conductance ($g_s$) made at the leaf level, as described in Chapter 2, did not vary significantly over the three years at MPB-06 (Fig. 3.16). At MPB-03, conifer $g_s$ also followed a trend similar to $g_c$, increasing slightly in 2008 and then falling in 2009 due to the effects of drought.

![Figure 3.16. Average growing season stomatal conductance ($g_s$) of canopy trees, small trees, and seedling and saplings. Bars are standard deviations. Average $g_s$ of broadleaf vegetation was 0.15 (0.06), 0.14 (0.07) and 0.27 (0.71) mmol H$_2$O m$^{-2}$ s$^{-1}$ from 2007-2009 at MPB-06, and 0.13 (0.07), 0.13 (0.09) and 0.14 (0.16) mmol H$_2$O m$^{-2}$ s$^{-1}$ from 2007-2009 at MPB-03 (numbers in parentheses are standard deviations).]
3.4.4 Water balance

MPB-03 had much higher drainage values than MPB-06 due to higher rainfall. At MPB-06 there was a steady decrease in $D_r$ over the three years, due to decreasing totals of $P$. Despite this decrease, $E$ actually increased from 2007 to 2009 (1 June – 30 September) causing $\Delta S$ to be negative in 2009. Uunila et al. (2006) suggested that there would be an increase in annual water yield and late summer/fall low flows in even-aged stands without secondary structure following MPB attack but at MPB-06 this has not been the case. Although there are few studies on the effects of beetle attack on the hydrology of forested stands (Hélie et al. 2005), the assumption that beetle attack would led to an increase in $\theta$ and runoff due to earlier snowmelt, and lower rates of transpiration (BCMFR 2008) were not observed in this study. Although EC measurements were not made before the site was first attacked, $E$ during August and September 2006 and 2007 was 1.91 mm day$^{-1}$ and 2.24 mm day$^{-1}$, respectively, suggesting $E$ was not much different prior to attack (Appendix 1). This lack of a difference in $E$ could be due to a soil water limitation in 2006, as average $\theta$ was 0.05 m$^3$ m$^{-3}$ and 0.11 m$^3$ m$^{-3}$ during August and September 2006 and 2007, respectively. As evidence that the August 2006 measurements were representative of pre-attack stand conditions, foliar photosynthesis and stomatal conductance of attacked trees were not significantly different than those of the non-attacked trees sampled during that period (see Chapter 2 for details).

The values of $\alpha_{\text{max}}$ at high values of $D$ were much less than the theoretical maximum $\alpha$ of 1.26 identified by Priestley-Taylor (1972) for well-watered vegetation. Shuttleworth and Calder (1979), however, noted that using the value of 1.26 is likely unrealistic in forest ecosystems due to physiological controls, which under dry conditions reduce $E$ to levels much lower than those observed over well-watered crops. At MPB-06 in 2009 there were only 19 days when $\theta$ was >
\( \theta_{\text{threshold}} \), thus using only data from that year to model \( \alpha_{\text{max}} \) was likely not as robust as combining data from all three years, even though the cumulative WD was similar using the two methods. This was likely not an issue in 2009 at MPB-03, as there were a larger number of values available for calculating \( \alpha_{\text{max}} \) (N = 59).

By including an \( \alpha_{\text{max}} \) term that varied with \( D \), Eq.4 was able to produce values of \( E_{\text{pot}} \) that incorporate both the influence of \( R_a \) and \( D \) on the capacity vegetation to transpire. For instance, under well-watered conditions low \( D \) resulted in higher \( \alpha \) values, as the stomata were more open during these times, which acted as a positive forcing on \( E \). However, \( R_a \) tended to be low under such conditions, which limited \( E \). This interplay of the influences of \( D \) and \( R_a \) helps explain the low variability in interannual \( E \), despite the variation in climate. The growing season WD shows that these stands are water limited and thus the stomata must close to restrict water loss. However, since the WD was small, even if \( \theta \) remained high throughout this period, \( E \) would not have been dramatically higher. The WD was likely low because \( E_{\text{pot}} \) would have been less than if the stands had not been attacked by the beetle. The effect of beetle on the WD depends on how much the effect of the beetle reduces \( E_{\text{pot}} \) (i.e., \( E \) when \( \theta \) is not limiting) compared to how much it reduced \( E \). The observation of a WD indicates that in spite of the beetle attack, stands with either an understory or un-killed trees respond to the atmospheric demand for water.

### 3.5 Conclusions

Although it has been predicted that the MPB outbreak in BC would significantly alter transpiration rates and thus induce changes in annual water yields (BCMFR 2008; Hélie et al. 2005), there has not been a significant change in \( E \) at these two sites over the tree years EC measurements were made. The increase in \( E \) from the growth release of the secondary structure,
understory vegetation and mosses and lichens at MPB-03 has compensated for the reductions in $E$ due to the death of the overstory. At MPB-06, the growth of the surviving trees and understory vegetation, and mosses and lichens in response to the beetle attack maintained $E$ at relatively stable levels over the three years following attack. Canopy conductance was largely controlled by $D$ but the response varied with $Q$. The use of the Priestley-Taylor equation with a varying $\alpha$ resulted in reasonable values of $E_{pot}$ for these stands at their current stage of recovery from MPB attack. As the stands continue to recover and canopy closure is once again attained, $E_{pot}$ will likely increase. The large difference in growing season drainage between sites was due to difference in $P$ at the two sites, with MPB-03 having the higher $P$ and $D_r$. 
4. The carbon balance of two lodgepole pine stands recovering from mountain pine beetle attack in British Columbia

4.1 Introduction

Recently, the impact of disturbance on forest carbon (C) cycling in North America is receiving increased attention from researchers (e.g. Amiro et al. 2010, Coops and Wulder 2010, Kurz et al. 2008). Forests fires, insect attacks and harvesting can all shift forests from C sinks to sources (Amiro et al. 2010). In Canada, insect infestations can result in greater annual tree mortality than either fires or harvesting (Kurz et al. 2008), thus quantifying their impact is central to furthering our understanding of forest C dynamics. The recent mountain pine beetle (MPB) (Dendroctonus ponderosae) outbreak in British Columbia (BC) is unprecedented in terms of tree mortality and area affected and could severely impact the C balance of BC’s forests. Lodgepole pine (Pinus contorta var. latifolia), the main host of the beetle, is found throughout the interior of BC. A 2009 aerial survey reported just under 9 million ha of forests showing some current beetle impact, down from the peak infestation of 10 million ha in 2007 (Westfall and Ebata 2009). Insect attacks can influence net ecosystem production (NEP), the net uptake of atmospheric CO₂ by the forest, via their impact on gross ecosystem photosynthesis ($P_g$) and ecosystem respiration ($R_e$). The reduction in leaf area associated with tree mortality would likely lead to a decline in $P_g$, and the increase in dead organic matter (needles, roots, stems and branches) would be expected to lead to an increase in decomposition. However, the time scale at which these processes occur is not well known. While $P_g$ might be expected to show an immediate response to attack, an increase in $R_e$ could take years.
There are few published results of the impact of insect attacks on C cycling. Eddy covariance (EC) measurements made in a hardwood forest in Wisconsin that had been 37% defoliated by forest tent caterpillars (*Malacosoma disstria*) suggested a 24% reduction in $P_g$ compared to non-outbreak years (Cook *et al.* 2008). Similarly, Clark *et al.* (2010) reported a decrease in the magnitude of annual net ecosystem exchange (NEE) in New Jersey oak (*Quercus* sp.) and pine (*Pinus* sp.) dominated upland forests defoliated by the Gypsy moth (*Lymantria dispar*), though the impact varied among three sites. A modelling study predicted the cumulative impact of the BC MPB outbreak from 2000-2020 to be a net loss 270 Mt C, with the impact peaking in 2009 with a net biome production (NEP plus the impacts of disturbance but excluding the effects of additional harvesting) of -53 g C m$^{-2}$ (Kurz *et al.* 2008). MODIS-based estimates of $P_g$ over the BC MPB infestation area from 2002 to 2005 showed a decrease of 10-20% from pre-outbreak levels (Coops and Wulder 2010), with more severely attacked stands having a greater reduction in $P_g$.

Although the previous two studies cited reported a decline in $P_g$, previous results of eddy covariance measurements from two beetle-attacked stands in the central interior of BC showed that in the first two years of measurement (first and second and fourth and fifth years after initial attack) NEP was negative but then increased following a boost in the productivity of the residual trees and vegetation (Chapter 2). These two sites also showed little change in evapotranspiration following the attack, a result of the compensating effect of the surviving trees and below-canopy vegetation (Chapter 3). This study examines how these two stands continue to recover from the attack using four years of EC data focusing on how $P_g$ and $R_e$ have responded by examining their relationships with climate variables.
4.2 Methods

4.2.1 Site description

NEP and climate measurements were made in two stands dominated by lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.), located in the northern interior of BC, in the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar 1991). The first stand (MPB-06) (55°06′42.8″N, 122°50′28.5″W) is located at Kennedy Siding, approximately 35 km southeast of the town of Mackenzie. The first large scale attack by the beetle at this ~80-year-old stand was in the summer of 2006. This site contained few non-pine trees, and the understory consisted mainly of pine seedlings, scattered shrubs and a ground cover of moss and lichen. The second, ~110 year-old stand (MPB-03) (54°28′24.8″N, 122°42′48.4″W) is in Crooked River Provincial Park, approximately 70 km north of Prince George, BC and approximately 100 km south of MPB-06. The overstory was comprised of about 92% lodgepole pine and 8% subalpine fir (*Abies lasiocarpa*), and had a developed secondary structure (tree seedlings and saplings, and sub-canopy and canopy trees that survive the attack) consisting of lodgepole pine, subalpine fir and hybrid white spruce (*Picea glauca*) sub-canopy trees and saplings, and seedlings of all three tree species. The ground cover was dominated by mosses, lichens and dwarf shrubs. MPB-03 was first attacked in 2003, and by March 2007, when NEP measurements began, more than 95% of the pine canopy had been killed by the beetle. Both sites are flat and on coarse textured gravelly soils of glacio-fluvial origin. The fine soil bulk density is approximately 1180 and 1160 kg m\(^{-3}\) and soil coarse fragment content is about 34 and 70 % (by volume >2 mm) at MPB-06 and MPB-03, respectively. In 2007, stand density was ~1235 and ~560 stems ha\(^{-1}\) and stand basal area was 12.0-20.1 m\(^2\) ha\(^{-1}\) and 8.8-17.9 m\(^2\) ha\(^{-1}\) (live and dead trees with height > 10 m) at MPB-06 and MPB-03, respectively. LAI decreased at MPB-06 from 1.4 in 2007 to 1.3 in 2010. Live
LAI at MPB-06 was 0.42, 0.31, 0.30 and 0.22 in 2007, 2008, 2009 and 2010, respectively. At MPB-03, LAI decreased from 0.9 in 2007 to 0.55 in 2010. For further information on stand characteristics see Chapter 2.

### 4.2.2 Flux, climate and ecophysiological measurements

A 32-m-tall scaffold flux tower (~2.1 m long x ~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. Fluxes of CO$_2$ ($F_c$), sensible ($H$) and latent heat ($\lambda E$) were measured directly using the EC technique. 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 turbulent fluctuations of CO$_2$ and H$_2$O concentration were measured using an open-path infrared gas analyzer (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. At both sites, EC sensors were mounted at the height of 26 m, which was ~8 m and ~6 m above the top of the canopy at MPB-06 and MPB-03, respectively. Following Webb et al. (1980), $F_c$ and $\lambda E$ were calculated as the product of the dry air density and the covariance of the CO$_2$ and water vapour mixing ratios, respectively, measured at 10 Hz. Further details of the measurements system and the data processing procedure are provided in Chapter 2.

