Multiscale observations of snow accumulation and peak snowpack following widespread, insect-induced lodgepole pine mortality

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ABSTRACT
Seasonal snowpack in forested lands is the primary source of fresh water in western North America, where mountain pine beetle (MPB) infestation has resulted in rapid and extensive tree die-off. Forests significantly influence the amount and spatial distribution of peak seasonal snowpack, but the impacts of large-scale tree mortality on the processes controlling peak snowpack are not well understood. We evaluate the effects of widespread tree mortality on winter snow accumulation and peak seasonal snowpack across multiple spatial scales and several levels of MPB impact in the Central Rocky Mountains. Observations for winters 2010 and 2011 include continuous snow depths in 20 plots, distributed snow surveys at peak accumulation and climate observations above and below canopy including precipitation, temperature, humidity, wind and shortwave radiation. Stable water isotopes were observed for fresh snowfall and for snowpack. Plot-scale snowfall observations showed 20% lower interception (p < 0.05) in grey-phase stands (needles lost) than in unimpacted stands. However, distributed snow surveys found no differences in peak seasonal snow water equivalent between unimpacted and grey-phase stands. Water isotopes of snowpack from MPB-killed stands indicated kinetic fractionation; enriched values demonstrated higher winter snowpack sublimation in MPB-killed forest. Following MPB infestation, reduced canopy sublimation of intercepted snow appeared to be compensated by increased snowpack sublimation, consistent with observations of higher snowpack insolation. Consequently, the effects of widespread tree mortality on peak seasonal snowpack, which is crucial for downstream water resources, will be influenced by compensation for lower interception by higher snowpack sublimation. Copyright © 2012 John Wiley & Sons, Ltd.

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INTRODUCTION
Snow dominates the water cycle inputs to the semi-arid western portions of Canada and the USA (Connaughton, 1935; Troendle, 1983; Bales et al., 2006) and is the primary control on the fluxes of energy and biogeochemicals. More than 60 million people in the Western United States rely on montane snowmelt as a primary source of water (Bales et al., 2006). Most of this water is derived from forested areas, where accumulation and ablation of snow are strongly controlled by vegetation (Troendle and King, 1987; Jost et al., 2007; Musselman et al., 2008; Rinehart et al., 2008; Molotch et al., 2009; Veatch et al., 2009; Varhola et al., 2010). Vegetation influences how montane catchments capture, store, partition and release snow water, yet the impacts of insect-induced tree mortality on snow–vegetation interactions are not well understood, especially against the backdrop of changing or extreme climate (Varhola et al., 2010). Many seasonally snow-covered areas in western North American have recently suffered rapid and extensive tree die-off caused by mountain pine beetle (MPB; Dendroctonus ponderosae; Kurz et al., 2008; Raffa et al., 2008). Although MPB is endemic to the region, its activity has reached unprecedented levels during the last 15 years. In 2010, MPB infested 2.77 million hectares of forests, accounting for 75% of all US tree mortality related to insects and other pathogens (USFS 2012). Causes of the present epidemic are thought to include historically high stocks of mature pine trees following a century of fire suppression, increasing beetle survival and reproduction rates due to longer summers and warmer winters (Mitton and Ferrenberg, 2012), and greater tree susceptibility due to water stress from a warmer and dryer climate (Ayres and Lombardo 2000; Logan et al. 2003; Logon et al., 2003; Hicke et al., 2006). Understanding the effects of insect-induced changes to canopy structure on snow accumulation and peak seasonal snowpack is critical to effective management of forest and water resources (Troendle, 1983; Troendle and King, 1987) and the prediction of ecosystem response and recovery following MPB (Edburg et al., 2012).

Forest canopy controls snowpack through interception, sublimation of snow from the canopy, attenuation of wind speeds, creation of wind eddies and alteration of the radiation
balance. A variable fraction of snowfall is retained in the forest canopy (Schmidt and Troendle, 1992; Hedstrom and Pomeroy, 1998; Link and Marks, 1999), and sublimation of this canopy snow may reduce peak seasonal snowpack by 25–45% in mature pine forest (Pomeroy et al., 1998). Studies by Boon (2012) and Pugh and Small (2011) attributed greater peak seasonal snowpack under grey phase than living lodgepole forest to reduced sublimation of intercepted snow. Modelling studies have predicted increased peak water yield following MPB infestation using model equations that increased snowpack as interception (modelled as a function of canopy density) was decreased (Bewley et al., 2010; Mikkelsen et al., 2011, Pomeroy et al., 2012), reinforcing the expectation of reduced interception as a dominant response. Vegetation interacts with wind to affect spatial distribution of snow through development of eddies across the top of forest canopy that may preferentially deposit snow in canopy gaps (Golding and Swanson, 1978) and by altering redistribution of snow on the ground (Troendle, 1983). Canopy also attenuates wind (Bergen, 1971), thus offering protection against wind scour (e.g. Winstral and Marks, 2002) and sublimation (Bernier, 1990). A forest canopy protects snowpack from ablation by attenuating solar radiation and reducing near-surface wind speeds (Link and Marks, 1999; Lopez-Moreno and Stahli, 2008; Musselman et al., 2008; Molotch et al., 2009; Veatch et al., 2009). A significant body of literature indicates the importance of shading from solar radiation in determining snowpack ablation both during winter and spring melts (e.g. Anderson, 1956; Lopez-Moreno and Stahli, 2008; Musselman et al., 2008; Rinehart et al., 2008; Molotch et al., 2009; Veatch et al., 2009).

