The impact of beetle-induced conifer death on stand-scale canopy snow interception

Evan T. Pugh and Eric E. Small

ABSTRACT

Bark beetles have killed more than 100,000 km^2 of pine forest in western North America, causing trees to lose the majority of their canopy material and potentially leading to enhanced subcanopy snow accumulation. Over a 45-day period, we tested this hypothesis by measuring daily snow accumulation in three living and two dead lodgepole pine stands and in three adjacent clearings. The largest clearing was selected as our reference clearing based on previous studies. At maximum pre-melt snow water equivalent (SWE), this clearing had accumulated 50.4-cm SWE, while 45.6-cm SWE accumulated under dead stands and 38.1-cm SWE accumulated under living stands. Dead stand snowpacks were both denser and deeper than those in living stands. We attribute higher subcanopy accumulation under dead stands, compared to living stands, to diminished canopy snow interception and sublimation. Storm-scale canopy interception was also estimated by comparing SWE in forests and clearings before and after storm events. Over 10 storms, dead and living stands intercepted 18 and 41% of snowfall, respectively. The amount of interception increased linearly with storm size in the living stands, but not dead stands. We estimate more than half of snow falling on living stands sublimated, with measurably less sublimation in dead stands.

Key words | canopy snow interception, forest disturbance, forest snow processes, mountain pine beetle, snow accumulation, water budget

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INTRODUCTION

Snow that falls on a needleleaf forest either passes through the canopy to the ground or is intercepted by the canopy on needles, branches or bark (Hedstrom & Pomeroy 1998). The magnitude of intercepted snow impacts the water budget because this snow is more likely to sublimate than subcanopy snow. Compared to snow on the ground, intercepted snow is more likely to sublimate because the forest canopy experiences faster wind speeds (Raynor 1971; Bernier 1990). In addition, the forest canopy has a lower albedo (~0.15) than the snow-covered ground (Pomeroy & Dion 1996). Low canopy albedo often persists with snow present on trees because intercepted snow is usually thin and translucent (Ni & Woodcock 2000), though some studies suggest intercepted snow can alter the top-of-canopy energy balance (Nakai *et al.* 1999; Stähli *et al.* 2009). The sublimated portion of intercepted snow is water that does not contribute to snowmelt (Lundberg 1994). The magnitude of canopy snow interception depends on local climactic factors such as air temperature, wind speed and precipitation (Pomeroy *et al.* 1998; Schmidt *et al.* 1998; Pomeroy & Essery 1999; Suzuki & Nakai 2008) as well as forest structure characteristics such as canopy density and canopy height (Winkler & Moore 2006; López-Moreno & Latron 2008; Veatch *et al.* 2009; Varhola *et al.* 2010). Forest structure can be drastically and rapidly altered by forest disturbance, such as insect attack, wildfire and blowdown. This study examines the impact that altered forest characteristics wrought by beetle infestation have on canopy snow interception.

The mountain pine beetle (*Dendroctonus ponderosae*; MPB) is currently impacting more than 100,000 km^2 of predominantly lodgepole pine (*Pinus contorta*) forest

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in western North America (MFR 2011; USFS 2011). During the first 2 years following infestation, pine needles turn reddish-brown and begin to fall off dead trees. This stage of mortality is called the ‘red phase’ (Wulder *et al.* 2006). Increased needlefall can reduce snow surface albedo under the canopy and advance snowmelt (Pugh & Small 2012). Within 3 years of the initial attack, the pines have been completely denuded of needles and the trees appear grey. The thinner canopies transmit more sunlight and are expected to intercept less snowfall (Boon 2009; Pugh & Small 2012). This needle-less stage of tree death is termed the ‘grey phase’ (Wulder *et al.* 2006). During the grey phase, pine twigs and branches are sloughed (Klutsch *et al.* 2009; Teste *et al.* 2011), leading to even greater canopy thinning.

Beetle-induced tree death impacts hydrologic processes including snow accumulation and melt, soil infiltration and evapotranspiration (Boon 2009; Pugh & Small 2012; Pugh & Gordon 2013). Because forest canopy characteristics control snow interception, which in turn affects subcanopy snow accumulation, reductions in canopy density have important implications for net snow accumulation on the forest floor (Molotch *et al.* 2009; Veatch *et al.* 2009; Varhola *et al.* 2010). Tree death drastically reduces available interception platforms. In previous studies it was hypothesized that this will lead to greater subcanopy snow accumulation under dead trees, compared to pre-infestation conditions (Boon 2007, 2012; Pugh & Small 2012). In this study, we test this hypothesis using data collected from living and dead forest stands and adjacent clearings.