Climate variables measured included above-canopy upwelling and downwelling shortwave and longwave radiation (at 30-m height) and above-canopy upwelling and downwelling (30-m height), and below-canopy downwelling (3-m height) photosynthetically active radiation (PAR), precipitation at just-below-canopy height, wind speed, air temperature
and relative humidity at the 25-m height, soil temperature at depths of 5, 10, 20 and 50 cm, soil
heat flux at a depth of 5 cm and water content at the 0-10 cm and 30-50 cm depths at MPB-06
and at the 10-cm, 20-cm and 50-cm depths at MPB-03. Meteorological measurements were made
every second, and 30-min average values calculated. Snow-pack depth was also measured at a
clearcut weather station located ~1 km from MPB-06, using an acoustic distance sensor and
precipitation calculated from these data and manual measurements of liquid water equivalent.
Instrument names and model numbers can be found in Chapter 2. 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), hemispherical photography
(Egginton et al. 2008). Live LAI at MPB-06 was determined by canopy photo analysis.
Photographs of the forest canopy were taken each year in 8 directions from the tower. The
images were adjusted to ensure the same area of the canopy was analysed each year and the
fraction of green leaf area was determined by overlaying a 240-point grid on each image and
counting the number of grid points on green forest canopy. Each year, live LAI was determined
as the LAI measured in 2006 adjusted by the fraction of green canopy from the photographic
analysis.

Foliar gas-exchange (CO₂ and water vapour) measurements were made every two to four
weeks throughout the 2007-2009 growing seasons (1 May- 30 September) at MPB-06 and 2007-
2010 growing seasons at MPB-03 (Bowler 2010). The measurement periods were 23 May – 23
August 2010 (measurements were made at MPB-03 only in 2010). Shoots were clipped at
random from the lower branches of the canopy exposed to sun at a height of approximately 6 m
using a pruning pole and shoots from smaller understory trees were clipped using handheld shears from random branches and measured within 5 minutes of sampling. Samples were taken from the same trees on consecutive occasions. Measurements were made between 10:00 and 16:00h PST in ambient light conditions. Foliar net assimilation ($A_n$) and stomatal conductance ($g_s$) measurements were made using a portable photosynthesis measurement systems (model LI-6400, LI-COR Inc.) with a clear acrylic conifer chamber (model 6400-05, LI-COR Inc.), following the approach of Pypker and Fredeen (2002). Needles intact to the branchlet were placed in the conifer chamber under ambient light conditions. Broadleaf vegetation gas-exchange measurements began in early June when leaves were estimated to be fully expanded. Samples were randomly selected from many different species of several classes of vegetation including small trees such as trembling aspen (Populus tremuloides), deciduous and evergreen shrubs, herbaceous annuals, and lycopods (the latter occur at MPB-03 only). The physiological response to excision of broadleaves has been found to be more rapid than needles (Richardson and Berlyn 2002); therefore to minimize stomatal closure due to leaf water potential changes following excision, broadleaf gas-exchange measurements were conducted on intact foliage, except for very small evergreen shrubs such as wintergreens (Pyrola spp.). These species were too close to the ground to effectively enclose in the conifer chamber. It was assumed the effects of excision were minimal due to the similarity in leaf structure and cuticle thickness compared to conifers (Taneda and Tateno 2005). During the measurements a CO$_2$ concentration and air flow rate was maintained for 3 min at 380 ppmv and 500 µmol s$^{-1}$ (300 mL min$^{-1}$), respectively. Air temperature, vapour pressure deficit ($D$) and PAR were continuously recorded during each measurement along with $A_n$ and $g_s$. Area-based estimates of $A_n$ were calculated after determining half the total leaf area, using the volumetric displacement technique, for each branchlet sampled.
and leaf area to dry leaf biomass ratios (specific leaf area, SLA) were determined. Broadleaf sample one-side surface areas were determined optically using a flat bed scanner (Epson Expression 1640 XL) and analyzed using WinFolia (version Pro 2003d) image processing software (Régent Instrument Inc., Quebec, Canada).

There are three main stages to MPB attack in terms of its effects on the host tree. The green attack stage generally occurs during the first year of attack, when the needles remain green. The red attack stage occurs after the first winter of attack when the tree has been killed and the needles turn red. Finally, the tree enters the grey attack stage one or two years later when the needles begin to fall. By 2007, MPB-03 was already in the red and grey stage of attack. Tree health status inventories at MPB-06 were conducted each year from 2006 to 2010 (Fig. 4.1). The attack status of individual trees was determined along two 350-m long x 2-m wide transects. 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 grey 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 response to partial retention logging of MPB attacked stands (Seip and Jones 2007). Tree health was also determined by canopy photo analysis.
Figure 4.1. Mountain pine beetle attack status at MPB-06. July and October 2007 are values from Hilker et al. (2009). August 2007-2009 are mean values from this study and of Seip and Jones (2008). August 2010 are mean values of Spittlehouse et al. (2010) and Dale Seip (personal communication).

4.2.3 Flux quality control and data analysis

Quality control procedures included rejection of flux data when a 30-minute period had more than 30\% of an individual trace with an instrument diagnostic warning flag that indicated a bad measurement, and setting minimum (300 μmol mol\(^{-1}\)) and maximum (1000 μmol mol\(^{-1}\)) bounds on CO\(_2\) concentrations as measured by the open-path IRGA. Fluxes were not rejected on the basis of wind direction since the fetch of beetle-affected forest was greater than 1 km in all directions around the tower, and when wind passed through the tower before passing through the
sonic anemometer array, which was rare, there was no detectable effect. An additional quality control procedure was applied to winter flux data to address the issue of wintertime CO$_2$ uptake commonly observed with the use of the LI-7500 open-path IRGA (described in detail in Chapter 2).

Nighttime EC measurements 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 $u_*$ ($u_{*th}$) of 0.30 m s$^{-1}$ were considered for analysis, thus ensuring sufficient turbulent mixing (Baldocchi 2003). The value of $u_{*th}$ was determined by plotting half-hourly CO$_2$ flux against $u_*$ and selecting the value for which a further increase in $u_*$ no longer led to an increase in the flux (Massman and Lee 2002). The value was not clearly defined, which, unfortunately, is commonplace in EC studies (Gu et al. 2005); however, it was within ±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 the following empirical logistic relationship between nighttime $R_e$ ($u_*$ > $u_{*th}$) and soil temperature at 5-cm depth ($T_s$) can be applied to the daytime:

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

(1)

where $r_1$, $r_2$ and $r_3$ are parameters set by the model. Following the FCRN protocol, a moving window parameter ($r_w(t)$), which estimates the seasonal variation of the parameters in Eq. (1) was added so that:

$$R_e = \frac{r_w(t)r_1}{1 + \exp[r_2(r_3 - T_s)]]}$$

(2)

The moving window parameter is calculated as the slope of the linear regression between estimates of $R_e$ obtained from the annual relationships (Eq. 1) and $R_e$ from the measurements.
Barr et al. (2004). The window is 100 data points wide and is moved in an increment of 20 points at a time.

\[ P_g \] 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 modelled using the following FCRN standard algorithm, which assumes a rectangular hyperbolic (Michaelis–Menten) relationship between \( P_g \) and downwelling PAR (\( Q \)):

\[
P_g = \frac{\alpha P Q P_{g_{\text{max}P}}}{\alpha P Q + P_{g_{\text{max}P}}}
\]  

(3)

where \( \alpha P \) is the quantum yield, \( P_{g_{\text{max}P}} \) is ecosystem photosynthetic capacity (i.e., asymptotic value when \( Q \) approaches infinity). An additional moving window parameter (\( p_w(t) \)) is added, resulting in:

\[
P_g = \frac{p_w(t)\alpha P Q P_{g_{\text{max}P}}}{\alpha P Q + P_{g_{\text{max}P}}}
\]  

(4)

where the moving window parameter was used as in Eq (2) above. The gap-filling procedure was altered from that described in Barr et al. (2004) in that, the moving window was not applied during the winter (when \( T_s \) was <1 °C). 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 (Chapter 2 (Brown et al. 2010)), a single 100 point window was found to span weeks or 2-3 months. Over such time spans climatic variability, such as changes in air temperature (\( T_a \)), resulted in variations in \( R_e \) even though \( T_s \) varied little. To fill gaps in \( H \) and \( \lambda E \) a procedure described in Chapter 3 was used.
In this paper, the seasonal and annual C balance values of $R_e$ and $P_g$ were obtained using the nighttime $R_e - T_s$ relationship (Eq. (2)) and the $P_g$ and $Q$ relationship (Eq. (4)) when daytime NEP values were missing.

The growing season photosynthetic and respiratory characteristics of the two ecosystems were also determined without using the nighttime relationship (Eq. 1) to obtain daytime $R_e$. These estimates were obtained by applying the Michaelis–Menten light response relationship to daytime NEP measurements as follows:

$$\text{NEP} = \frac{\alpha_N Q P_{g\max N}}{\alpha_N Q + P_{g\max N}} - R_{edN}$$

where $\alpha_N$ is the quantum yield, $P_{g\max N}$ is ecosystem photosynthetic capacity and $R_{edN}$ is the daytime ecosystem respiration.

To examine the seasonal variation in daytime ecosystem respiration and its response to $T_s$, 3-day values of daytime ecosystem respiration ($R_{ed}$) were determined as the intercept of the linear relationship between 3-day half-hourly values of measured NEP and $Q$ when $Q$ was <300 μmol m$^{-2}$ s$^{-1}$ (Jassal et al. 2007). $R_{ed}$ values binned by a width of 2.0 °C were then used with average 3-day daytime $T_s$ (5-cm depth) to develop a $R_{ed}$ function using Eq. 1. Only values of $R_{ed}$ were included for the analysis when the $r^2$ was > 0.2 for the 3-day fitting procedure. Annual and growing season totals of $R_{ed}$ were calculated by applying this $R_{ed}$ function to nighttime and daytime half-hourly $T_s$ values.

The light response parameters of the foliage were determined using the following equation:

$$A_n = \frac{\alpha_i Q A_{\max}}{\alpha_i Q + A_{\max}} - R_{id}$$

(6)
where $\alpha_l$ is the leaf quantum yield, $A_{max}$ is the leaf photosynthetic capacity $R_{ld}$ is the leaf daytime respiration.

In the ecosystem respiration and light response analysis the fitted models (Eq. (1) and (3)) were compared to null models (containing only an intercept parameter) with a likelihood ratio test (Seber and Wild 2003). $P$-values were determined by comparing the change in the log likelihood between the full and null models to a chi-squared distribution with degrees of freedom equal to the difference in the number of model parameters. To test for changes in the models over time, models with parameters being constant across years were compared to fitting separate models to each year's data using a likelihood ratio test. The log likelihood for the temporally constant model was compared to the sum of the log likelihoods for the separate models, with the difference compared to a chi-squared distribution with degrees of freedom equal to the number of extra parameters used when fitting separate models for each year.

The quality of the EC data was assessed by determining energy balance closure, although a closure correction was not applied. A detailed energy balance closure analysis was reported in Chapter 3. Briefly, half-hourly measurements of net radiation flux ($R_n$), surface soil heat flux ($G$), $H$ and $\lambda E$ were used together with estimates of the rate of change in energy storage (per unit ground area) in the air and biomass between the EC sensors and the ground surface ($S_t$). The slopes of plots of half-hourly values of $H + \lambda E$ vs. available energy flux ($R_n - G - S_t$) for both sites were always >0.89 on an annual basis, and >0.92 for the growing season data.
4.3 Results

4.3.1 Climate

The main difference between the climates at the two sites is the precipitation, with approximately twice as much growing season rainfall at MPB-03 compared to MPB-06 (Fig. 4.2) due to the presence of convective storms which frequently pass over MPB-03. Despite the large difference in precipitation, the region of both sites often experiences a period with little rainfall in late July and August. While rainfall during the 2007 and 2008 occurred quite steadily throughout the growing seasons, 2009 and 2010 were quite dry. At MPB-06 soil fine fraction (soil particle size < 2 mm) volumetric water content ($\theta$) was at its lowest level (< 0.05 m$^3$ m$^{-3}$) from 29 July to 7 September 2009, during which time there was a total of 29 mm of rainfall. In 2010 between 24 July and 22 August, MPB-06 received only 1 mm of rainfall and $\theta$ fell to 0.05 m$^3$ m$^{-3}$. MPB-03 also experienced a prolonged drought in 2010, lasting from 13 July to 22 August (10 mm of rainfall), during which time $\theta$ was approximately 0.12 m$^3$ m$^{-3}$. There was a similar, though shorter drought at MPB-03 in 2009 lasting from 17 July to 10 August. Over the four years, 2009 had the warmest growing season at both sites (Fig. 4.2; Table 4-1) when $T_a$, $Q$ and daytime $D$ were all highest. The winter was much milder in 2010 than the previous years, with 5-day-average $T_a$ never falling below -8 °C after 10 January at both sites. While snowmelt was not complete until mid-May in 2007 to 2009, it was complete by late April in 2010 at MPB-06, while at MPB-03 snowmelt was complete by 20 April in 2007 and 2010, and by 15 May and 7 May in 2008 in 2009. Wintertime daily $T_s$ (5-cm depth) never fell below -1.0 °C at MPB-06 and 0.0 °C at MPB-03. Further climate details are provided in Chapters 2 and 3.
Table 4-1. Average values of climate variables for the growing season.