Because canopy can both prevent snowfall from reaching the snowpack and protect the snowpack from ablation (Musselman et al., 2008; Rinehart et al., 2008; Molotch et al., 2009; Veatch et al., 2009; Pugh and Gordon, 2012), reduced canopy density following MPB tree mortality is likely to lead to compensatory process changes (Somor et al., in preparation). Prior studies of canopy removal by harvest (e.g. Hoover and Leaf, 1967; Gary, 1974; Golding and Swanson, 1978, 1986; Troendle, 1983; Troendle and King, 1987; Woods et al., 2006) found more snow water equivalent (SWE) in harvested clearings than in nearby forest plots for clearing sizes ranging up to about 5–8 times the mean surrounding tree height. However, these studies reported a mix of increased and unchanged SWE at the stand or hillslope scales, leading to the ideas that (1) increases in clearings were supplied by decreases in undisturbed forest (Gary, 1974; Golding and Swanson, 1986) and (2) reduced interception could be compensated by increased sublimation (Troendle, 1983; Golding and Swanson, 1986; Troendle and King, 1987). Differences were observed at plots scales but sometimes not at larger scales, demonstrating the importance of multiscale observation. Understanding snow process responses (e.g. interception reduction) may require observation at the scale of individual trees to plot, but understanding larger-scale snowpack response to canopy reduction calls for observations across multiple stands. Insect-induced mortality may have some similar effects to harvest, but it differs because much of the tree remains intact and may continue to intercept snow, attenuate wind and alter radiation fluxes (Edburg et al., 2012).

Prediction of hydrologic response to forest mortality should cover a range of scales allowing process-based understanding to inform the larger-scale impacts on ecosystem function and water resource availability. Studies comparing adjacent stands within a given site are often hampered by lack of stands with similar structure but differing MPB impact (Pugh and Small, 2011), but comparison of multiple sites requires consideration of topography, forest structure and climate forcing. To address the effect of MPB tree mortality on peak seasonal snowpack, we used nested multiscale observations of snow depth and SWE, onsite climate data and isotopic tracers of hydrologic partitioning to answer two questions: (1) How does MPB tree mortality affect the balance of canopy-mediated snow processes influencing peak SWE? and (2) What is the net effect of MPB tree mortality on peak SWE at the scale of small headwater catchments?

**METHODS**

Two sites with varying levels and timing of forest mortality from MPB infestation were studied during winters 2010 and 2011, with observations organized in a nested fashion at multiple spatial scales (Figure 1). Each study site comprised a small headwater catchment of approximately 1 km² containing one or more precipitation gauges and a tower for above-canopy climate observation. Within each site, forest stands were categorized by their level of MPB mortality and year of initial major infestation (e.g. Unimpacted, MPB-2007). Stand-scale observations included canopy characteristics, snow depth, SWE, snow chemistry and subcanopy wind speed. Within three stands chosen for intensive study from the Unimpacted, MPB-2008 and MPB-2007 types, 20 plots were instrumented for continuous observation of snow depth and subcanopy temperature, humidity and downward shortwave radiation.

**Study sites**

Two study sites were identified in late 2009 along the Front Range of the Central Rocky Mountains in northern Colorado and southern Wyoming (Figure 1), a region of the USA severely affected by MPB during the present epidemic (since ca 1996). Sites with adjacent uninfested and infested stands of otherwise similar characteristics were not found. The sites at Chimney Park, WY and Niwot, CO offered observations of meteorology and snowpack from prior and concurrent studies. To isolate the effects of vegetation mortality from those of topography, we selected headwater catchments with similar elevation (2750–3000 m) and gentle terrain (Table 1). Both sites have annual mean precipitation of about 800 mm and mean annual air temperatures of 1–3 °C. Forest characteristics and MPB infestation status were obtained from the Niwot Ameriflux project (http://ameriflux.ornl.gov), from H. Barnard (personal communication) and from ground-based vegetation surveys conducted annually since 2008 at
Chimney Park. Although of similar species and age, the Chimney Park stands had larger mean tree height and diameter at breast height as well as lower stem density than the Niwot stands (Table 1).

The Niwot site (Figure 1) is within the University of Colorado’s Long-Term Ecological Research site, 8 km east of the continental divide and 50 km northwest of Denver. It includes an above-canopy Ameriflux tower (Blanken and Monson, 2012) and a Natural Resources Conservation Service snowpack telemetry (SNOTEL) station (NRCS, 2012) all within approximately 400 m distance and 30 m elevation of the forest stands studied. Forest cover is natural regrowth following logging a century ago, dominated by 97% lodgepole pine (Pinus contorta) with a few individuals of Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa). MPB activity was not observed within the forest stands studied, and these were labelled Unimpacted.

The Chimney Park site (Figure 1) is in the Medicine Bow National Forest 110 km north of the Niwot site and 50 km southwest of Laramie, WY. It includes a tower with above-canopy observations of wind velocity, temperature, humidity and shortwave radiation, which began collecting data in January 2009. The site is primarily an even-aged forest of lodgepole pine (82%) with small amounts of aspen (Populus tremuloides, 11%), Douglas fir (Pseudotsuga menziesii, 5%) and Engelmann spruce (1%) (Reed et al., in preparation), with the last stand-replacing fire 135 years ago (Knight et al., 1985). Chimney Park experienced extensive MPB infestation beginning in 2007, with approximately 75% of mature lodgepole pine killed by 2011. MPB travel to new host trees during summer, where they introduce a blue stain fungus that inhibits sap flow and usually kills the tree within several weeks to months (Yamaoka et al., 1990). Dead trees retain their needles for 1–3 years (Wulder et al., 2006), termed the red phase of mortality. Once the needles are lost, trees are said to be in the grey phase of mortality, which lasts 5–20 years or more, until the stems fall. Study stands at Chimney Park were categorized by their year of initial MPB infestation including MPB-2007, MPB-2008 and MPB-2009. The MPB-2007 and MPB-2008 stands experienced approximately 75% mortality, nearly all in the first year of infestation. Most dead trees (75% of total) in the MPB-2007 stand were in the grey phase during the entire study. Most dead trees in the MPB-2008 stand (75% of total) were in the red phase during the first winter of the study (2010) but lost their needles and progressed to the grey phase in the second winter (2011). The MPB-2009 stand experienced 10% mortality before winter 2010 and an additional 15% by winter 2011.