Previous studies have employed various techniques to measure canopy snow interception, at both the tree and stand scales (Lundberg 1993; Lundberg & Halldin 2001a, b). A widely used method for measuring canopy interception on an individual tree is to weigh intercepted snow on real and artificial trees or branches. This method is also useful for measuring snow mass lost to sublimation and unloading (Schmidt 1991; Schmidt & Gluns 1991; Hedstrom & Pomeroy 1998; Lundberg *et al.* 1998; Montesi *et al.* 2004). Further, snow interception has been studied by observing branch deflection following snow storms (Schmidt & Pomeroy 1990; Bründl *et al.* 1999). To estimate intercepted load, these deflection measurements are compared to species deflection constants determined experimentally.

While tree-scale measurements are helpful for understanding the mechanics of interception processes, deployment of these techniques at the stand or watershed scale is not practical. To study interception at larger scales, subcanopy snow accumulation is compared to clearing snow accumulation resulting from individual storms. Measured canopy-clearing differences are then attributed to interception during the storm (McNay *et al.* 1988; Storck *et al.* 2002; Lundberg & Koivusalo 2003; Musselman *et al.* 2008). This approach is based on the assumption that the forested areas and clearings receive the same amount of precipitation. We used this method to estimate interception. We measured snow accumulation in living and grey phase dead lodgepole pine stands as well as in adjacent clearings of varying area. The ratio of snow accumulation in forested areas relative to accumulation in adjacent clearings has been found to depend on clearing size (Golding & Swanson 1978). For small to moderate sized clearings, peak snow accumulation is greater than surrounding forest because forest aerodynamics redirect falling snow into the clearings rather than carry it farther downwind (Gary 1974). Larger clearings (i.e., more than two times wider than surrounding tree height, $>2H$) may begin experiencing wind scour, reducing the potential for greater snow accumulation. Therefore our estimates of intercepted snow are sensitive to the size of the clearing we use as a reference for snowfall totals. This is discussed further in the site description (see the section ‘Study sites and methods’).

Because interception reduces the amount of snow that accumulates under forests, it is integral to many hydrologic and land surface models. Hedstrom & Pomeroy (1998) developed an interception model that predicts interception using effective leaf area index (LAI′), species-specific snow loading coefficient (B), snowfall density (ρ_{sf}) and storm size (P). This model is widely used (e.g., Gelfan *et al.* 2004) and has been incorporated into several hydrologic and land surface models (e.g., *CLASS*, *NOAH-MP*). A key concept in the model is that the percentage of incoming snowfall intercepted by a canopy is inversely proportional to storm size. The amount of snow stored in the canopy asymptotes at a maximum intercepted load determined by characteristics of both the canopy and the intercepted snow. In the Discussion, we identify how the effects of tree death could be better represented in snow interception models.

This study quantifies how conifer death impacts interception at the stand scale. Pugh & Small (2012) studied subcanopy accumulation beneath living and dead stands in multiple stages of tree death and did not observe additional accumulation under red phase trees, which retain most of their needles. However, MPB snow studies (Boon 2007, 2012; Pugh & Small 2012) have reported higher peak snow water equivalent (SWE) under grey phase canopies than under adjacent living stands. Boon (2007) reported 75% more snow under grey phase stands during a year of extraordinary snowfall (159% of average). Other results (Boon 2012; Pugh & Small 2012), from years with closer-to-average snowfall, indicate more modest increases in grey phase stand snow accumulation, ranging from 3 to 21%. Here we clarify how the canopy snow interception process responds to stand-scale tree death by addressing three questions: (1) on a storm-by-storm basis, do living stands intercept more snow than dead stands? (2) if so, is subcanopy SWE lower under living stands at the season scale? and (3) does more canopy sublimation occur in living stands compared to dead stands?

Below, we describe our study sites and experimental methods. The next section contains results from the 2011 snow accumulation field study. We then discuss potential reasons for different magnitudes of snow accumulation in living and dead stands and suggest specific changes to improve interception modelling.