<table>
<thead>
<tr>
<th></th>
<th>MPB-06</th>
<th></th>
<th></th>
<th></th>
<th>MPB-03</th>
<th></th>
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<td></td>
<td>2007</td>
<td>2008</td>
<td>2009</td>
<td>2010</td>
<td>2007</td>
<td>2008</td>
<td>2009</td>
<td>2010</td>
</tr>
<tr>
<td>Air temperature (26-m height) (° C)</td>
<td>11.8</td>
<td>12.4</td>
<td>12.9</td>
<td>12.0</td>
<td>12.8</td>
<td>13.0</td>
<td>14.0</td>
<td>12.7</td>
</tr>
<tr>
<td>Soil temperature (5-cm depth) (° C)</td>
<td>10.4</td>
<td>11.1</td>
<td>11.9</td>
<td>11.7</td>
<td>10.3</td>
<td>10.3</td>
<td>10.8</td>
<td>10.9</td>
</tr>
<tr>
<td>Rainfall total (mm)</td>
<td>246</td>
<td>250</td>
<td>177</td>
<td>219</td>
<td>576</td>
<td>620</td>
<td>477</td>
<td>422</td>
</tr>
<tr>
<td>$\theta$ (m³ m⁻³) (0-10-cm depth)</td>
<td>0.11</td>
<td>0.11</td>
<td>0.08</td>
<td>0.09</td>
<td>0.17</td>
<td>0.16</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>$Q$ (μmol m⁻² s⁻¹)</td>
<td>396</td>
<td>396</td>
<td>421</td>
<td>396</td>
<td>413</td>
<td>410</td>
<td>442</td>
<td>418</td>
</tr>
<tr>
<td>$D$ (kPa)</td>
<td>0.80</td>
<td>0.83</td>
<td>0.94</td>
<td>0.88</td>
<td>0.86</td>
<td>0.84</td>
<td>1.04</td>
<td>0.92</td>
</tr>
<tr>
<td>GSL (days)</td>
<td>136</td>
<td>141</td>
<td>134</td>
<td>147</td>
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<td>$R_n$ (GJ m⁻²)</td>
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<td>1.57</td>
<td>1.57</td>
<td>1.50</td>
<td>1.70</td>
<td>1.63</td>
<td>1.72</td>
<td>1.60</td>
</tr>
</tbody>
</table>

1 Daytime average values.
2 Growing season length (half-hourly values of air temperature and soil temperature (5-cm depth) > 0 and 1°C, respectively).
3 Growing season total.
Figure 4.2. Cumulative totals of growing season precipitation ($P$) and 5-day-averages of air temperature at 26 m ($T_a$), soil temperature at 5-cm depth ($T_s$) and volumetric water content 0-30-cm depth ($\theta$) for 2007 (black line), 2008 (dashed line), 2009 (dotted line) and 2010 (grey line).

4.3.2 Ecosystem respiration analysis: based on the nighttime approach

The logistic relationship between nighttime half-hourly measured $R_e$ and $T_s$ at the 5-cm depth (Eq. (1)) was significant ($P < 0.001$) at both sites each year and varied significantly between successive years at both sites (Fig. 4.3 and Table 4-2) ($P < 0.001$). To compare with the logistic equation, the response of $R_e$ to $T_s$ using the following exponential equation was also determined,

$$R_e = R_{e0}Q_{10}^{(T_s-10)/10}$$

(7)
where $R_{e10}$ and $Q_{10}$ are the respiration rate at 10 °C and the relative increase in respiration per 10 °C increase in $T_s$, respectively (Table 4-2). The logistic equation (Eq. (1)) provided a slightly better fit than the exponential equation at both sites. $R_e$ normalized to 10 °C ($R_{e10}$) calculated with the logistic equation was highest at MPB-06 and MPB-03 in 2008 and 2007, respectively, and lowest in 2010 at both sites. At MPB-06, when $T_s$ was < 10 °C, the rate of increase in $R_e$ with $T_s$ was most rapid in 2010 and most gradual in 2008, but at higher $T_s$, $R_e$ increased most rapidly in 2010. Although there was a smaller variation in the response of $R_e$ to $T_s$ between years at MPB-03, $R_e$ was both highest for $T_s < 5.0$ °C and lowest for $T_s > 10$ °C in 2010. Over the four years the annual totals of $R_e$ calculated using the logistic equation were approximately 15 and 5% lower than those calculated with the exponential equation at MPB-06 and at MPB-03, respectively. $Q_{10}$ values (Eq. (7)) were between 2.70 and 2.93 at MPB-06 and 2.48 and 4.27 at MPB-03. There was no direct relationship observed between half-hourly $R_e$ and $\theta$. While $\theta$ has often been found to have a positive impact on $R_e$ (Krishnan et al. 2006), the negative correlation between $T_s$ and $\theta$ can make determining the nature of its influence problematic. When values of half-hourly measured $R_e$ were normalized by dividing by modelled $R_e$ ($R_{eN}$) and plotted against $\theta$ (Jassal et al. 2007), a significant relationship was observed at MPB-06 when $\theta$ was > 0.13 m$^3$ m$^{-3}$ in 2007 and 2008 and >0.11 m$^3$ m$^{-3}$ in 2009 and 2010, and for $\theta$ > 0.17 m$^3$ m$^{-3}$ in 2007 at MPB-03 (Fig. 4.4). The rate of the increase in $R_{eN}$ with $\theta$ was greatest at MPB-06 in 2008 and 2010. There was also a significant decline in $R_{eN}$ for $\theta$ < 0.085 m$^3$ m$^{-3}$ at MPB-06 in 2009.
Figure 4.3. Relationship between annual measured half-hourly values of ecosystem respiration ($R_e$) and soil temperature at the 5-cm depth ($T_s$) (Eq.1). Values are bin averages of 10 measurements starting from the smallest value.
Table 4-2. Parameters from the annual relationships between half-hourly values of measured nighttime ecosystem respiration ($R_e$) and soil temperature at the 5-cm depth ($T_s$) and daily daytime derived respiration ($R_{ed}$) and daily daytime $T_s$. $R_{10}$ values are ecosystem respiration at 10 °C. $R_{tot}$ and $R_{totd}$ are the annual totals (g C m$^{-2}$) of modelled ecosystem respiration using the nighttime and daytime methods.

<table>
<thead>
<tr>
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<td>0.92</td>
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<td>$R_{ed10}$</td>
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<td>1.31</td>
<td>2.17</td>
<td>1.90</td>
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<td>$R_{ed}^1$</td>
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</table>

$R_{e10}$ and $R_{ed10}$ values are in μmol m$^{-2}$ s$^{-1}$.

$^1$ Annual totals (g C m$^{-2}$).

$^2$ Growing season totals (1 May – 30 September) (g C m$^{-2}$).

$^3$ Numbers in parentheses are upper and lower 95% confidence intervals.
4.3.3 Comparison of ecosystem respiration derived using the nighttime and daytime approaches

$T_s$ explained most of the variation in $R_{ed}$ for the majority of the years at both sites and the response varied significantly between successive years ($P < 0.001$) (Fig. 4.5 and Table 4-2). The values of $R_{ed10}$ were less than those of $R_{e10}$ at both sites, with the exception of 2009 at MPB-03.
Over the four years, the ratio of the annual total ecosystem respiration obtained using the daytime approach to that obtained using the nighttime approach varied from 0.69 to 0.97 at MPB-06 and from 0.81 to 1.34 at MPB-03. As can be seen in Fig. 4.6, the agreement between $R_e$ and $R_{ed}$ was worse during the winter at both sites, with winter $R_{ed}$ being about 35% lower and 100% higher in 2009 at MPB-06 and MPB-03, respectively.

**Figure 4.5.** Relationship between annual 3-day daytime values of ecosystem respiration ($R_{ed}$) and daily daytime soil temperature at the 5-cm depth ($T_s$) (Eq. 1). Data were sorted into 2 °C wide bins.
Figure 4.6. Daily values of ecosystem respiration calculated using the nighttime ecosystem respiration ($R_e$) and daytime ecosystem respiration ($R_{ed}$) approaches.

**4.3.4 NEP and $P_g$ light response analysis**

At both sites $Q$ was an important determinant of NEP and $P_g$ (calculated using the nighttime $R_e$ – $T_s$ relationship) during the growing season (Eqs. (3) and (5); Table 4-3), with the relationship being significant each year at both sites and varying significantly between successive years ($P < 0.001$). However, the proportion of NEP and $P_g$ variance explained by $Q$ was greater at MPB-06 than MPB-03. In every year, both $P_{g\text{max}N}$ and $P_{g\text{max}P}$ were higher at MPB-06 than MPB-03. At MPB-06, $P_{g\text{max}N}$ increased from a low value in 2007 to similar values in 2008, 2009 and 2010, while $P_{g\text{max}P}$ was highest in 2010. At MPB-03, both $P_{g\text{max}N}$ and $P_{g\text{max}P}$ were highest in 2008 and
lowest in 2010. The agreement between \( P_{\text{gmaxN}} \) and \( P_{\text{gmaxP}} \) was very good, especially at MPB-03 where the values were within 0.3 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) of each other every year. Growing season values of \( \alpha_N \) and \( \alpha_P \) also agreed very well at both sites. As the PAR reflectivity was \(~4.5\) and \(5\%\) at MPB-06 and MPB-03, respectively, and given that some \( Q \) was absorbed by dead needles and tree boles, actual \( \alpha \) values were likely slightly higher than those reported here. At both sites, the relationship between both daytime NEP and \( P_g \) and \( Q \) levelled off at a \( Q \) of approximately 1400 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (Fig. 4.7). In 2007 at \( Q \) values higher than this there was a significant reduction in NEP and \( P_g \) at both sites. There was also a slight decline in NEP at high \( Q \) in 2008, 2009 and 2010, more strongly at MPB-03 than MPB-06. Growing season \( R_{\text{edN}} \) values were highest in 2008 and lowest in 2010 at both sites.

Table 4-3. Regression parameters (Eqs.3 and 5) for the growing season (1 May -30 September) for net ecosystem production (NEP) and gross ecosystem photosynthesis (\( P_g \)) (nighttime method).