Winter climate
We defined the winter snow accumulation season as lasting from the first day of persistent snow cover on the Niwot SNOTEL station 663 (NRCS, 2012) in mid-October to our 7–9 April peak accumulation surveys, conducted approximately 1 week prior to the snowpack becoming isothermal.

Table 1. Mean characteristics of the two sites and four stand types.

<table>
<thead>
<tr>
<th>Site</th>
<th>Stand</th>
<th>Elevation (m)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Age (yr)</th>
<th>Stem density (per ha)</th>
<th>Tree height (m)</th>
<th>DBH (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niwot, CO</td>
<td>Unimpacted</td>
<td>3000</td>
<td>40° 02’</td>
<td>-105° 33’</td>
<td>100</td>
<td>3900</td>
<td>11.4</td>
<td>12.1</td>
</tr>
<tr>
<td>Chimney Park, WY</td>
<td>MPB-2009</td>
<td>2750</td>
<td>41° 04’</td>
<td>-106° 07’</td>
<td>90–110</td>
<td>2250</td>
<td>14.0</td>
<td>14.2</td>
</tr>
<tr>
<td></td>
<td>MPB-2008</td>
<td>2750</td>
<td>41° 04’</td>
<td>-106° 07’</td>
<td>90–110</td>
<td>1160</td>
<td>17.6</td>
<td>20.1</td>
</tr>
<tr>
<td></td>
<td>MPB-2007</td>
<td>2750</td>
<td>41° 04’</td>
<td>-106° 07’</td>
<td>90–110</td>
<td>1310</td>
<td>17.0</td>
<td>19.9</td>
</tr>
</tbody>
</table>

DBH, diameter at breast height; MPB, mountain pine beetle.
and commencing to melt. We will refer to this snow accumulation period as ‘winter’ hereafter. We characterized winter climate at each site with above-canopy observations of temperature, vapour pressure deficit, wind and incident shortwave radiation (Table 2). Wind speed at the Niwot site was corrected to the same height above canopy as the Chimney Park observations (3.7 m above canopy) using a neutral atmosphere logarithmic profile with zero-plane displacement height of two-thirds the mean tree height and a roughness length of 1.1 m. Open-area winter precipitation observations were made at the Niwot SNOTEL supplemented with data from a nearby (~200 m) NOAA Climate Reference Network site when necessary. Chimney Park precipitation was observed by a cluster of weighing-type gauges located 250 m west of the site meteorological tower in a small forest clearing similar in dimension to the clearing at the Niwot SNOTEL. These different instruments within the cluster were bias-corrected to a Geonor T-200B reference weighing precipitation gauge at the site.  

**Intensive study plots**

During February and March 2010, digital Judd ultrasonic snow depth sensors (Judd Communications, Salt Lake City, Utah, USA) were installed at 20 plots. Eight sensors were located in an Unimpacted stand, six in an MPB-2008 stand and six in an MPB-2007 stand. In each stand type, half of the depth sensors were located under tree canopy, whereas the others were located in canopy gaps. Gaps were defined by open areas with widths approximately 1/4 to 1/2 of the mean surrounding tree height. Although the timing of precipitation at the two sites was correlated at better than 99% (p < 0.0001), Chimney Park received 10–14% more precipitation. Depth records were therefore normalized to the mean snow depth in gaps from each stand at peak accumulation to account for this difference; this approach treats gap sensors as experimental controls for analysis of new snowfall. Sensor power was lost for portions of the winter in the MPB-2007 and MPB-2008 plots (Figure 2), and manual snow depth observations were made to supplement the record at the MPB-2007 plots on the days bracketing the 2011 snow survey. New snowfall inputs during each storm (mean value in gaps) were quantified for each stand, with storms defined as periods of precipitation rate ≥1.0 mm h⁻¹ (water equivalent) and total precipitation ≥5 mm (water equivalent).

Subcanopy climate observations included temperature, humidity, incoming shortwave radiation and wind speeds. Silicon cell pyranometers (model SP, Apogee Instruments, Logan, Utah, USA) measured downward shortwave radiation below the canopy at a height of 2 m in all 20 plots (half under canopy and half in gaps) beginning in April 2010. These sensors directly sample wavelengths from 300 to 1100 nm, the spectral range containing 80–90% of solar radiation reaching the land surface, and estimate the remaining 10–20% of radiation in wavelengths of 1100–2800 nm. Vegetation or high humidity can bias incoming shortwave radiation towards shorter wavelengths, reducing the accuracy. Power loss issues disrupted observation in the MPB-2007 plots, but comparisons were made between the Unimpacted and MPB-2008 plots for winter 2011. Temperature and relative humidity sensors (model EM50, Decagon Devices, Pullman, Washington, USA) were installed in all 20 plots at 2 m height in April 2010. These were gill-shielded and aspirated with solar-powered fans. Two subcanopy (3 m) sonic anemometers (model CSAT3, Campbell Scientific, North Logan, UT) were deployed from 16 April 2011 to 29 July 2011 in the MPB-2009 stand near the Chimney Park MET tower, and another two were deployed in Unimpacted study plots to investigate the effects of MPB mortality on wind attenuation. Above-canopy winds were on average 13% lower at each site during this spring/summer season than during the two winters of the study.