STUDY SITES AND METHODS

Study sites

Our goal was to observe snow interception and accumulation processes in living and grey phase stands. During the winter of 2011, we studied five lodgepole pine stands and three forest clearings in the subalpine headwaters of the Colorado River in north-central Colorado (Figure 1; Table 1). Study sites ranged in elevation from 2,693 m above sea level (asl) to 2,699 m asl and were effectively flat, with slopes ranging from 0° to 0.5°. The maximum distance between any two site centres was 238 m (between Sites 3 and 8). Within each stand, a 2,450 m^2 experimental zone was demarcated and sampled during the study. Each stand was composed of more than 95% lodgepole pine. The stands were classified based on the percentage of trees in the grey phase. The two grey stands selected had 69 and 83% trees in the grey phase (Table 1). The three other forested stands had less than 4% of trees in the grey phase. We refer to these non-grey stands as ‘living stands’, even though up to 41% of the trees in the stands are in the red phase of tree death (Table 1). LAI′ values for red phase trees can be intermediate between living and grey, potentially causing intermediate effects on interception and radiation transmission processes (Pugh & Gordon 2013). However, the red phase trees found in our living stands retained a significant majority of their needles, and thus likely affected interception and radiation in a similar fashion to living trees (Pugh & Small 2012).

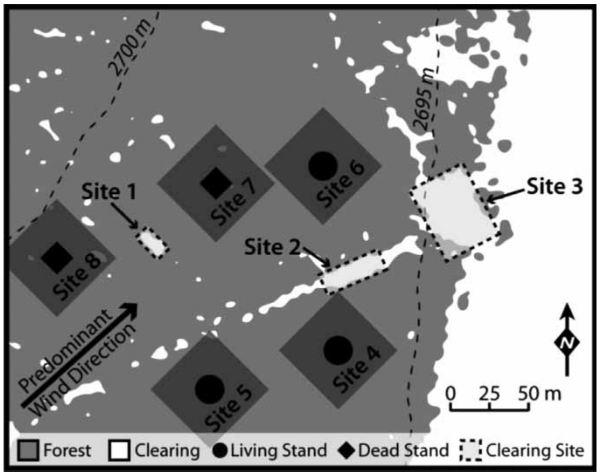

Figure 1 | Site locations along the headwaters of the Colorado River in north-central Colorado. Circle markers represent living stands, diamonds represent grey phase dead stands, and clearing sites are boxed in dashed lines. Shaded areas surrounding stand markers represent stand-scale experimental zones. During the study period, wind direction was predominantly from the southwest (73% of the time).

Previous studies comparing snow processes in living and MPB-impacted stands were complicated by the fact that forest characteristics were different in the living and dead stands, including stand density, trunk diameter and canopy coverage (Boon 2007, 2009; Pugh & Small 2012). This complication is unavoidable because severe MPB infestations may kill the majority of suitable host trees (Schmid & Mata 1996). The trees in living stands are largely

Table 1 | Site characteristics measured in April 2011. Additionally, all sites were between 2,693 and 2,699 m above sea level, had flat topography, and were composed of more than 95% lodgepole pine (*Pinus contorta*). Tree height and stem diameter at breast height (DBH) are stand averages calculated from tree census data. Canopy density and effective leaf area index (LAI′) values are stand averages calculated from hemispherical photos

Site #	Designation	Area (m^2)	Basal area ($m^2\,ha^{-1}$)	Tree height (m)	DBH (cm)	Stem density stems (ha^{-1})	Mortality % of stems	% Grey phase	Canopy density (%)	LAI′ ($m^2\,m^{-2}$)
1	Clearing	360	•	•	•	•	•	•	•	•
2	Clearing	800	•	•	•	•	•	•	•	•
3	Clearing	2,500	•	•	•	•	•	•	•	•
4	Living	2,450	45.3	19.3	15.4	2,432	20	3	71.7	1.28
5	Living	2,450	40.4	19.2	10.6	4,618	35	6	71.4	1.15
6	Living	2,450	43.6	18.3	14.5	2,642	41	4	72.6	1.18
7	Grey phase	2,450	45.3	19.3	18.3	1,721	89	87	63.6	0.86
8	Grey phase	2,450	43.9	20.8	17.9	1,746	69	69	57.8	0.75

uninfested because they differ from those in the dead stands in terms of age, species composition or stand density. As in previous studies, we faced the same challenge when choosing study sites. The living and impacted stands in our study were very similar with respect to basal area and tree height. However, the living stands had lower diameter at breast height (DBH) and higher stem density (Table 1). The effects of these differences in forest structure are evaluated in the Discussion.