<table>
<thead>
<tr>
<th></th>
<th>MPB-06</th>
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<th>MPB-03</th>
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<td>2010</td>
<td>2007</td>
<td>2008</td>
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<td>2010</td>
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<tr>
<td>( P_{\text{gmaxN}} )</td>
<td>6.69</td>
<td>7.64</td>
<td>7.62</td>
<td>7.46</td>
<td>6.29</td>
<td>7.51</td>
<td>6.77</td>
<td>6.00</td>
</tr>
<tr>
<td>( \alpha_N )</td>
<td>0.021</td>
<td>0.024</td>
<td>0.023</td>
<td>0.019</td>
<td>0.029</td>
<td>0.037</td>
<td>0.031</td>
<td>0.029</td>
</tr>
<tr>
<td>( R_{\text{edN}} )</td>
<td>2.36</td>
<td>2.47</td>
<td>2.19</td>
<td>1.80</td>
<td>2.56</td>
<td>2.79</td>
<td>2.37</td>
<td>2.22</td>
</tr>
<tr>
<td>( r^2 )</td>
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<td><strong>( P_g )</strong></td>
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<tr>
<td>( P_{\text{gmaxP}} )</td>
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<td>8.04</td>
<td>8.63</td>
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<td>7.39</td>
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<td>( \alpha_P )</td>
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<td>( r^2 )</td>
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<td>0.43</td>
<td>0.16</td>
<td>0.14</td>
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</table>

Only measured daytime values (\( Q > 5 \mu \text{mol m}^{-2} \text{s}^{-1} \)) were used in the analysis. \(^1\) values are in \( \mu \text{mol m}^{-2} \text{s}^{-1} \).
Figure 4.7. Relationship between daytime ($Q > 5 \text{ } \mu\text{mol m}^{-2}\text{ s}^{-1}$) measured net ecosystem production (NEP) and photosynthetically active radiation ($Q$) (Eq. 3) (upper panels) and gross ecosystem photosynthesis ($P_g$) (calculated using nighttime $R_e - T_a$ relationships) and $Q$ (Eq. 5) (lower panels) during the growing season. Symbols are bins of 50, starting with the smallest value while the lines have been fit to all the data (see Table 4-3 for parameter values).

4.3.5 Seasonal and annual NEP, $R_e$ and GEP: based on the nighttime approach

Wintertime (1 January to 31 March and December) average daily NEP, which is comprised almost entirely of $R_e$, averaged -0.57, -0.49, -0.53 and -0.29 g C m$^{-2}$ day$^{-1}$ at MPB-06 and -0.45, -0.39, -0.49 and -0.42 g C m$^{-2}$ day$^{-1}$ at MPB-03, in 2007 to 2010, respectively (Fig. 4.8). Small rates of $P_g$ did occasionally occur in the winter, mainly in March and especially in 2010, when $T_a$ warmed above freezing. Higher rates of $P_g$ typically began to occur in April, when daytime $T_a$
was often several degrees above freezing. During this time NEP was often quite high as $R_e$ was limited because the ground was still covered with snow, keeping $T_s$ just slightly above 0 °C. Once the snow melted and the ground surface was exposed, both $T_s$ and $R_e$ increased rapidly. During the mid-summer, maximum 5-day average NEP increased from $0.8 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2007 to $1.4 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2009 and 2010 at MPB-06. Maximum 5-day average $P_g$ ranged from $3.6$ in 2007 to $4.3 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2010, while maximum 5-day $R_e$ increased from $3.1 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2007 to $3.8 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2010. At MPB-03, maximum 5-day average NEP was $1.0$, $1.8$, $1.6$ and $1.6 \, \text{g C m}^{-2} \, \text{day}^{-1}$ for 2007 to 2010, respectively, while maximum 5-day average $P_g$ increased from $4.0 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2007 to $5.3 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2008 before falling to $4.7$ and $4.2 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2009 and 2010, respectively. 5-day average $R_e$ ranged from a high of $3.4 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2007 and 2010 to $3.8 \, \text{g C m}^{-2} \, \text{day}^{-1}$ in 2008.
At both sites, annual total NEP increased each year from 2007, when both sites were small C sources, to 2009 when both were C sinks (Fig. 4.9; Table 4-4). In 2010 annual NEP diverged at the two sites, increasing considerably at MPB-06, but becoming negative at MPB-03. At MPB-06, the yearly increase in annual NEP was due to increasing photosynthesis, as annual $P_g$ increased by 136 g C m$^{-2}$ over the four years. Annual $R_e$ was very stable at MPB-06, varying by just 36 g C m$^{-2}$ over the four years. The relatively low annual $R_e$ in 2010 helped lead to the high NEP that year. At MPB-03, annual $P_g$ increased from 2007 to 2008, was stable in 2009 and then fell in 2010. At MPB-03, annual $R_e$ was also very stable ranging from 487 to 513 g C m$^{-2}$.
between 2007 and 2010. Annual $P_g$ was similar at both sites each year, except in 2010 when $P_g$ was much higher at MPB-06. Growing season NEP was highest in 2010 and 2009 at MPB-06 and MPB-03, respectively (Table 4-4). The growing season accounted for 88 and 87% of annual $P_g$ and 74 and 75% of $R_e$ at MPB-06 and MPB-03 over the four years.

Table 4-4. Annual and growing season totals of net ecosystem production (NEP), gross ecosystem photosynthesis ($P_g$) and ecosystem respiration ($R_e$) (nighttime method).

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<td>379</td>
</tr>
<tr>
<td>2010</td>
<td>98</td>
<td>487</td>
<td>389</td>
<td>38</td>
<td>398</td>
<td>360</td>
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$^1$Annual and growing season totals of $R_e$ differ from $R_{e\text{tot}}$ values in Table 4-2 in that these values include the effect of the moving-window parameter (Eq. 2).
Figure 4.9. Annual courses of cumulative net ecosystem production (NEP) for 2007 to 2010.

4.3.6 Foliar CO₂ exchange

Growing season averages of net foliar photosynthesis ($A_n$) of un-attacked canopy trees (dbh > 9 cm, height > 1.3 m), small trees (< 9 cm dbh, > 1.3 m tall), seedlings/saplings (< 9 cm dbh, < 1.3 m tall) and broadleaf vegetation are shown in Fig. 4.10. Broadleaf $A_n$ values were highest at both sites, having higher values than each of the conifer classes. At MPB-06, $A_n$ for all conifer classes increased from 2007 to 2009 and each year the small trees had slightly higher $A_n$ than the other two conifer classes. The small trees in 2009 had the highest average $A_n$ (6.2 μmol m⁻² s⁻¹) of all the conifer classes over the three years. Average broadleaf $A_n$ was greatest in 2008 at 7.5 μmol m⁻²
2 s⁻¹, although the variation was high in all years. At MPB-03, $A_n$ for all conifer classes was greatest in 2008 and lowest in 2010, and was similar among conifer classes each year. Broadleaf $A_n$ was greatest in 2007 with an average of 7.5 μmol m⁻² s⁻¹ and was slightly lower in the following years, although in each year there was a large variation.

Figure 4.10. Growing season averages of foliar net photosynthesis ($A_n$) for canopy trees, small trees, seedling and saplings and broadleaf vegetation. Mean photosynthetically active radiation for all conifer and broadleaf measurements was 845 and 613 μmol m⁻² s⁻¹ in 2007, 752 and 716 μmol m⁻² s⁻¹ in 2008 and 863 and 650 μmol m⁻² s⁻¹ in 2009 at MPB-06, and 1195 and 924 μmol m⁻² s⁻¹ in 2007, 922 and 869 μmol m⁻² s⁻¹ in 2008 and 1042 and 937 μmol m⁻² s⁻¹ in 2009, and 1009 and 774 in 2010 at MPB-03. Measurements were not made at MPB-06 in 2010 and were not made on seedlings and saplings at MPB-03 in 2007. Bars are standard deviations.

There was a significant relationship between $Q$ and $A_n$ for 2007-2009 at MPB-06 and in 2008 at MPB-03 ($P<0.05$) (Fig. 4.11), and there was a significant difference in the relationships
between years at MPB-06 (P < 0.05). No measurements were made at MPB-03 in 2007 and 2009 when \( Q \) was < 220 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) making it difficult to fit a light response curve to the data. Generally there was little response to increasing \( Q \) for \( Q > 500 \mu \text{mol m}^{-2} \text{s}^{-1} \). There was much more variation in \( A_n \) at MPB-03, especially for \( Q > 1100 \mu \text{mol m}^{-2} \text{s}^{-1} \) when values were often low. At MPB-06, \( A_{\text{max}} \), \( \alpha_l \), and \( R_{\text{ld}} \) were all highest in 2008.

Figure 4.11. Relationship between net foliar photosynthesis \( (A_n) \) (half of the total needle area basis) and photosynthetically active radiation \( (Q) \) of (coniferous) trees. Values are binned averages of 10 starting with the smallest value. Leaf photosynthetic capacity \( (A_{\text{max}}) \), leaf quantum yield \( (\alpha_l) \), leaf daytime respiration \( (R_{\text{ld}}) \) and the \( r^2 \) were 9.4 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), 0.11, 3.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 0.53 in 2007, 14.2 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), 0.29, 7.6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 0.39 in 2008 and 7.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), 0.02, -1.0 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 0.44 in 2009 at MPB-06 and 15.1 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), 0.42, 8.8 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 0.21 in 2008 at MPB-03.
4.3.7 Water use efficiency

Monthly April to October water use efficiency (WUE = \( P_g / E \)), varied from a low of 0.9 g C (kg H\(_2\)O)\(^{-1}\) in April 2008 to a high of 3.3 g C (kg H\(_2\)O)\(^{-1}\) in August 2010 at MPB-06, and from 0.1 g C (kg H\(_2\)O)\(^{-1}\) in April 2008 to 2.5 g C (kg H\(_2\)O)\(^{-1}\) in October 2009 at MPB-03 (Fig. 4.12). At MPB-06, monthly \( E \) varied conservatively over the years (Chapter 3) causing interannual differences in monthly values of WUE to be dominated by changes in \( P_g \). Growing season average WUE was lowest in 2007 at both sites due to low \( P_g \). Maximum growing season WUE occurred in 2010 at MPB-06 and in 2008 and 2009 at MPB-03 (Table 4-5). At MPB-06, the highest monthly WUE, which occurred in August 2010, was a result of high \( P_g \) and a slightly low \( E \) due to drought. At MPB-03 variation in WUE was due to changes in both \( P_g \) and \( E \). Maximum interannual variation in monthly \( E \) occurred in July and August, where values were low in 2009 (August) and 2010 (July and August) due to drought. In August 2009, \( P_g \) did not respond as strongly to drought as \( E \) did, resulting in a slightly high WUE, while the 2010 drought resulted in a decline in both \( P_g \) and \( E \), leading to little change in WUE.
Figure 4.12. Monthly means of gross ecosystem photosynthesis ($P_g$), evapotranspiration ($E$), and water use efficiency (WUE).

Table 4-5. Growing season evapotranspiration ($E$), gross ecosystem photosynthesis ($P_g$) and water use efficiency (WUE).

<table>
<thead>
<tr>
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<th>MPB-06</th>
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<td>$E$ (mm)</td>
<td>176</td>
<td>177</td>
<td>191</td>
<td>176</td>
<td>228</td>
<td>236</td>
<td>226</td>
<td>208</td>
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<tr>
<td>$P_g$ (g C m$^{-2}$)</td>
<td>388</td>
<td>448</td>
<td>478</td>
<td>487</td>
<td>383</td>
<td>463</td>
<td>446</td>
<td>399</td>
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<tr>
<td>WUE</td>
<td>2.2</td>
<td>2.5</td>
<td>2.5</td>
<td>2.8</td>
<td>1.7</td>
<td>2.0</td>
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<td>1.9</td>
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<td>(g C (kg H$_2$O)$^{-1}$)</td>
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4.4 Discussion

4.4.1 The response of $R_e$, $P_g$ and NEP to environmental variables

The larger proportion of $R_e$ explained by $T_s$ at MPB-06 than MPB-03 could be a result of the latter site having a high fraction of subalpine fir and white spruce and greater abundance of broadleaf vegetation whose respiratory response to $T_s$ might differ from that of lodgepole pine, which dominates MPB-06. The logistic equation best described the response of $R_e$ to $T_s$. Annual totals of $R_e$ calculated using the exponential equation were unrealistically high due to an overestimation of $R_e$ when $T_s$ was high. This conclusion was reinforced by the annual totals of $R_{ed}$ which were more similar to those of $R_e$ calculated using the logistic equation than those calculated using the exponential equation. $Q_{10}$ values obtained using the exponential equation were higher at MPB-03 than MPB-06 every year, except 2010, showing a greater temperature sensitivity of respiration at that site. The decline in $Q_{10}$ in 2009 and 2010 at MPB-03 was likely due to low $\theta$. Normalized $R_e$ ($R_{eN}$) showed that at MPB-06, once $\theta$ exceeded the threshold of approximately 0.12 m³ m⁻³, $R_e$ increased rapidly with $\theta$. In 2009, when growing season $\theta$ reached the lowest values over the four years at MPB-06, $R_{eN}$ declined significantly, showing a clear water limitation of $R_e$. At MPB-03, $\theta$ only had a positive influence on $R_{eN}$ in 2007, the year $\theta$ reached the highest values, suggesting that had similar values been reached in the following years, $R_{eN}$ would also have responded positively.