**Snow surveys at peak accumulation**

Snow surveys were conducted on 7–9 April 2010 and 2011 (Figure 1) over small headwater catchments including 5–6 stands at each site (somewhat less area was surveyed at Niwot

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Winter precipitation (mm)</th>
<th>Temperature (°C)</th>
<th>Wind speed (m s⁻¹)</th>
<th>Vapour pressure deficit (kPa)</th>
<th>(R_{\text{sw}}) (W m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>NWT above canopy</td>
<td>379</td>
<td>−3.0 (4.8)</td>
<td>3.3 (1.7)</td>
<td>0.26 (0.19)</td>
<td>158 (80)</td>
</tr>
<tr>
<td></td>
<td>CP above canopy</td>
<td>433</td>
<td>−3.0 (4.5)</td>
<td>3.2 (1.1)</td>
<td>0.24 (0.17)</td>
<td>165 (80)</td>
</tr>
<tr>
<td>2011</td>
<td>NWT above canopy</td>
<td>422</td>
<td>−2.1 (6.8)</td>
<td>4.1 (2.4)</td>
<td>0.28 (0.22)</td>
<td>131 (65)</td>
</tr>
<tr>
<td></td>
<td>Unimpacted subcanopy</td>
<td>−1.9 (5.1)</td>
<td>0.38 (0.15)*</td>
<td>0.23 (0.17)</td>
<td>14 (9)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CP above canopy</td>
<td>466</td>
<td>−2.0 (7.1)</td>
<td>3.6 (1.3)</td>
<td>0.27 (0.25)</td>
<td>126 (65)</td>
</tr>
<tr>
<td></td>
<td>MPB-2007 subcanopy</td>
<td>−1.8 (5.3)</td>
<td>–</td>
<td>0.20 (0.21)</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MPB-2008 subcanopy</td>
<td>−0.9 (2.4)</td>
<td>–</td>
<td>0.21 (0.14)</td>
<td>25 (15)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MPB-2009 subcanopy</td>
<td>–</td>
<td>0.43 (0.30)*</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

NWT = Niwot, CO and CP = Chimney Park, WY. Standard deviations are shown to reflect the variability in daily climate variables. MPB, mountain pine beetle

*All data are for the winter snow accumulation season except subcanopy wind speeds, which were observed from 16 April 2011 to 29 July 2011, during which the means of daily above-canopy wind speeds were NWT = 2.7 (1.3) m s⁻¹ and CP = 3.0 (0.9) m s⁻¹.

during the second year because of overall lower variability in canopy cover and snow distribution). In recognition of the potentially important roles of slope and aspect on snow accumulation and ablation, we focused on areas of low slope at both sites. Chimney Park snow surveys had slopes ranging from 1.9% to 17% with mean (standard deviation) of 4.3% (1.8%) and a relatively uniform mixture of all aspects. The Niwot surveys were made on gentle opposing hillslopes with northeast (15% of survey) and southeast (85% of survey) aspect and slopes ranging from 3.7 to 18% with mean (standard deviation) of 9.0% (2.3%). Surveys were made along orthogonal transects (e.g. Anderton et al., 2004) aligned with cardinal magnetic directions. Depth measurements were made at 5-m centres as well as 1 m to the front, back, left and right for a total of 100 depth observations along each 100 linear metres of survey. An observation of canopy density was made at each 5-m centre point using the categories none, sparse, medium and dense. Transects were selected to characterize Unimpacted, MPB-2009, MPB-2008 and MPB-2007 stand types but extended beyond these to broadly characterize small headwater catchments of ~1 km² at each site (Figure 1) with over 8000 total observations. The present analysis focused on MPB mortality in mature forests and used the 4634 observations in mature lodgepole pine stands, excluding those closer to a stand edge than twice the mean tree height to minimize edge effects (Woods et al., 2006). Determination of differences among mean SWE of stand types and canopy densities was performed by one-way ANOVA followed by a t-test-based comparison of multiple means (MATLAB R2012a).

Patterns of spatial correlation were studied within each stand type using experimental and modelled semivariograms (e.g. Schabenberger and Gotway, 2004). The experimental semivariogram

\[ \gamma = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2 \]  

(1)

is half the average squared difference in depth observation pairs \( z \) at locations \( x \), separated by a lag distance \( h \). \( N(h) \) is the number of such depth observation pairs in the given dataset. Snow depth variability may be anisotropic, so semivariograms were calculated separately for 200-m South–North and West–East transect portions using the 120 depth observations falling along the centerline of each survey at positions of 0, 1, 2, 5, 6, 7, . . . , 199, 200, 201 m. Experimental semivariograms were fitted with exponential models (MATLAB R2012a) to allow calculation of the sill, or variance approached at large lag distances, and the range, calculated as the lag distance at which the model semivariogram reaches 95% of the sill variance. Observations closer to one another than the range are considered autocorrelated, whereas those farther apart than the range are considered independent.

With each peak seasonal snow survey, densities were determined from 2 to 4 snow pits at each site using the method described by Cline et al. (2001) in a variety of forest stands.
and both under canopy and in gaps. Pits were excavated to the ground surface, taking snow density, grain type and size, and temperature measurements at 10-cm vertical increments. Fewer snow density measurements were required than snow depths because density varies in space much less than depth (Elder et al., 1998; Anderton et al., 2004). Densities did not vary significantly in space within each site, so mean density values (range: 261 to 342 kg m$^{-3}$) for each site and date were applied in calculation of SWE (Anderton et al., 2002; Jost et al., 2007).

**Isotopic tracers of sublimation**

Stable water isotopes of snowpack were compared with the isotopic content of fresh snowfall. Snowfall samples were collected within 24–36 h of storms in forest clearings, which minimized potential contamination by previously intercepted snow sloughed from the canopy, where it would be more likely to have partially sublimated. Fresh snowfall determined the local meteoric water line (LMWL) at each site, which was considered the starting point for any snowpack isotopic enrichment. Snowpack isotope samples were collected from snow pits dug approximately monthly at paired under canopy and gap locations. Samples were collected from each 10-cm vertical layer, with composite values volume-weighted using the snow density measurements. The samples were analysed for stable water isotope ratios ($\delta^{18}$O) at the University of Arizona using a DLT-100 liquid water isotope analyser (Los Gatos Research, Inc., model 908-000). Further analytical details are described in Lyon et al. (2009).