In addition to observing five pine stands, we took measurements in three nearby forest clearings that varied in size: 360 m^2 (Site 1), 800 m^2 (Site 2) and 2,500 m^2 (Site 3). Golding & Swanson (1978) measured snow accumulation in a variety of cut clearings that varied in size. Clearings with a width of two times tree height accumulated the most snow, relative to nearby treed areas. When computing canopy snow interception as the difference between subcanopy accumulation and clearing accumulation, interception magnitude will vary depending on the clearing size that is used as reference. In her study investigating snow accumulation processes following beetle infestation, Boon (2012) used a 2,500 m^2 reference clearing size. We adopt the same reference clearing size (Site 3) to allow for comparable forest-to-open (F:O) snow-accumulation ratios. We compare snow accumulation in the three study clearings to relationships derived in previous studies to assess the suitability of the reference clearing (e.g., Golding & Swanson 1978). The size of the reference clearing only affects the absolute magnitude of calculated canopy interception. The differences in snow accumulation between living and dead stands reported below are independent of the reference clearing used.

Field snow measurements

Regular measurements of snow depth, snow density, and snow and air temperatures were made at the eight study sites between 1 March and 15 April 2011. Daily, pre-storm and post-storm snow depth measurements were taken. The timing of pre- and post-storm snow depth measurements was guided by snowfall predictions from National Oceanic and Atmospheric Administration hourly weather forecasts (NWSFO 2011), which accurately predicted the beginning and end of storms. On each sampling trip, 28 snow-depth samples were taken at each study site with measurements every 5 m along four 35-m long, cardinally oriented transects. Depth measurements were made 1.5 m to the right of the transects to avoid anthropogenic contamination from repeated travel. This design yields 224 measurements per survey (Pugh & Small 2012).

The 28 snow depths from each site were combined with a single, high quality measurement of snowpack density from the same site to calculate stand-scale SWE. Snowpack density at each site was measured in a snowpit with a 250-cc SnowMetrics density cutter. Average snowpit density was calculated from measurements made every 10 cm. Density measurements were taken every 2 days at new locations within each site. This method of measuring average snowpack density was chosen because it produced the least error in a density measurement method comparison (Boon *et al.* 2009).

Snowpack and air temperatures were measured every 2 hours at each site using iButton temperature sensors (Maxim 2009). Snow temperatures were taken using sensors that were stratified throughout the snowpack at heights of 33, 66 and 100 cm above the soil. Air temperature was measured 2 m above the ground surface. All iButton temperature sensors were calibrated against a CS500 temperature sensor for 2 weeks prior to deployment. Wind speed and direction were measured at a weather station 7 km south of the study sites. Wind measurements were taken every 15 min from a height of 2 m using an RM Young 05103 wind monitor. Predominant wind direction was calculated from this data set. During storms, wind commonly (89% of the time) came out of the southwest and almost always exceeded 1 m s^{-1} (96% of the time).

Hemispherical photos were taken of the forest canopy in August 2011 at the same locations within each study site as snow depth measurements. Photos were acquired using a Nikon D700 camera with a Sigma EX Fisheye 8-mm lens. The camera was positioned 1 m above the ground, levelled to gravity, and oriented to true north. The hemispherical photos were analysed to calculate per cent canopy openness and LAI′ using the Gap Light Analyzer 2.0 software (GLA; Frazer *et al.* 1999). LAI′ is defined as the product of a clumping factor (Nilson 1971) and the LAI′ (Black *et al.* 1991) and is a measure of total plant area, including both leaves and woody material. Canopy density is calculated from these data by subtracting per cent canopy openness from complete (100%) canopy cover. Reported LAI′ was integrated over the zenith angles 0° to 60° (Stenberg *et al.* 1994). Average LAI′ values for living and grey phase stands are 1.20 and 0.80, respectively. These values are consistent with regional estimates of LAI′ in living and grey phase lodgepole pine stands (Pugh & Gordon 2013).

Seasonal accumulation trends

Differences in SWE between forest sites and the reference clearing represent SWE lost up to a given date due to the effects of the forest canopy on interception and sublimation. This loss of potential snow accumulation was termed *SWE Loss* by Storck *et al.* (2002) and is calculated here as:

$$SWE\,Loss = \mathrm{SWE}_{\mathrm{clearing}} - \mathrm{SWE}_{\mathrm{forest}} \tag{1}$$

where SWE is stand-scale snow water equivalent calculated from mean stand snow depth and snowpack density. We only completed this analysis for the accumulation period, after which the effects of melt and interception cannot be separated.