At MPB-06, annual totals of $R_{ed}$ were consistently less than, and outside the 95% confidence intervals of the $R_e$ annual totals, with the exception of 2008 when the totals agreed well (Table 4-2). At MPB-03, annual totals of $R_{ed}$ were also outside the bounds of the $R_e$ annual totals 95% confidence intervals (below in 2008 and above in 2009 and 2010), except in 2007 when the agreement was very good. Much of the disagreement between the two approaches at
MPB-06 occurred during the winter. When restricted to the growing season, the agreement between the two approaches was much better, with the exception of 2010 when the $R_e$ annual total was considerably higher than the $R_{ed}$ annual total. At MPB-03, the agreement between growing season totals of $R_e$ and $R_{ed}$ was also much better than that for the annual totals. Still, the annual totals of $R_{ed}$ seemed unreasonably high at MPB-03 in 2009 and 2010. While the flux footprint of daytime and nighttime measurements was quite different (the 80% cumulative flux contour was typically 400 and 1500 m upwind of the tower along the longitudinal axis of the footprint during the daytime and nighttime, respectively (Appendix 2)), since the stand is relatively homogenous this would not be expected to have much effect on NEP measurements. Although the $r^2$ of the fit between binned values of $R_{ed}$ and $T_s$ was high at MPB-03, the average number of 3-day $R_{ed}$ values included in the analysis over the four years was only 32, adding some uncertainty in the $R_{ed}$ estimates. Annual totals of $R_{ed}$ may have been less than those of $R_e$ because leaf respiration has been found to be lower during the day than night due to light inhibition of dark respiration (Brooks and Farquhar 1985); however, annual totals of $R_{ed}$ were not consistently lower at MPB-03. The good agreement between $P_{gmaxN}$ and $P_{gmaxP}$ indicates values of $R_{eN}$ were similar to daytime $R_e$ obtained from the nighttime approach and provides confidence in using the nighttime approach to estimate daytime $R_e$.

While the response of $R_e$ to $T_s$ and $θ$ did vary over the years at both sites, it is difficult to attribute this to the impact of the beetle attack. At MPB-06, the ratio of autotrophic ($R_a$) to heterotrophic ($R_h$) respiration might have fallen as a result of the dramatic reduction in the fraction of un-attacked trees from 2007. However, the strong growth of the surviving trees may have had the opposite effect of increasing $R_a$. Although no measures of $R_a$ and $R_h$ were made, their relative contributions to $R_e$ can be estimated (Amiro et al. 2010). Assuming that $R_a$ is about
55% of \( P_g \), as various studies have suggested (e.g., Waring et al. 1998; Jassal et al. 2007), annually, \( R_a \) comprised 46, 50, 56 and 61% of \( R_e \) from 2007 to 2010 at MPB-06, and 49, 55, 56 and 52% of \( R_e \) at MPB-03 from 2007 to 2010. The increase in the contribution of \( R_a \) to \( R_e \) at MPB-06 seems likely, given the large increase in \( P_g \) over the four years.

At MPB-06, the steady annual increase in \( P_g \) resulted in the corresponding increase in NEP. At MPB-03, variation in NEP was also mainly controlled by changes in \( P_g \), as \( R_e \) varied little over the four years. The decline in \( P_g \) in 2010 at MPB-03 corresponded to a significant reduction in \( P_{g\max N} \) and \( P_{g\max P} \). The mid-growing season drought in 2009 and 2010 limited \( P_g \) at MPB-03. As reported in Chapter 3, at MPB-03 there was a significant drop in canopy conductance during the growing season drought in 2009, and there was an even greater drop in 2010 as the stomata closed to limit water loss. The resulting decline in \( P_g \) and NEP during late July and August 2009 and 2010 can be seen in Fig. 4.8. At a 78-year old jack pine (\textit{Pinus Banksiana}) stand in Saskatchewan, Kljun et al. (2006) observed little effect of a three year drought on \( P_g \) owing to the trees being able to access water at deep soil depths. During the growing season at MPB-03, \( \theta \) increased slightly (~1.5%) from the 10 cm to 20 cm soil depths and then decreased 0.5% from the 20 to 50 cm soil depth. At MPB-06, although \( \theta \) was also lowest during the mid-growing season droughts in 2009 and 2010, there was not a significant impact on \( P_g \). Perhaps the different response to drought observed at the two sites is due to the trees being almost exclusively lodgepole pine at MPB-06, which are known to be drought tolerant, while at MPB-03 a large fraction of the remaining live trees were subalpine fir and white spruce, which are more vulnerable to drought (Bigler et al. 2007). Also, although \( \theta \) was always higher at MPB-03, the soil coarse fragment content is 70% by volume, compared to 35%
at MPB-06, much of which is composed of large rocks, resulting in a smaller quantity of fine soil from which tree roots could extract water.

In 2010, the spring months of April and May were extremely productive at MPB-06 (Fig. 4.13). It was during this period when NEP in 2010 mainly differed from the previous years, although NEP was also high during April-May in 2009. During this period $T_a$ was high in 2010, averaging 6.5 °C, compared to the 5.0 °C average of the previous three years. $T_a$ was particularly high between 14-20 April 2010, when maximum daytime values were between 15 and 22 °C, compared to the same period in 2007-2009 when $T_a$ never reached 14 °C. Similar values of spring $T_a$ at MPB-03 also led to a high April-May NEP in 2009 and 2010. Spring growing conditions are thus an important determinant of the annual C balance of these sites.
4.4.2 Foliar CO$_2$ exchange

Foliar gas-exchange measurements provided an important validation of the tower-based NEP measurements and helped determine how the different components of the stand responded to the beetle attack. $A_n$ followed similar trends as $P_g$ at both sites. Although the sampling frequency was much lower than the continuous tower-based measurements, there was a clear annual increase in average $A_n$ of all conifer classes at MPB-06, comparing well with the growing season $P_g$ trends. Both the EC and foliar gas-exchange data showed the surviving MPB-06 canopy trees,
as well as younger sub-canopy trees and broadleaf vegetation increasing photosynthesis as the stand recovered. At MPB-03, the trend in $A_n$ was also similar to that of growing season $P_g$, although the decline in 2009 in $A_n$ was greater than that observed with the EC data. This discrepancy in 2009 could be due to the low sampling frequency of $A_n$. Average $A_n$ from the broadleaf vegetation, which was much more developed at MPB-03, was relatively stable during the four years; however, the large variation in the measurements made it difficult to determine any trends. The light response analysis of conifer $A_n$ also agreed well with that of $P_g$ at MPB-06, both showing an increase in the photosynthetic response to $Q$. Conifer $\alpha_L$ values were greater than values of $\alpha_p$ in 2007 and 2009 at MPB-06 but the agreement between the two was good in 2008 at both sites. In 2008 at MPB-03, conifer $A_n$ showed a strong response to $Q$, and values were the highest of the three years, agreeing well with $P_g$. A relationship between $A_n$ and $Q$ could not be determined for 2007, 2009 and 2010. During these years there was high variability in the measurements, but like $P_g$, $A_n$ decreased at high $Q$. The low $A_n$ values in 2010 were a result of measurements only being made during the drought period. Thus, both the foliar gas-exchange and NEP measurements showed the effects of water stress on photosynthesis during the 2010 growing season at MPB-03.

### 4.4.3 Interannual variability in WUE

While the surviving trees increased their $P_g$, the total amount of water transpired and evaporated from the ground surface remained rather constant, leading to an increase in growing season WUE at MPB-06. At MPB-03, growing season $E$ followed the same as pattern as $P_g$, increasing from 2007 to 2008, and then decreasing in 2009 and 2010, although the magnitude of change was much less. The higher WUE at MPB-06 was due to the lower $E$ and generally higher $P_g$
compared to MPB-03. During the drought in August 2009, WUE remained relatively high at MPB-03 because $P_g$ remained similar to previous August values despite the drop in $E$ in 2009, while in 2010, both $P_g$ and $E$ decreased in July and August, probably because the drought was more severe that year, keeping WUE similar to non-drought years. This reduction in both $E$ and $P_g$ in response to water stress is not surprising given that trees must optimize the trade off between C uptake and transpiration (Beer et al. 2009) and has been frequently observed in other forests (Ponton et al. 2006; Barr et al. 2007). As the stomata close to restrict water loss, a reduction in photosynthesis also occurs.

4.4.4 Recovery of NEP following MPB attack

Both these stands demonstrated resilience to MPB attack. The prediction that stands in the central interior of BC would quickly become C sources and remain so for several years (Kurz et al. 2008) has not proven to be true at these two contrasting sites. While MPB-06 was a moderate C source for the first two years following attack, the surviving trees and vegetation showed increased vigour in the third and fourth years resulting in an increase in $P_g$ and as a result, NEP. At MPB-03, measurements were not made until the fourth year following attack, and that year the site was also a moderate C source. While NEP was slightly positive in the following two years, the site became, as a result of drought, a C source in the seventh year (2010) after attack. While the fraction of healthy trees at MPB-06 decreased rapidly in 2007 and 2008, and almost the entire canopy had been killed at MPB-03, the surviving trees and vegetation appeared to benefit from a reduction in competition for nutrients and soil water and an increase in $Q$ reaching the lower levels of the canopy crown and understory (Mitchell et al. 1983; Waring and Pitman 1985). At MPB-06, between 2007 (prior to any loss of needles) and 2009, direct and diffuse solar
radiation transmissivity increased from 29 to 44% and 41 to 51%, respectively, while at MPB-03 solar radiation transmissivity increased from 48% in 2007 to 60% in 2009. Evidence suggests that in beetle-attacked stands nutrient levels remain similar to undisturbed stands, increasing the availability for surviving trees (Knight et al. 1991). In a clearcutting and thinning by girdling experiment where 40% of the trees were left alive, Knight et al. (1991) found that a thinned lodgepole stand retained nitrates and total nitrogen, while there was large decrease in both in the clearcut stand. Although the drop in NEP at MPB-03 appeared to be a response to drought, it may be the start of a longer term trend if the initial growth release following attack slows down. However, Berg et al. (2006) found that in spruce forests which had experienced spruce-beetle (Dendroctonus rufipennis) outbreaks, the surviving trees experienced rapid growth for decades, until the canopies began to close and competition suppressed annual growth. Thus, it seems likely the trees at these two sites will continue to experience high rates of growth until the canopies begin to close and there is more competition for light and nutrients. In both stands most of the killed trees remained standing. However, as tree fall increases and the stems, branches and roots begin to decompose, there could be a significant increase in R_e, negating any increase in NEP from the enhanced P_g. Tree fall began to occur in 2008 and 2009 (5 and 6 years after attack) and many more fell in 2010 at MPB-03, while at MPB-06 a few trees began to fall in 2009 and 2010, but not in great numbers. In Oregon, trees killed by the beetle began falling five years following death and 50% had fallen after nine years and 90% after 14 years (Mitchell and Preisler 1998). Busse (1994) reported that MPB-killed trees in Oregon took a minimum of 26 years for 50% of their wood biomass to decompose after they had fallen. They did not detect any decomposition in tree boles that were either standing or elevated above the soil surface by branches, but once the boles were in contact with the soil surface the decay was relatively rapid.
Similarly, Brown et al. (1998) reported wind-thrown lodgepole pine boles in a subalpine forest in Colorado persist on the forest floor for many decades with most of their volume intact. A 10-year-old clearcut (CC-97; see Chapter 2 for site details) located 1 km from MPB-06 still had dead branches and coarse woody debris on the ground left from when the site was harvested a decade ago, indicating the decay of the dead organic material could take many years at both these sites.