The isotopic enrichment of snow is similar to that of evaporating water, with mass exchange between snow and vapour (Moser and Stichler, 1975). The sublimated fraction of snowpack, $f$, was estimated via the method given by Clark and Fritz (1997) and demonstrated in a recent field study by Gustafson et al. (2010) using both $\delta^{18}$O and $\delta^2$H (deuterium) values. Equation (2) dictates the equilibrium fractionation enrichment factor expressed as per mil (‰) due to the transition of water from the solid to vapour phase:

$$e^{18}O_{Ice} = 1 - \alpha \times 10^3 \tag{2}$$

where $e^{18}O_{Ice}$ is the per mil (‰) fractionation and $\alpha$ is the fractionation factor ($\alpha = 1.015$) (O’Neil, 1968, cited in Clark and Fritz, 1997). Kinetic fractionation is governed by Equation (3), where $h$ is the humidity at the snow–atmosphere boundary.

$$\Delta e^{18}O_{Ice} = 14.2 \times (1 - h) \tag{3}$$

Deuterium excess of snow pit isotopic values, relative to the LMWL, showed a humidity of approximately 80–90% at the snow–atmosphere boundary. The total fractionation of $^{18}$O ($e^{18}Op$) due to sublimation is the sum of equilibrium and kinetic fractionation, expressed as

$$e^{18}Op = e^{18}O_{Ice} + \Delta e^{18}O_{Ice} \tag{4}$$

The fractional water loss $f$ from the snowpack due to sublimation enrichment then was calculated according to Rayleigh distillation:

$$\delta^{18}O_{Obs} - \delta^{18}O_{Snowfall} = e^{18}Op \cdot \ln(f) \tag{5}$$

where $\delta^{18}O_{Obs}$ was the maximum snowpack value and $\delta^{18}O_{Snowfall}$ was the intercept of the least-squares linear regression of snowpack samples with the LMWL (MATLAB R2012a). The sublimation estimates were not sensitive to temperature and relative humidity, which were assumed on the basis of conservative conditions to be $-2 \, ^\circ C$ and 90%.

**RESULTS**

Cold temperatures and frequent storms (mean interstorm interval of 4.2 days) prevailed throughout the winter snow accumulation seasons (winters) of 2010 and 2011, resulting in the development of continuous snow cover across the study sites. Snowpack temperatures and crystal stratigraphy excluded melt during the winters. Winter precipitation of 2010 was climatologically average (379 mm at Niwot and 422 mm at Chimney Park), whereas 2011 winter precipitation was 113% (calculated from 30-year Niwot SNOTEL history) of average (422 mm at Niwot and 466 mm at Chimney Park). The Niwot and Chimney Park sites received comparable climate forcing as characterized by temperature, vapour pressure deficit, wind speed, and downward shortwave radiation (Table 2) and largely experienced the same regional-scale winter storms, evidenced by similar timing and magnitude of snow depth increases in plots (Figure 2). Cumulative daily winter precipitation plots (Chimney Park vs Niwot, plots not shown) had slopes of 1.10 and 1.14 for winters 2010 and 2011, respectively, reflecting the 10–14% greater winter precipitation at Chimney Park (see methods). However, these plots showed linear correlation greater than 99% ($p < 0.0001$), meaning the precipitation timing was quite similar.

To address this study’s first question about the balance of canopy-mediated snow process responses (see Introduction), continuous snow depth records were used to compare new snowfall under canopy and gaps in the Unimpacted, MPB-2008 and MPB-2007 plots. In the Unimpacted plots, locations under gaps accumulated deeper snow than under adjacent canopy throughout the winter (Figure 2). Differences between canopy and gaps were smaller in the MPB-2008 plots and slightly reversed in the MPB-2007 plots, where the under-canopy mean depth was slightly larger than in gaps. At the end of the winter, differences in mean snow depth under canopy as compared with gaps were 11%, 4% and $-7\%$ for the Unimpacted, MBP-2008 and MBP-2007 plots, respectively. Taking one minus the ratio of new snowfall during storms under canopy to that in gaps (Figure 3) as an estimate of interception, we calculated interception of 20%, 14% and 0% in the Unimpacted, MBP-2008 and MBP-2007 plots, respectively. Assuming 60% of intercepted snow sublimates and the remaining 40% is unloaded to the snowpack (Pomeroy et al., 1998), these correspond to reductions in peak seasonal snowpack of 12.0%, 8.4% and 0.0%.

Marked contrasts in spatial distribution of peak snow depth across the different stages of MPB infestation were used to make further inferences about the balance of
canopy-mediated snow process responses. Representative South-to-North transects (Figure 4) show least depth under denser canopy and greatest depth under canopy observed to be 'sparse' or 'none', but the overall variability decreased with increasing time since MPB infestation. Standard deviations of depth were 21.9, 10.6 and 6.4 cm for Unimpacted, MPB-2008 and MPB-2007 transects (Figure 4), respectively. Numerous field observations indicated that gaps larger than half the surrounding tree height had deepest snow at their southern edges and least snow at their northern edges (e.g. Figure 4a, Unimpacted transect near 0 and +70 m); the phenomenon was weaker in grey stands that had lost their needles than in healthy or red-phase stands as illustrated in Figure 4b (MPB-2008) near 0 and +75 m and in Figure 4c (MPB-2007) just south of 0 m. Semivariograms (Figure 5) had clear sills, indicating that snow surveys were of sufficient extent to characterize the mean and variability (Figure 6) of each stand type (Cressie, 1993; Legendre and Legendre, 1998; Jost et al., 2007). Semivariograms of normalized 2010 peak snow depth were anisotropic (Isaaks and Srivastava, 1989), showing an order of magnitude lower sill variance along South–North transects in an MPB-2007 stand (grey phase, sill = 0.015) than an Unimpacted stand (sill = 0.120) with an MPB-2008 stand (red phase, sill = 0.053) of intermediate variability (Figure 5). In the Unimpacted forest (Figure 5a), the sill variance along a South–North transect (0.120) was double the sill variance along a West–East transect. The semivariogram ranges, which represent the distance beyond which depths were independent, decreased from 12.2 m in an Unimpacted stand to 7.4 in an MPB-2008 stand (red phase) to 3.3 m in an MPB-2007 stand (grey phase) along South–North transects.