Interception event calculations

We estimate interception during individual storms by measuring stand SWE before and directly after storms. Mean stand snow depths were combined with the snowpack density measurements taken closest in time to the snow depth measurements (within 1 day) to calculate stand SWE. Changes in stand SWE during storms are calculated as the difference in SWE before and after storms:

$$\Delta\mathrm{SWE}_{\mathrm{storm}} = (\mathrm{Depth}_{\mathrm{after}}\rho_{\mathrm{after}} - \mathrm{Depth}_{\mathrm{before}}\rho_{\mathrm{before}}), \tag{2}$$

where Depth is mean stand depth and ρ is average snowpack density.

The SWE intercepted by the forest canopy (living or dead) is assumed to equal the difference in new snow accumulation between forested stands and the reference clearing:

$$I = \Delta\mathrm{SWE}_{\mathrm{clearing}} - \Delta\mathrm{SWE}_{\mathrm{forest}} \tag{3}$$

where I is intercepted SWE and ΔSWE is the change in SWE during the storm event. Storms during which mean air temperatures rose above $-3\,^{\circ}$C were excluded to ensure that storms with rainfall did not obfuscate the analysis. Analyses were performed on all stands individually and for averages by mortality class. Both stand and class analyses yielded very similar results. In all figures, results are reported as class averages.

RESULTS

Snow depth and density surveys were completed daily over a 45-day interval from 1 March to 15 April. In the reference clearing, SWE increased from 33.0 to 51.3 cm during this interval. This represents approximately 35% of total accumulation during the entire snow season. The snowpack temperatures in clearings and under grey phase stands became isothermal at 0 °C on 17 March (Day of Year (DoY) = 76) and stayed so for 6 days. The snowpack then refroze before returning to 0 °C on 2 April. The initial period of isothermal snowpack did not occur under living stands. Instead, living stand snowpacks became isothermal later, reaching 0 °C for the first time on 3 April and staying isothermal for the remainder of the study period (Figure 2). The first precipitation event that was primarily rain occurred on 2 and 3 April. Given the isothermal conditions and rainfall at this time, we define the end of the pre-melt period as 3 April, and report maximum pre-melt SWE on this date. SWE increased monotonically prior to this date. After this date, snow events were interspersed with periods of melt and rainstorms.

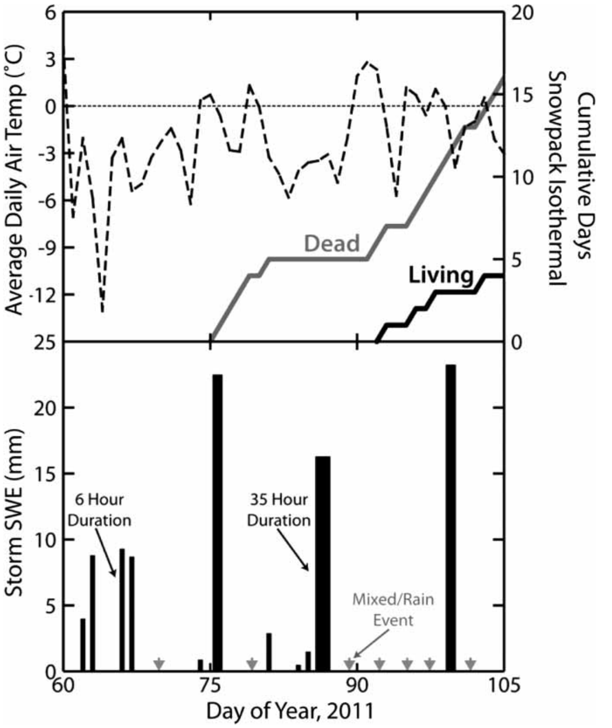

Figure 2 | Average 2-m air temperatures, cumulative days when snowpacks were isothermal in living and dead stands, and storm size reported by Day of Year, 2011. Storms where air temperatures were less than −3 °C are shown in black lines (those included in our analysis); other storms are indicated with grey arrows. Storm size column widths vary with storm duration. Clearing snowpacks became isothermal at the same times as snowpacks under dead canopies.