4.5 Conclusion

The logistic equation provided a consistently better description of the response of $R_e$ to $T_s$ than the exponential equation at both sites. The good agreement between $\alpha_N$ and $\alpha_P$ and between $P_{g\text{max}P}$ and $P_{g\text{max}N}$ indicates that $P_g$ and daytime $R_e$ derived using the nighttime approach, were realistic estimates of the true fluxes. Foliar gas-exchange measurements of $A_n$ validated tower-based estimates of $P_g$, with both increasing from 2007 to 2009 at MPB-06, and decreasing in response to drought in 2009 and 2010 at MPB-03. The annual C balance of both sites was strongly affected by spring NEP.

The recovery of NEP from beetle attack occurred much quicker than hypothesized, with MPB-06 and MPB-03 reaching C neutrality in the third year and fifth years after attack. The increase in NEP at both sites was due to an increase in $P_g$. Furthermore, NEP and foliar gas-exchange measurements indicated a significant increase in the photosynthetic capacity of both stands. In neither stand was there a significant increase in $R_e$ as it recovered, indicating slow decomposition of the large amounts dead organic matter. In both stands solar radiation transmissivity increased significantly from 2007 to 2009. As these stands continue to open, more light will reach the lower tree crowns and understory, enhancing the growth of the surviving
trees, seedlings and saplings, as well as shrubs, mosses and lichens. Thus, the future C status of these sites depends on the interplay between the individual responses of $P_g$ and $R_e$. 
5. Conclusions

This study has examined four years of EC data from two MPB-attacked lodgepole pine stands in the central interior of BC. The differences in the characteristics of MPB-06 and MPB-03, and the several years over which NEP was measured provided insight on the spatial and temporal effects of the MPB outbreak, and the effect of climate variability on C and water cycling in these stands. The major findings of this study are presented below.

1. The recovery of NEP from beetle attack occurred much more quickly than hypothesized at the onset of this study. MPB-06 was a moderate C source for the first two years following attack, but became a sink in the third and fourth years. MPB-03 was a moderate C source in the fourth year, had a slight C uptake in the fifth and sixth years, and, due to drought, was a C source in the seventh year after attack. The increase in NEP was due to an increase in $P_g$ from the canopy trees that survived the beetle attack, the seedlings and saplings and other understory vegetation at MPB-06, and from the canopy subalpine fir, the sub-canopy trees, the seedlings and saplings and the other understory vegetation at MPB-03. The increase in the photosynthetic capacity ($P_{g\text{max}}$) of the surviving vegetation was likely a response to the canopy transmissivity of solar radiation, as well as a reduction in competition for nutrients and soil water due to tree mortality. Foliar gas-exchange measurements of $A_n$ for canopy trees, small trees, seedling and saplings and broadleaf vegetation confirmed the increase in the $P_{g\text{max}}$ observed at stand level $P_g$, although the response varied among the stand classes.
2. Ecosystem respiration did not increase significantly in both stands, indicating slow decomposition of the large amounts of dead organic matter. Although $R_e$ did increase from a low in 2007 at MPB-03, there was not a significant increase in $R_{e10}$ values between 2007 and 2010. While $R_h$ is expected to increase in the coming years due to the decomposition of the fallen dead needles and dead roots, the killed trees will likely take several years to fall and decades to decompose. Studies in Oregon and Colorado suggest that $R_h$ will likely increase following tree fall at MPB-06 and MPB-03 due to an increase in decomposition. The increase could be small, but could be sustained for many years. Autotrophic respiration could also increase if the growth release of the stands continues, which would further augment $R_e$.

3. Drought had a major effect on NEP at MPB-03 in 2009 and 2010, as shown by reductions in both $P_g$ and $A_n$. The reduction in $P_g$ was likely due to a reduced C uptake by the subalpine fir and white spruce trees, which are drought sensitive and made up a significant fraction of the live trees at MPB-03. MPB-06 did not show the same response to drought as MPB-03, likely because it contained few non-lodgepole pine trees. As a result, if less drought tolerant trees, such as subalpine fir and white spruce become more dominant than prior to the beetle outbreak, drought could play a more important role in determining the future C balance of these stands.

4. The good agreement between $P_{g\text{max}P}$ and $P_{g\text{max}N}$ indicated that values of $P_g$ and daytime $R_e$ derived using the nighttime approach were likely representative of the actual fluxes.
Furthermore, the relatively good agreement between growing season totals of \( R_e \) and \( R_{ed} \) also provided confidence in the use of the nighttime approach to determine daytime \( R_e \).

5. NEP measurements at the site harvested in 1997 (CC-97) showed that ten years following harvesting this replanted stand remained a growing-season C source. As expected, the site harvested in 2005 (CC-05) was a significant C source during the 2007 growing season, since the stand was clearcut harvested only two years earlier. The comparison of growing season NEP from the harvested and beetle-attacked stands showed the potential consequence of the increase in forest harvesting approved by the British Columbia Ministry of Forests and Range following the beetle outbreak, which could lead to much higher C emissions over extended time periods than if stands were allowed to recover naturally.

6. Increased \( E \) from the growth release of the surviving trees and understory vegetation at MPB-06 and MPB-03 appeared to compensate for a reduction in \( E \) due to the tree mortality from beetle attack. The result was little change in \( E \) at either of these sites between 2007 and 2010. It had been predicted that the MPB outbreak in BC would significantly alter transpiration rates and thus induce changes in annual water yields. During August and September 2006, shortly after MPB-06 was first attacked, \( E \) was slightly less than the following year when 50% of the trees had been killed (Appendix 2). As evidence that the August and September 2006 measurements were representative of pre-attack stand conditions, foliar photosynthesis and stomatal conductance of attacked
trees were not significantly different than those of the non-attacked trees sampled in late August 2006 (Table 2-3). However, $\theta$ was low in 2006, which may have limited $E$.

7. The growing season WD showed both stands were water limited, even though a high proportion of the trees were dead, implying that the remaining live vegetation was consuming a significant amount of water. The variability in the WD between 2007 and 2009 was small due to little year-to-year variability in values of $E_{pot}$ and $E$ during the 15 May – 30 September period. There was no apparent increase in $D_t$ in both stands due to the beetle attack; however, if $E$ had been greater at MPB-03 prior to the beetle attack, it is possible $D_t$ has increased since then. There is no evidence for this at MPB-06, as $E$ did not change significantly in the first two years following the first year of attack, and in August and September 2006, shortly after MPB-06 was first attacked, $E$ was not higher than the following year. The large difference in growing season $D_t$ between sites was due to the similarly large difference in $P$, with MPB-03 having both higher $P$ and $D_t$.

Both of these stands were still in the early stages of recovery from beetle attack when NEP measurements were made. The future C balance of these stands will depend on the individual responses of $R_e$ and $P_g$. A modelling study by Kurz et al. (2008) predicted the cumulative impact of the BC MPB outbreak from 2000-2020 to be a net loss 270 Tg C (36 g C m$^{-2}$ year$^{-1}$) over 374,000 km$^2$ of forest, due to a decrease in net primary production ($P_n = P_g - R_a$) and an increase in $R_h$. That study predicted both the direct effects of the beetle and the additional salvage harvesting response to reduce $P_n$ from pre-outbreak values of 440 g C m$^{-2}$ year$^{-1}$ to 391 g C m$^{-2}$ year$^{-1}$ during the 2015-2018 period, after which, $P_n$ was predicted to recover. $R_h$ was
predicted to increase from 408 to 424 g C m$^{-2}$ year$^{-1}$ during the 2003 to 2007 period. These values were calculated for a much larger area than the stand level at which NEP measurements were made, and thus the two results are not directly comparable; however, they predict a different trend than observed in this study. MODIS-based estimates of $P_g$ (at a 1-km spatial resolution) over the BC MPB infestation area from 2002 to 2005 showed a decrease of 10-20% from pre-outbreak values (Coops and Wulder 2010), with more severely attacked stands experiencing a greater reduction. While NEP measurements were not made at MPB-06 or MPB-03 prior to the beetle attack, measurements made at MPB-06 shortly after the site was first attacked in 2006 were not significantly different than those made during the same period in 2007, when 50% of the trees were dead (Fig. 2-3). While it is possible the stands studied here were not representative of the MPB infestation region as a whole, it is important to note that while the EC technique provides a direct measure of NEP at the stand level, MODIS-based estimates of $P_g$ are made at a coarser spatial and temporal resolution and rely on an algorithm relating $P_g$ to the fraction of absorbed $Q$ through a radiation-use conversion efficiency term which depends on vegetation type (Running et al. 2004, Coops and Wulder 2010). The contrasts in the results of these approaches highlight the importance of continuing EC measurements at the stand scale, as well as using other techniques, such as MODIS-based and modelling approaches, to study the landscape-scale recovery from the beetle outbreak.

The results presented here indicate that the future C status of these forests is not yet clear and a number of research areas can be indentified which merit further work. EC measurements should continue at both of these stands to continue to track the recovery. The trees will fall in the coming years, which will increase the canopy transmissivity of solar radiation and enhance forest re-growth, as well as add a large supply of dead organic matter to the soil surface. Soil
respiration measurements in both control and root exclusion plots (e.g., Gaumont-Guay et al. 2008) would enable $R_c$ to be partitioned into $R_h$ and $R_a$ and the response of $R_h$ to the influx of dead organic matter (roots, needles, branches and boles) to be tracked. Foliar gas-exchange measurements should also be continued as they can play an important role in determining the recovery of various components of the stand, as demonstrated in this study. Finally, EC measurements made in healthy stands as well as other beetle-attacked stands that differ from these two, but are still representative of the infestation region, would provide important information on the variability of the impacts of the outbreak and help advance our understanding of the processes involved in this type of forest disturbance.
References


Appendix 1: Comparison of evapotranspiration in the year of and the year following the MPB attack at MPB-06

Average daily $E$ measured by eddy covariance during 1 August to 30 September was 1.91 and 2.24 mm day$^{-1}$ in 2006 and 2007, respectively (Fig. A.1). During this period $\theta$ was 0.05 m$^3$ m$^{-3}$ and 0.11 m$^3$ m$^{-3}$ in 2006 and in 2007, respectively.

Figure A.1. Evapotranspiration ($E$) at MPB-06. Bars are standard deviation.
Appendix 2: Flux footprint analysis

Flux footprint analysis was conducted following the methods of Kormann and Meixner (2001) who developed a simple analytical model to describe the crosswind integrated and crosswind-distributed footprint under all conditions of atmospheric stability.

Figure A. 2. A typical daytime source area calculated with input parameters that reflect the average conditions for July (between 10:00 – 14:00 PST) at MPB-06 in 2009. Blue and red lines are the 80 and 90% source area contours.
Figure A.3. A typical daytime source area calculated with input parameters that reflect the average conditions for September (between 10:00 – 14:00 PST) at MPB-06 in 2009. Blue and red lines are the 80 and 90% source area contours.
Figure A.4. A typical daytime source area calculated with input parameters that reflect the average conditions for July (between 10:00 – 14:00 PST) at MPB-03 in 2009. Blue and red lines are the 80 and 90% source area contours.
Figure A.5. A typical daytime source area calculated with input parameters that reflect the average conditions for September (between 10:00 – 14:00 PST) at MPB-03 in 2009. Blue and red lines are the 80 and 90% source area contours.

Table A-1. Mean July and September climate values for MPB-06 and MPB-03 used to calculate the flux source area (Figs. A.2 - A.5).