Amounts and spatial distribution of SWE were used to compare mean effects of MPB infestation on peak seasonal SWE as well as the role of canopy within each stand type. SWE at the snow surveys ranged from 23.0 to 29.3 cm over the 2 years (Table 3). SWE values were normalized by onsite observations of winter precipitation for each site and year, with the ratio SWE:P indicating the fraction of snowfall remaining in the snowpack at peak seasonal accumulation. Consistent with expectations based on low slope, there was no significant relationship between peak SWE:P and slope at either site. At Niwot, the small portion (15%) of the dataset with Northeast aspect had higher SWE:P than the points with Southeast aspect (SWE:P of 0.658 and 0.625, respectively).
Mean normalized peak seasonal snowpack (SWE:P) was used to address this study’s second question regarding the net impact of forest mortality on SWE. Unimpacted, MPB-2008 and MPB-2007 stand types were statistically indistinguishable with a mean SWE:P of 0.62 (Figure 6), whereas the MPB-2009 stand had 2% greater SWE:P \((p < 0.05)\). Total winter season ablation was therefore 36–38% of snowfall. When SWE:P values were categorized by canopy density (i.e. none, sparse, medium and dense), the number of unique \((p < 0.05)\) canopy groups was highest in stands with ~75% mountain pine beetle (MPB)-induced tree mortality.
Table III. Distributed snow depth and SWE and SWE:P values from surveys conducted in headwater catchments (~1 km²) near peak accumulation for winters 2010 and 2011.

<table>
<thead>
<tr>
<th>Year</th>
<th>Stand</th>
<th>Depth (cm)</th>
<th>SWE (cm)</th>
<th>SWE:P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>Unimpacted</td>
<td>88.3 (0.6)</td>
<td>23.0 (0.2)</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>MPB-2009</td>
<td>92.9 (0.3)</td>
<td>28.2 (0.1)</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>MPB-2008</td>
<td>96.4 (0.8)</td>
<td>29.3 (0.2)</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>MPB-2007</td>
<td>94.0 (0.3)</td>
<td>28.6 (0.1)</td>
<td>0.66</td>
</tr>
<tr>
<td>2011</td>
<td>Unimpacted</td>
<td>87.8 (0.7)</td>
<td>27.0 (0.2)</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>MPB-2009</td>
<td>82.6 (0.5)</td>
<td>28.2 (0.2)</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>MPB-2008</td>
<td>83.2 (1.5)</td>
<td>28.5 (0.5)</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>MPB-2007</td>
<td>79.0 (1.6)</td>
<td>27.0 (0.5)</td>
<td>0.58</td>
</tr>
</tbody>
</table>

The enrichment of stable water isotopes in snowpack differed between Unimpacted and MPB-impacted stands. Unimpacted stand snowpack plotted along the LMWL, indicating no kinetic fractionation. This does not exclude equilibrium fractionation (saturated conditions at the snow–air interface), which is not detectable with this method. MPB-impacted stand snowpack plotted on a line below (Figure 7) and statistically different from the LMWL ($p < 0.05$) with a slope of 6.2, indicating kinetic sublimation at an average relative humidity of 90%. We calculated $\delta^{18}O_{\text{react}} - \delta^{18}O_{\text{react}}$ as 3.6 and $\delta^{2}H_{\text{react}} - \delta^{2}H_{\text{react}}$ as 22.2. The fraction of SWE lost from the combined MPB-impacted stand snowpack via kinetic sublimation is estimated at 24% using $^{18}O$ and 18% using $^{2}H$. These estimates of snowpack kinetic sublimation loss would include neither sublimation of intercepted snow completely sublimated from the MPB canopy nor sublimation of snowpack under equilibrium (saturated) conditions. The estimate may be further reduced by condensation back into the snowpack, which may bring the isotopic signature of snowpack back towards the LMWL and obscure the sublimation signal. These 18–24% snowpack loss estimates are therefore lower bounds of total winter snowpack sublimation in the MPB stands, consistent with estimates of an additional 0–8.4% lost by canopy sublimation and snow surveys showing a total of 36–38% winter season ablation of snowfall.

**DISCUSSION**

In this study, we observed shifts in two canopy-mediated snow processes following MPB forest mortality: decreased interception (Figure 3) and increased snowpack sublimation (Figure 7). Ultimately, these compensated for one another, resulting in no difference to peak normalized SWE (Figure 6), in contrast with the few previous direct observations of snowpack than Unimpacted snowpack during the winter. During the April–July 2011 assessment of subcanopy (3-m height) wind speeds, above-canopy and below-canopy wind speeds were 2.73 and 0.36 m s$^{-1}$ in the Unimpacted stand and 3.00 and 0.43 m s$^{-1}$ in the MPB-2009 stand.

Figure 7. Water isotopic contents of fresh snowfall and evolved snowpack for (a) Unimpacted stands and (b) combined mountain pine beetle (MPB) stands. ‘+’ symbols denote fresh snowfall and ‘*’ denote snowpack. The MPB stands snowpack slope was significantly less than that of the Local Meteoric Water Line or LMWL ($p < 0.05$).
accumulation following insect-induced mortality (Boon 2007, 2012; Pugh and Small, 2011). Sublimation of intercepted snow from the canopy is often considered the dominant flux representing differences between snowfall and peak SWE (Schmidt and Troendle, 1992; Hedstrom and Pomeroy, 1998), leading to an expectation of increased peak SWE following forest mortality. Sublimation requires available energy for the change of phase between ice and water vapour and the turbulence to transport vapour away from the ice surface, both of which are high in the forest canopy and much lower at the level of the snowpack on the forest floor. Given sufficient energy and turbulence, however, snowpack sublimation may represent a large fraction of winter snowfall (Hood et al., 1999; Molotch et al., 2009). Molotch et al. (2009) reported winter snowpack sublimation rates averaging 0.41 mm d⁻¹ and a mean contribution by snowpack to total sublimation of 45% for healthy forest at the Niwot site used in this study. Our results indicate that the sum of winter sublimation losses from the canopy and snowpack remained constant (Figure 6). Snowpack sublimation increased (Figure 7), compensating for lower sublimation of snow from the canopy. These results were similar to studies in which canopy removal treatments altered spatial distribution of snow with little to no effect on peak SWE at larger scales (e.g. Gary, 1974; Troendle and King, 1987; Woods et al., 2006). A recently developed method (Gustafson et al., 2010) of comparing stable water isotopes in fresh snowfall to those in snowpack confirmed greater sublimation of snowpack in insect-killed forest (Figure 7), and season-long observations of temperature, vapour pressure deficit, solar radiation and wind speed (Table 2) provide inferences to explain why snowpack sublimation increased, compensating for reduced canopy snow sublimation.