The magnitude of snow accumulation in the three study clearings varied with clearing size, as expected given the results of Golding & Swanson (1978) (i.e., maximum accumulation at $H = 2$). For Sites 1–3, clearing width-to-tree-height ratios were 0.86, 1.73 and 3.76, respectively. At maximum pre-melt SWE, the reference clearing (Site 3) had accumulated 50.4 cm SWE. Pre-melt maximum SWE at the 0.86H clearing (Site 1) was 11% less than at the 3.76H reference clearing (Site 3). The 1.73H clearing (Site 2) accumulated 17% more snow than the reference clearing. The differences observed throughout the accumulation period were similar to those measured at maximum pre-melt SWE.

Compared to the reference clearing, there was less snow accumulation on the ground beneath both dead and living forest stands. At maximum pre-melt SWE, dead and living pine stands had SWE of 45.6 and 38.1 cm, respectively, compared to 50.4 cm in the reference clearing. Therefore, dead stands accumulated 7.5 cm more subcanopy SWE than living stands. Both snow depth and density were lower in the living stands than in the reference clearing. In contrast, snow density in the dead stands equalled that in the clearing, but snow depths were lower (Figure 3). Differences in stand-scale SWE between living and dead stands are the result of both differences in snowpack density and depth (Figure 3 inset). The observed differences in depth, density and SWE between the mortality classes were consistent, on a percentage basis, throughout the observation period, not just at the time of maximum pre-melt SWE (Figure 3). Differences in snowpack density within landcover classes (i.e., in the three living stands) were small (<4%), justifying the measurement of snowpack density at only one point within each study stand.

SWE Loss was greater under living stands than under dead stands. At maximum pre-melt SWE, living stand *SWE Loss* was 12.3 cm, while dead stand *SWE Loss* was 4.7 cm. These *SWE Loss* values represent 24 and 9% of the reference clearing snow accumulation, for living and dead stands, respectively. *SWE Loss* values from our study sites are similar to forest:open (F:O) SWE ratios reported

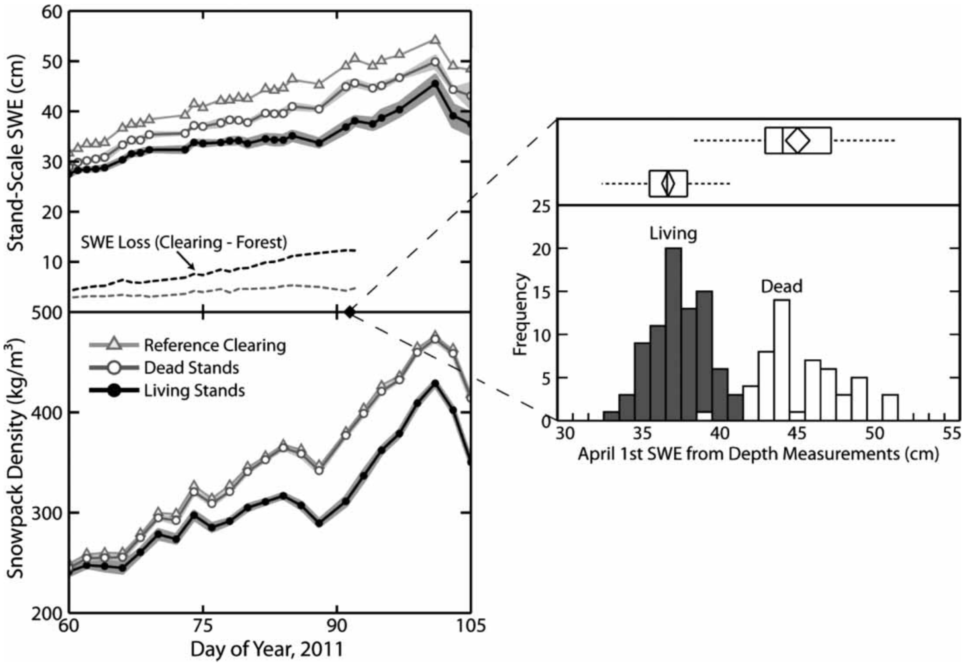

Figure 3 | Stand-scale SWE and snowpack density graphed against Day of Year, 2011. Dot markers in SWE and density graphs represent average measurements, and shaded regions represent 95% confidence intervals. *SWE Loss* in the stand-scale SWE graph was calculated as reference clearing SWE minus forest SWE. A histogram of snow depth values in living and dead forest stands for 1 April with average, maximum, median, minimum and quartile distribution values is inset.

in other studies (Table 2). *SWE Loss* in both living and dead stands increased throughout the accumulation period (Figure 3), thus the F:O ratio remained relatively constant (not shown).