<table>
<thead>
<tr>
<th></th>
<th>MPB-06 July</th>
<th>September</th>
<th>MPB-03 July</th>
<th>September</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative humidity (%)</td>
<td>47</td>
<td>59</td>
<td>45</td>
<td>57</td>
</tr>
<tr>
<td>$T_a$ (°C)</td>
<td>20</td>
<td>15</td>
<td>22</td>
<td>16</td>
</tr>
<tr>
<td>$u$ (m s$^{-1}$)</td>
<td>2.1</td>
<td>2.9</td>
<td>2.15</td>
<td>2.4</td>
</tr>
<tr>
<td>wind direction (°)</td>
<td>200</td>
<td>218</td>
<td>175</td>
<td>232</td>
</tr>
<tr>
<td>$H$ (W m$^{-2}$)</td>
<td>250</td>
<td>127</td>
<td>266</td>
<td>133</td>
</tr>
<tr>
<td>$\lambda E$ (W m$^{-2}$)</td>
<td>110</td>
<td>77</td>
<td>129</td>
<td>100</td>
</tr>
</tbody>
</table>

$T_a$ is air temperature at 26 m, $u$ is the mean horizontal wind speed at 26 m, $H$ is the sensible heat flux and $\lambda E$ is the latent heat flux.
Appendix 3. Evapotranspiration at clearcut harvested sites

Average daily and daytime (600-1800 PST) measured $E$ during the 29 June-23 July measurement period was 3.97 and 3.16 mm day$^{-1}$ and 0.12 and 0.11 mm hour$^{-1}$ at CC-07 and MPB-06, respectively, while during the 24 July – 16 August period, average daily and daytime measured $E$ was 4.64 and 2.87 mm day$^{-1}$ and 0.14 and 0.10 mm hour$^{-1}$ at CC-05 and MPB-06, respectively (Fig. A.6). During the first and second period, average daily $Q$, $T_a$ and total rainfall as measured at MPB-06, were 460 and 405 μmol m$^{-2}$ s$^{-1}$, 16 and 14 °C and 35 and 32 mm, respectively.

Figure A.6. Evapotranspiration ($E$) at (a) MPB-06 and CC-97 and (b) MPB-06 and CC-05 during the 2007 growing season. Bars are standard deviation.
NEP values during the two measurement periods were -0.37 and -0.87 g C m\(^{-2}\) day\(^{-1}\) at CC-97 and CC-05, respectively, both slightly lower than MPB-06 values during the same period (Fig 2.10). These negative NEP values suggest that \(P_g\) was relatively low at these two harvested stands, although \(P_g\) was not estimated due to an insufficient amount of data to fit the \(R_e\) and \(P_g\) models (Eq. 4.1 and 4.2). Light response characteristics were determined using the following equation:

\[
\text{NEP} = \frac{\alpha_N Q P_{\text{max}N}}{\alpha_N Q + P_{\text{max}N}} - R_{dN}
\]

(1)

where \(\alpha_N\) is the quantum yield, \(P_{\text{max}N}\) is ecosystem photosynthetic capacity and \(R_{dN}\) is the daytime ecosystem respiration. The photosynthetic capacity of the sites was low (Fig. A.7), thus, the higher daytime \(E\) at the harvested stands was likely from evaporation from the soil surface rather than from transpiration. This was likely especially true at CC-05 which was only harvested two years before the measurements were made and only had a sparse covering of lichen and moss, as well as planted seedlings of lodgepole pine and hybrid white spruce. Had the vegetation cover been greater, the photosynthetic uptake during the day might have been higher. Under such conditions there would have probably been a higher contribution of transpiration to \(E\). Still, \(E\) was higher than expected considering the sandy soils of the site.
Figure A.7. Relationship between net ecosystem production (NEP) and photosynthetically active radiation \((Q)\) during the 2007 growing season. \(P_{\text{maxN}}, \alpha_{\text{N}}\) and \(R_{\text{dN}}\) were 3.05 \(\mu\text{mol m}^{-2}\text{s}^{-1}\), 0.025 and 1.79 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) at CC-97, and 2.74 \(\mu\text{mol m}^{-2}\text{s}^{-1}\), 0.020 and 2.24 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) at CC-05.
Appendix 4: Climate and eddy covariance measurement system design

A 32-m-tall scaffold flux tower (~2.1 m long x ~1.5 m wide) (Fig.A.8) was erected at each of MPB-06 and MPB-03 in July 2006 and March 2007, respectively (Fig. A.8). Flux and climate measurements began on 18 July 2006 and 20 March 2007 at the respective sites. 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 turbulent fluctuations of CO$_2$ and H$_2$O were measured using an open-path infrared gas analyzer (IRGA) (model LI-7500, LI-COR, Inc, Lincoln, Nebraska,) (Fig. A.9). At both sites, EC sensors were mounted at the height of 26 m, which was ~8 m and ~6 m above the top of the canopy at MPB-06 and MPB-03, respectively. Signals were measured with a data logger (CSI, model CR1000) with a synchronous-device-for-measurement (SDM) connection (Fig. A.10). High frequency (10 Hz) data were stored on a compact flash card that was replaced every 2-4 weeks. During the winter the sampling rate was reduced to 5 Hz to conserve power. Half-hourly covariances and other statistics were calculated on the data logger and transmitted with climate data daily by cell phone to the laboratory. Following Webb et al. (1980), $F_c$ and $\lambda E$ were calculated as the product of the dry air density and the covariances of vertical velocity and CO$_2$ mixing ratio and vertical velocity and water vapour mixing ratio, respectively, measured at 10 Hz (see Appendix 7).
Figure A.8. Diagram of the flux tower design at MPB-06 and MPB-03.

Figure A.9. Sonic anemometer, infrared gas analyser (IRGA) and fine-wire thermocouple (at 26-m height) at MPB-06.
Climate variables measured included above-canopy upwelling and downwelling shortwave and longwave radiation (model CNR1, Kipp and Zonen B.V., Delft, The Netherlands) (at 30-m height) and above-canopy upwelling and downwelling (30-m height), and below-canopy downwelling (3-m height) 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 (model 05103 R.M. Young Inc., Traverse City, MI), air temperature and relative humidity (model HMP45C, Vaisala Oyj, Helsinki, Finland) at the 25-m height, 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 (model CS616, CSI) at the 0-10 cm and 30-50 cm depths at MPB-06 and (model EC-5, Decagon Devices Inc, Pullman, Washington) at the 10-cm, 20-cm and 50-cm depths at MPB-03. Climate instruments were connected to a data logger (CSI, model CR1000) via a multiplexer (CSI, model AM25T) (Fig.A.8). Meteorological measurements were made every second and 30-min average values calculated.
The systems were powered using 3 100-W solar panels (CTI-130, Carmanah Technologies Corp., Victoria, BC) (Fig. A.11) with an 800-Ah battery unit consisting of 8 absorbent glass mat batteries (EX-1000, Carmanah Technologies Corp.) stored in an insulated box (63.5 cm tall, 122 cm wide and 61 cm deep) (2448, Greenlee Textron, Inc., Providence, Rhode Island) (Fig. A.12). The system consumed 1A continuous current (12 W), and 24-Ah during per day. 1 hour of summer charging was enough to power the system for a full day. The reserve provided > 20 days of power without any additional solar charging. During the winter, when the power drained below 11.7 V, due to a lack of solar charging, the climate program turned off the IRGA, which reduced the power consumption to ~0.2 A. When the batteries reached 14.4 V from solar recharging, the IRGA was automatically switched back on. As the open-path IRGA often does not make reliable measurements under adverse weather conditions (raining, snowing or ice or condensation on the instrument), during such times, the IRGA was often manually switched off to conserve power. The IRGA was switched back on when weather conditions were generally clear and accurate measurements could be made. Although insulated, the temperature inside the power box during the winter would occasionally reach a minimum of -10 °C, which reduced the capacity of the batteries. At a flux tower similar to MPB-06 and MPB-03, located near Summit Lake, ~30 km south of MPB-03, burying the power box to a soil depth of 30 cm and covering it with an insulated plywood box kept wintertime temperatures inside the box several degrees warmer than at MPB-06 and MPB-03 (temperature was not measured inside the box at Summit Lake). This increased the battery capacity at this site and enabled the IRGA to run continuously through the winter.
Figure A.11. MPB-06 32-m-tall tower with eddy covariance (EC) and net radiometer booms and three solar panels.
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 (Fig. A.13). CC-97 is a 10-year-old clearcut, which was left to naturally regenerate. The same 0.25-m x 3-m tall triangular tower was used at each site, first at CC-05 and then at CC-97. Measurements included the same EC instrumentation as used on the two main towers as well as above-canopy upwelling and downwelling shortwave and longwave radiation (model CNR1, Kipp and Zonen B.V.) (at 3-m height), air temperature and relative humidity (model HMP45C, Vaisala Oyj) at the 3-m height, soil temperature (chromel-constantan 30 gauge thermocouple wire) at depths of 2, 10, 20 and 50 cm, soil heat flux (3 heat-flux plates) at a depth of 5 cm and water content (model EC-5, Decagon Devices Inc, Pullman, Washington) at the 5-cm, 15-cm and 30-cm depths. EC and climate signals were measured with a data logger (CSI, CR5000). The system was powered using a 100-W solar panels (CTI-130, Carmanah...
Technologies Corp.) with an 100-Ah battery unit consisting of 1 absorbent glass mat battery (EX-1000, Carmanah Technologies Corp.).

Figure A.13. Eddy covariance and climate measurement tower at a) CC-97 and b) CC-05 during the 2007 growing season.
Appendix 5: Canopy photographs

Figure A.14. MPB-06 canopy photographs.
Figure A.15. MPB-03 canopy photographs.
Appendix 6: Test of significance

In the ecosystem respiration and light response analysis the fitted models (Eq. (1) and (3)) were compared to null models (containing only an intercept parameter) with a likelihood ratio test (Seber and Wild 2003). *P*-values were determined by comparing the change in the log likelihood between the full and null models to a chi-squared distribution with degrees of freedom equal to the difference in the number of model parameters. To test for changes in the models over time, models with parameters being constant across years were compared to fitting separate models to each year's data using a likelihood ratio test. The log likelihood for the temporally constant model was compared to the sum of the log likelihoods for the separate models, with the difference compared to a chi-squared distribution with degrees of freedom equal to the number of extra parameters used when fitting separate models for each year.

Matlab code for determining significance in $R_c$ between years at MPB-06:

```matlab
%% MPB_NEP_annual;
MPB1_ts = [siteDataMPB1_2007.ts; siteDataMPB1_2008.ts; siteDataMPB1_2009.ts; siteDataMPB1_2010.ts];
MPB1_R_meas = [siteDataMPB1_2007.erm; siteDataMPB1_2008.erm; siteDataMPB1_2009.erm; siteDataMPB1_2010.erm];
% FCRN R Model
fTs2R = inline(['b(1)./(1+exp(b(2)*(b(3)-Ts)))'],'b','Ts');
bRGuess = [20 0.10 20];
iReg = find(~isnan(MPB1_R_meas+MPB1_ts));
nReg = length(iReg);
[bR,b,c] = FCRN_function_fit_rmse(fTs2R,bRGuess,MPB1_R_meas(iReg),[],MPB1_ts(iReg));
deviance_combined= n * (log(c.SSE) - log(n))
R_analysis;

n1=length(find(siteData(1).iReg(:,1) >0));
n2=length(find(siteData(1).iReg(:,2) >0));
n3=length(find(siteData(1).iReg(:,3) >0));
n4=length(find(siteData(1).iReg(:,4) >0));
```
deviance\_separate = n1 * (log(siteData(1).SSE(1)) - log(n1)) + n2 * (log(siteData(1).SSE(2)) - log(n2)) + n3 * (log(siteData(1).SSE(3)) - log(n3)) + n4 * (log(siteData(1).SSE(4)) - log(n4))

lr = deviance\_combined - deviance\_separate
1 - chi2cdf(lr, 12)

% 2007 and 2008
MPB\_NEP\_annual;
MPB1\_ts = [siteDataMPB1\_2007.ts; siteDataMPB1\_2008.ts];
MPB1\_R\_meas = [siteDataMPB1\_2007.erm; siteDataMPB1\_2008.erm];

% FCRN R Model
ftS2R = inline(['b(1)./(1+exp(b(2)*(b(3)-Ts)))'], 'b', 'Ts');
bRGGuess = [20 0.10 20];
iReg = find(~isnan(MPB1\_R\_meas+MPB1\_ts));
nReg = length(iReg);

[bR,b,c] = FCRN\_function\_fit\_rmse(ftS2R, bRGGuess, MPB1\_R\_meas(iReg), [], MPB1\_ts(iReg));

deviance\_combined = n * (log(c.SSE) - log(n))

R\_analysis;
n1 = length(find(siteData(1).iReg(:,1) >0));
n2 = length(find(siteData(1).iReg(:,2) >0));
n3 = length(find(siteData(1).iReg(:,3) >0));
n4 = length(find(siteData(1).iReg(:,4) >0));

% compare 2007 with 2008
lr = deviance\_combined - (n1 * (log(siteData(1).SSE(1)) - log(n1)) + n2 * (log(siteData(1).SSE(2)) - log(n2))
1 - chi2cdf(lr, 4)
Appendix 7: Eddy covariance data logger program and flux calculations

The program for the EC data logger (CSI CR1000) was obtained from Laval University and, modifications were made by Joe Kidston, Zoran Nesic, Dominic Lessard and Mathew Brown. It calculated half-hourly means, variances and covariances of CO₂ and H₂O densities, u, v, w, Tₐ (from sonic anemometer and fine-wire thermocouple) and IRGA and sonic anemometer diagnostics. These half-hourly data were transmitted to UBC daily and used to assess EC system performance.