Continuous snow depth sensors identified the expected pattern of lower interception in the high mortality forests (Figure 3), presumably in response to reduced canopy density (Hedstrom and Pomeroy, 1998; Pomeroy et al., 2002). Interception is a function of canopy area, temperature, humidity and snowfall characteristics (e.g. Strobel, 1978; McNay et al., 1988; Hedstrom and Pomeroy, 1998; Pomeroy et al., 2002), and has been implicitly accepted as a driver of increased snowpack in modelled response to MPB (Bewley et al., 2010; Mikkelsen et al., 2011, Pomeroy et al., 2012). Interception rates observed in healthy forest (Figure 3) were similar to recent regional observations (Musselman et al., 2008; Molotch et al., 2009), suggesting that differences in new snowfall under canopy and in gaps are due primarily to interception and not influenced by redistribution of canopy snowfall preferentially deposited in gaps (Golding and Swanson, 1978). Although unloading of intercepted snow from the canopy may also influence estimates of interception (Clark et al., 2011), low new snow densities result in an immediate depression of snow depth following unloading (Musselman et al., 2008, Molotch et al., 2009), which allowed us to exclude these events from the analysis summarized in Figure 3. It is possible that higher subcanopy wind speeds (Table 2) during storm events reduced the observed interception below impacted stands and that both lower stem density and taller trees (Table 1) could enhance this effect. However, the 20% difference in interception between the Unimpacted and MPB-2007 plots (Figure 3) is of similar magnitude to findings by Pugh and Small (2011) in lodgepole pine forests in Colorado and by Boon (2012) in British Columbia.

Despite reduced interception, peak SWE was unchanged by widespread (~75%) MPB tree mortality (Figure 6), indicating that lower interception (Figure 3) was compensated by higher winter snowpack sublimation. Differences in topography between the Niwot and Chimney Park sites could have influenced the SWE comparison. The Unimpacted stands at Niwot showed slightly higher (~5%) peak normalized SWE in an area with 9% slope and Northeast aspect as compared with an area with 9% slope and Southeast aspect. Because 85% of the dataset was collected on the Southeast aspect, this may have led us to underestimate SWE: P in the Unimpacted stands, meaning that net snow accumulation at the larger scale might actually be lower in the MPB-impacted stands than that in the Unimpacted stands. Melt was excluded during the winter because profiles of cold content and crystal structure indicated a continuously cold snowpack. Wind scour was excluded by more than 8000 snow depth observations collected over areas of approximately 1 km² at the two sites in 2 years, which showed no major areas of net deposition. Minimal wind redistribution is consistent with our observations of low subcanopy wind speeds (Table 2).

With melt and wind excluded as important process of winter snowpack ablation at these sites, we infer that reduced canopy sublimation in MPB-impacted stands was compensated by increased snowpack sublimation. Snowpack sublimation is difficult to observe, especially when concurrent with canopy sublimation, which confounds stand-scale vapour flux observations (Molotch et al., 2009). Increases in concentrations of snowpack solute ions have been used successfully in open areas (Gustafson et al., 2010), but ion contamination from throughfall and needle litter in MPB-impacted stands made stable isotopes preferable in this study (Stichler, 1986; Sommerfeld et al., 1987; Sommerfeld et al., 1991; Gustafson et al., 2010). Comparison of stable water isotopes in snowpack with those in fresh snowfall offered evidence that snowpack sublimation was indeed higher in MPB-impacted stands (Figure 7). Although this method (Equations (2–5)) allows quantification of just the kinetic portion of sublimation, the significant difference in kinetic fractionation (i.e. snowpack sublimation loss under subsaturated conditions) between Unimpacted (no loss) and MPB-impacted (20–25% loss) stand types confirms a major increase in sublimation from the snowpack below the canopy following MPB mortality. Such a difference could have been caused by enhancement of vapour transport away from the surface (i.e. increased vapour pressure deficits and/or turbulent transport) or by increased available energy from solar radiation (Rinehart et al., 2008, Veatch et al., 2009, Gustafson et al., 2010). Isotopic contents of fresh snowfall inputs to the snowpack could be influenced by partial sublimation of snow initially retained in the canopy and then sloughed to the ground. The collection of samples in open areas immediately after storms was intended to minimize such
effects. Given the lower wind speeds and higher density of canopy available for interception, we would expect any such effect to be larger in Unimpacted stands. Because canopy sublimation would likely exhibit kinetic fractionation, the consistency with which snowfall and snowpack samples remained near the Global Meteoric Water Line in the Unimpacted stands (Figure 7a) suggests that partial canopy snow sublimation was of minimal influence on the isotope results.