We measured SWE prior to and immediately after storm events to estimate the magnitude of canopy interception. From 3 March to 27 March (DoY 62–88), there were 10 snowfall events during which air temperatures did not exceed −3 °C. These storms yielded 18.2 cm of new SWE accumulation. Individual snowfall events lasted from 7 to 35 hours (Figure 2). Storm size (in SWE) in the reference clearing ranged from 0.3 to 5.1 cm, spanning the range expected for the environment studied. There were two storms within this period when temperature was greater than −3 °C. Based on data from a nearby SNOTEL site, these storms yielded ~1 cm of SWE or ~5% of total accumulation during the interval. These two storms were excluded from our analysis. Because the fraction of precipitation delivered during warm storms was over 50% after day 88, we limit the analysis period up to that date.

On a storm-by-storm basis, SWE increased more in the reference clearing than in both living and dead stands. Sub-canopy snowfall SWE is strongly correlated with clearing snowfall SWE for both living and dead stands and significantly more snow is accumulated under dead than under living stands (Figure 4(a)). Intercepted SWE is significantly correlated with storm SWE for living stands, but not for dead stands (Figure 4(b)). The differences between each

Table 2 | Forest-to-open clearing SWE ratios (F:O) at maximum pre-melt accumulation from recent MPB snow accumulation studies as well as from this effort. Winkler & Boon (2009) presented a synthesis of many unpublished results and, as such, a range of applicable means are presented from that data set

Study	Location	Living F:O ratio	Grey phase F:O ratio
Spittlehouse (2006)	British Columbia, Canada	0.75	
Winkler & Boon (2009)	British Columbia, Canada	0.74–0.78	0.84–0.89
Bewley *et al.* (2010)	British Columbia, Canada		0.84; 0.98
Boon (2012)	British Columbia, Canada	0.73; 0.80	0.75; 0.94
This study	Colorado, USA	*0.76*	*0.91*

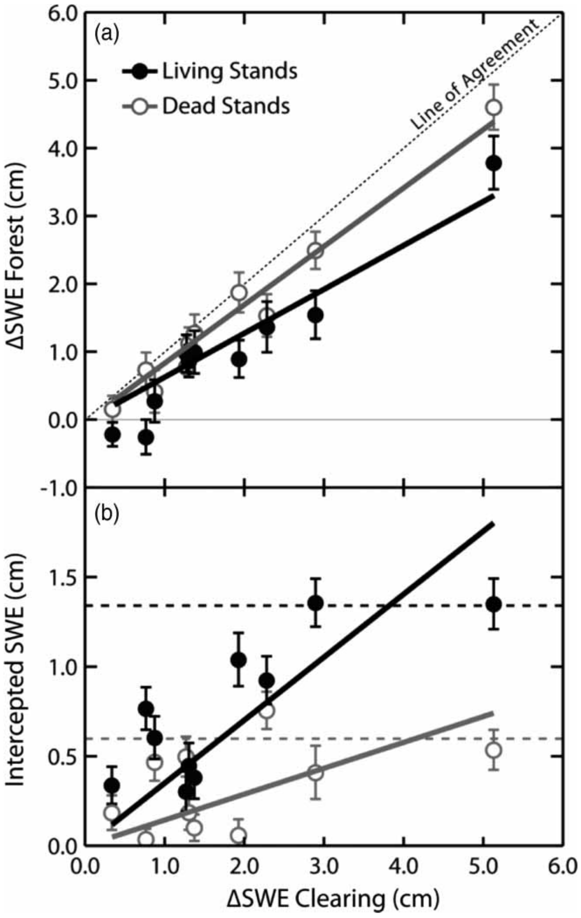

Figure 4 | (a) Event (storm) snowfall SWE: forest subcanopy versus clearing SWE for living ($y = 0.64x$; $p < 0.0001$; $r^2 = 0.89$) and dead ($y = 0.86x$; $p < 0.0001$; $r^2 = 0.97$) stands. (b)) Event (storm) forest intercepted SWE versus clearing SWE ($p < 0.001$; $r^2 = 0.40$) for living and dead stands ($p = 0.175$; $r^2 = 0.02$). Error bars represent one standard deviation and dashed lines are average maximum observed interception values (Living = 1.35 cm; Dead = 0.56 cm). Regressions were performed assuming zero subcanopy accumulation when zero clearing accumulation (i.e., forcing the y-intercept of linear regression lines through the origin).

forested area and the clearing were consistent across storm size, on a percentage basis. Under dead stands, the increase in SWE was 86% of that in the reference clearing ($r^2 = 0.97$). The difference was greater in the living stands, where SWE only increased by 64% as much as that observed in the clearing ($r^2 = 0.89$). Therefore, the increase in SWE during storms was greater in the dead stands than in the living stands. Additionally, for two small storms (<1 cm SWE) where living stands showed decreases in subcanopy 'accumulation' (i.e., effectively intercepted 100% of incoming precipitation), dead stands had positive subcanopy accumulation.