Variances and covariances calculated by the data logger program were:

```
'Public cov_out(21)
Public cov_out(15)
Alias cov_out(1) = CO2_CO2
Alias cov_out(2) = CO2_H2O
Alias cov_out(3) = CO2_u
Alias cov_out(4) = CO2_v
Alias cov_out(5) = CO2_w
Alias cov_out(6) = H2O_H2O
Alias cov_out(7) = H2O_u
Alias cov_out(8) = H2O_v
Alias cov_out(9) = H2O_w
Alias cov_out(10) = u_u
Alias cov_out(11) = u_v
Alias cov_out(12) = u_w
Alias cov_out(13) = v_v
Alias cov_out(14) = v_w
Alias cov_out(15) = w_w
Alias cov_3_out(1) = Ts_Ts
Alias cov_3_out(2) = Ts_u
Alias cov_3_out(3) = Ts_v
Alias cov_3_out(4) = Ts_w
Alias cov_4_out(1) = Tc_Temp_Tc_Temp
Alias cov_4_out(2) = Tc_Temp_u
Alias cov_4_out(3) = Tc_Temp_v
Alias cov_4_out(4) = Tc_Temp_w
```

The EC program:
```
'=================================================================
```
' Program starts here
'============================================================================

BeginProg
  'Calculate fluxes and save raw data on compile
  'Set all csat3 and irga variables to NaN
  For j = 1 To 5
    csat_in(j) = NaN
  Next j
  For j = 1 To 11
    irga_in(j) = NaN
  Next j

  ' Measure CSAT and LI-7500 data
  SDMSpeed (sdm_par)
  Scan (scan_interval,mSec,15,0)
  CSAT3 (csat_in(1),1,CSAT_SDM,CSAT_CMD,csat_opt)
  CS7500 (irga_in(1),1,IRGA_SDM,IRGA_CMD)

  ' Measure fine wire thermocouple
  PanelTemp (ref_temp,250)
  TCDiff (tc_temp(),3,mV2_5,1,TypeE,ref_temp,True,200,250,1.0,0)
  TCDiff (tc_temp(),2,mV2_5,1,TypeE,ref_temp,True,200,250,1.0,0)

  ' synchronization for Carmen's experiment
  VoltDiff (tc_temp(3),1,mV5000,3,True,0,250,1.0,0)

  RealTime (real_time)
  Hours_Tmp=Hours*100
  Hours_Mins=Hours_Tmp+Minutes
  rmsec=real_time(7)/1000000
  rsec=real_time(6)+rmsec

  ' Load tables containing raw high and low frequency data and system diagnostics
  CallTable RawHF
    CurrentRecord = RawHF.record
    HHourRecords = CurrentRecord - OldRecord

  ' Set file marks to break up high and low frequency data into 30 min files
  If (real_time( 5) = 29 AND real_time(6) = 59 AND real_time(7) >= 900000)
    FileMark(RawHF)
    OldRecord = CurrentRecord
  EndIf
  If (real_time(5) =59 AND real_time(6) = 59 AND real_time(7) >= 900000)
    FileMark(RawHF)
    OldRecord = CurrentRecord
  EndIf
' Load array used to calculate covariances

cov_in(1) = CO2
cov_in(2) = H2O
cov_in(3) = u_wind
cov_in(4) = v_wind
cov_in(5) = w_wind
cov_3_in(1)=Tsonic
cov_3_in(2)=u_wind
cov_3_in(3)=v_wind
cov_3_in(4)=w_wind

cov_4_in(1)=Eddy_Tc
cov_4_in(2)=u_wind
cov_4_in(3)=v_wind
cov_4_in(4)=w_wind

'=======================================
'Sample low frequency sensors
'=======================================
'Get info from status table
Battery(batt_volt)
PCcard_free=Status.CardBytesFree(1,1)
memory=Status.MemoryFree(1,1)
watchdog=Status.WatchdogErrors(1,1)

'************************Calculate Fluxes***************************
CallTable comp_cov
GetRecord(cov_out(1),comp_cov,1)
CallTable Tscov
GetRecord(cov_3_out(1),Tscov,1)
CallTable Tc_cov
GetRecord(cov_4_out(1),Tc_cov,1)
CallTable flux_30m
CallTable diag30m

'Add file marks to divide flux table into daily files
If (real_time(4) = 23 AND real_time(5) = 59 AND real_time(6) = 59 AND real_time(7) >=
900000)
  FileMark(flux_30m)
EndIf
NextScan
EndProg

Below is the Matlab code used to calculate coordinate rotations, convert CO2 and H2O densities
to mixing ratios, and calculate fluxes (reported in this thesis) from high frequency data. This
code comes from sub-functions of new_calc_and_save.m in the Biometeorology and Soil Physics Matlab library.

Coordinate rotation:

```matlab
function [Eddy_HF_data_rot] = fr_rotatn_hf(Eddy_HF_data,angles)
%   [Eddy_HF_data] = fr_plot_raw(Eddy_HF_data,angles)
% %
% Rotates the high frequency data assuming that the first the column in
Eddy_HF_data
% contain u v w
% % Do the rotation
if isnan(angles(3))
ce = cos(pi/180*angles(1));
se = sin(pi/180*angles(1));
ct = cos(pi/180*angles(2));
st = sin(pi/180*angles(2));
Eddy_HF_data_rot = Eddy_HF_data;
Eddy_HF_data_rot(:,1) = Eddy_HF_data(:,1)*ct*ce + Eddy_HF_data(:,2)*ct*se + Eddy_HF_data(:,3)*st;
Eddy_HF_data_rot(:,2) = Eddy_HF_data(:,2)*ce - Eddy_HF_data(:,1)*se;
Eddy_HF_data_rot(:,3) = Eddy_HF_data(:,3)*ct - Eddy_HF_data(:,1)*st*ce - Eddy_HF_data(:,2)*st*se;
else
ce = cos(pi/180*angles(1));
se = sin(pi/180*angles(1));
ct = cos(pi/180*angles(2));
st = sin(pi/180*angles(2));
cc = cos(pi/180*angles(3));
sb = sin(pi/180*angles(3));
means2(:,1) = Eddy_HF_data(:,1)*ct*ce + Eddy_HF_data(:,2)*ct*se + Eddy_HF_data(:,3)*st;
means2(:,2) = Eddy_HF_data(:,2)*ce - Eddy_HF_data(:,1)*se;
means2(:,3) = Eddy_HF_data(:,3)*ct - Eddy_HF_data(:,1)*st*ce - Eddy_HF_data(:,2)*st*se;
Eddy_HF_data_rot = Eddy_HF_data;
Eddy_HF_data_rot(:,1) = means2(:,1);
Eddy_HF_data_rot(:,2) = means2(:,2)*cc + means2(:,3)*sb;
Eddy_HF_data_rot(:,3) = means2(:,3)*cc - means2(:,2)*sb;
End

Mole fractions to mixing ratios:
if strcmp(configIn.Instrument(configIn.System(systemNum).Instrument(2)).Type,'7000')
chi = EngUnits(:,6);
EngUnits(:,5) = EngUnits(:,5)./(1-chi/1000);
EngUnits(:,6) = EngUnits(:,6)./(1-chi/1000);
configIn.System(systemNum).ChanUnits(5:6) = {'\mu mol/mol dry air','mmol/mol dry air'};
```

Flux calculations:

% Sensible heat calculations

\[
\text{Cp}_{\text{moist}} = \text{sp\_heat(h}_2\text{o\_bar)}; \quad \% \text{specific heat of moist air}
\]

\[
\text{SensibleSonic} = wT \times \rho_{\text{moist\_air}} \times \text{Cp}_{\text{moist}}; \quad \%
\]

Sensible heat (Sonic)

\[
\text{Eddy\_results} = \text{setfield(Eddy\_results,(1),char(rotation)},... \]
\[
\text{char(detrendType),}'\text{Fluxes}','Hs',\text{SensibleSonic});
\]

\[
\text{SensibleTc1} = wTc1 \times \rho_{\text{moist\_air}} \times \text{Cp}_{\text{moist}}; \quad \%
\]

Sensible heat (Tc1)

\[
\text{Eddy\_results} = \text{setfield(Eddy\_results,(1),char(rotation)},... \]
\[
\text{char(detrendType),}'\text{Fluxes}','Htc1',\text{SensibleTc1});
\]

\[
\text{SensibleTc2} = wTc2 \times \rho_{\text{moist\_air}} \times \text{Cp}_{\text{moist}}; \quad \%
\]

Sensible heat (Tc2)

\[
\text{Eddy\_results} = \text{setfield(Eddy\_results,(1),char(rotation)},... \]
\[
\text{char(detrendType),}'\text{Fluxes}','Htc2',\text{SensibleTc2});
\]

% CO2 flux calculations

\[
\text{convC} = \text{mol\_density\_dry\_air}; \quad \% \text{convert umol co2/mol dry air} \rightarrow \text{umol co2/m3 dry air (refer to Pv = nRT)}
\]

\[
\text{Fc} = wc \times \text{convC}; \quad \% \text{CO2 flux (umol m}^{-2} \text{ s}^{-1})
\]

\[
\text{Eddy\_results} = \text{setfield(Eddy\_results,(1),char(rotation)},... \]
\[
\text{char(detrendType),}'\text{Fluxes}','Fc',\text{Fc});
\]

% P energy calculation

\[
\text{Penergy} = -10.47 \times wc; \quad \% \text{Penergy}
\]

\[
\text{Eddy\_results} = \text{setfield(Eddy\_results,(1),char(rotation)},... \]
\[
\text{char(detrendType),}'\text{Fluxes}','MiscVariables','Penergy',\text{Penergy});
\]

% Latent heat calculations

\[
\text{convH} = \text{mol\_density\_dry\_air} \times \text{Mw}/1000; \quad \% \text{convert mmol h2o/mol dry air} \rightarrow \text{g h2o/m3 (refer to Pv = nRT)}
\]

\[
\text{wh\_g} = \text{wh} \times \text{convH}; \quad \% \text{convert m/s(mmols/mol)} \rightarrow \text{m/s(g/m}^\text{3})
\]

\[
\text{LELicor} = \text{wh\_g} \times L_v; \quad \% \text{LE LICOR}
\]

\[
\text{Eddy\_results} = \text{setfield(Eddy\_results,(1),char(rotation)},... \]
\[
\text{char(detrendType),}'\text{Fluxes}','LE\_L',\text{LELicor});
\]