Larger snowpack sublimation beneath MPB-impacted forest canopy could have been controlled by higher wind speeds (Stegman, 1996) and turbulence (Molotch et al., 2007) or by greater transmission of solar radiation (Boon, 2009; Pugh and Small, 2011), consistent with the major role that radiation plays in the energy balance of forested snowpacks (Link and Marks, 1999). Our observation of similar wind speeds in the Unimpacted and MPB-2009 stand types (Table 2) makes it unlikely that wind controlled differences in snowpack sublimation. Seventy-one percent more solar radiation reached the snowpack in the MPB-2008 plots than in the Unimpacted plots (Table 2). Although the type of pyranometer used might lead to over-estimation of below-canopy shortwave by 10–20% (see Methods), any bias should be larger for Unimpacted stands, suggesting that the true difference could be larger. The 71% difference we observed is much larger than the 11–13% shortwave difference calculated by Pugh and Gordon (2012) for grey-phase stands using a modified Beer–Lambert model (Hellstrom, 2000). More detailed canopy radiation transmission models could be more informative (e.g. Hellstrom, 2000; Hardy et al., 2004); caution is warranted in using spatially lumped models because winter season sublimation can vary among forest stands with similar average canopy density but different geometry (i.e. spatial arrangement of trees and gaps, Woods et al., 2006; Veatch et al., 2009) and/or topography (slope, aspect, elevation; e.g. Rinehart et al., 2008). Although vegetation is the most important control of SWE in forested terrain, even in complex topography (Varholak et al., 2010), solar interactions with slope and aspect may be of increased importance following canopy density reduction (Troendle and King, 1987; Somor et al., in preparation). Net shortwave inputs to the snowpack may be further increased by litter fall beneath killed trees and associated albedo reductions (Winkler et al., 2010; Pugh and Small, 2011). If the observed 11 W m\(^{-2}\) (Table 2) were the only difference in available energy from 1 December to 1 April, it would be sufficient to sublimate an additional 4.1 cm of SWE, or 14% of the mean peak SWE observed in this study, more than compensating for the estimated 12% reduction in canopy sublimation between the Unimpacted and grey-phase MPB-2007 stands (Figure 3).

Spatial observations from our distributed snow surveys supported the importance of solar radiation in controlling snowpack sublimation and net annual snow water input. First, the observation of greater snow depth at the shaded southern edges of forest gaps and less depth near the less-shaded northern edges (Figure 4) indicated the importance of solar shading (Golding and Swanson, 1986; Musselman et al., 2008, Molotch et al., 2009; Veatch et al., 2009). Second, snow surveys showed decreased snowpack (SWE:P) in gaps (Figure 6) of MPB-killed forest, which may be attributed to reduced shading by adjacent canopy. Third, the importance of solar shading was demonstrated by higher semivariogram sill variance along the South–North transect than the West–East transect of Unimpacted forest (Figure 5). A South–North transect in healthy forest crosses the deep, shaded southern portion and shallower, unshaded northern portion of snow in each gap traversed, whereas a West–East transect crosses each gap parallel to its snow depth contours, resulting in lower variability. This directional difference was not observed in MPB-killed forest, consistent with a reduction in canopy shading.

Compensatory process changes affect peak SWE following insect-induced tree mortality, with a potentially variable balance between lower interception and higher snowpack sublimation. Reduced sublimation of intercepted snow with reduced canopy density is intuitive, and our estimates of 8.4–12.0% more snowfall reaching the snowpack in grey-phase stands (Figure 3) are consistent with both empirical observations (Pugh and Small, 2011; Boon, 2012) and modelled results (Bewley et al., 2010; Pugh and Gordon, 2012) ranging from 7% to 19%. Much less is known about the effects of insect-induced tree mortality on winter snowpack sublimation. The present study’s conclusion of no change in peak seasonal SWE (Figure 6) contrasts with increased SWE observed following MPB in Colorado by Pugh and Small (2011) and for one of two winters in British Columbia by Boon (2012). We suggest that such contrast may arise because the observations in this study are nested across a larger range of spatial scales (tree, plot, stand, hillslope) than that in previous studies of snowpack following MPB. Earlier studies of harvest effects on snowpack reported forest-to-clearing snowpack differences, but no net change averaged over larger scales (Hoover and Leaf, 1967; Gary 1974; Troendle, 1983; Golding and Swanson, 1986; Troendle and King, 1987), highlighting the importance of large-scale snowpack characterization.

Peak SWE is a primary indicator of long-term water availability in forested mountain catchments, and this study has implications for ecosystem function and downstream water resources. The conventional wisdom is that widespread tree mortality results in increased water yield on the basis of harvest studies (see review by Pugh and Gordon, 2012), but the few empirical studies of water yield response to insect-induced mortality are inconclusive in this regard. Bethalhmy (1974) reported a small water yield increase that did not peak until 15 years following major infestation, whereas Potts (1984) found a small increase immediately, and Somor et al. (in preparation) found less runoff in one catchment and no change in seven others following widespread MPB forest mortality. These mixed responses in runoff likely reflect variable SWE response (i.e. changes to interception and winter sublimation), time-varying changes to transpiration (Edenburg et al., 2012), and mediation of impacts due to complex hydrologic flow paths and the patchy, transient nature of insect infestation. Our results showed that increased winter sublimation compensated for reduced interception and demonstrated that insect-induced forest mortality will not necessarily result in increased water availability.
CONCLUSIONS

This study provided extensive empirical evidence from two winters that snow process responses to insect-induced forest mortality can compensate for one another, resulting in no change to peak SWE. Observations of reduced interception were consistent with expectations from prior studies, but surprisingly, there was no difference in peak SWE between healthy and grey-phase forests. Higher rates of snowpack sublimation were confirmed by the recently developed method of comparing stable water isotopes in fresh snowfall to those in snowpack. Several lines of evidence suggested that vegetation shading of snowpack from solar radiation was a primary control on winter sublimation of snow at the study sites and that shading was reduced in insect-killed forest. The plot-scale observations of new snowfall and accumulated depth showed a decreased association between canopy density and snow depth, consistent with the decreased spatial variability of depth, the decreased spatial scale of variability and the lower importance of canopy density in controlling SWE:P at peak accumulation. The contrast between our results and those of two prior studies emphasizes the importance of winter snowpack sublimation as well as the need for large-scale observation when characterizing peak SWE.

The significance of peak SWE as an indicator of hydrologic response to forest disturbance highlights the need for improved understanding of the balance between greater net snow inputs and increased snowpack sublimation; factors needing further investigation include forest geometry, topographic exposure to radiation and wind, and the dynamics of a given disturbance.

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SNOWPACK FOLLOWING INSECT-INDUCED PINE MORTALITY


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