For each storm, we calculated intercepted SWE according to Equation (3). Simply summed over the storms, there was 18.2 cm of precipitation in the reference clearing. We measured 7.5 cm of interception in the living stands, and 3.2 cm in the dead stands. This is 41 and 18%, respectively; or a mortality-associated decrease of more than half of the interception. Intercepted SWE significantly varied with storm size in living stands ($r^2 = 0.40$), but not in dead stands ($r^2 = 0.02$), as expected given Figure 4(b). During the two smallest storms, the change in SWE on the ground was negative, equivalent to negative accumulation according to Equation (3). In these cases, interception in the living stand was assumed to equal the accumulation amount in the clearing. Together, these storms accounted for <1.0 cm of the total intercepted SWE. If instead we assumed zero interception in the living stands for these two storms, the total percent interception would be 35% instead of 41%. Values of interception (e.g., 41% in living stands) are not equal to 100% minus the slope of the best fit lines between subcanopy accumulation and clearing accumulation (Figure 4(a)) because those regressions include error associated with measurements in a natural system.

In order to compare our snowpack SWE record with our measurements of snowfall accumulation, we again limit the analysis period to the interval between DoY 62–88. This interval included 10 of the 11 cold storms observed during the 45-day study and occurred before snowmelt. During this 26-day period, SWE increased by 11.4 cm in the reference clearing, compared to ~19 cm of accumulation measured during the storms. Measured cold storm accumulation values are increased by 5% to account for accumulation during warm storms (see above). This difference between snowpack SWE increase (DoY 62–88) and accumulation during storms suggests that 40% of the precipitation reaching the reference clearing sublimated. Living stand SWE increased by 5.4 cm and dead by 10.3 cm during the same interval, suggesting that 72% of precipitation falling on living stands sublimated and 46% sublimated in dead stands.

Because we made our post-storm measurements immediately following storms, we do not know how much of the intercepted snow was unloaded mechanically subsequent to measurement. As such, we cannot quantify the portions of total sublimation that are due to sublimation in the canopy as opposed to the ground. However, when looking at the sign (±) of *SWE Loss* during storms versus non-storm intervals (Figure 5), it appears the majority of *SWE Loss* occurred during storms. Negative *SWE Loss*, or apparent snow accumulation relative to the reference clearing, could result from either canopy snow unloading or snow sublimation in the clearing. Since most of this negative *SWE Loss* occurred without actual additional accumulation in the forest, it is likely due to sublimation in the clearing. Positive *SWE Loss* that is coincident with precipitation events suggests that the majority of sublimation in our forest stands occurred from canopy snow.

DISCUSSION

At maximum pre-melt SWE, dead and living pine stands had accumulated 45.6 and 38.1 cm SWE, respectively. This represents 91 and 76% of accumulation in the reference clearing. This difference between dead and living stands likely results from dissimilar canopy snow interception during individual precipitation events. During the interval DoY 62–88, dead and living pine canopies intercepted 18 and 41% of incoming snowfall, respectively. Through a comparison of season- and storm-scale subcanopy snow accumulation, we estimated 46% of snow falling on dead stands sublimated and 72% of snow falling on living stands sublimated.

The sublimation of intercepted snow can be substantial, with up to 40% of the annual snowfall sublimating from conifer canopies (Troendle & Meiman 1986; Pomeroy & Gray 1995; Hedstrom & Pomeroy 1998; Lundberg *et al.* 2004). This statistic refers to the percentage of snowfall that was intercepted by the canopy and later sublimated. As mentioned in the Results, we were unable to partition our estimates of snow sublimation into canopy and ground components. For the interval DoY 62–88, our estimates of *total* sublimation (i.e., from both the ground and the canopy) are 72, 46 and 40% for living stands, dead stands and the reference clearing, respectively. Our measurements are very

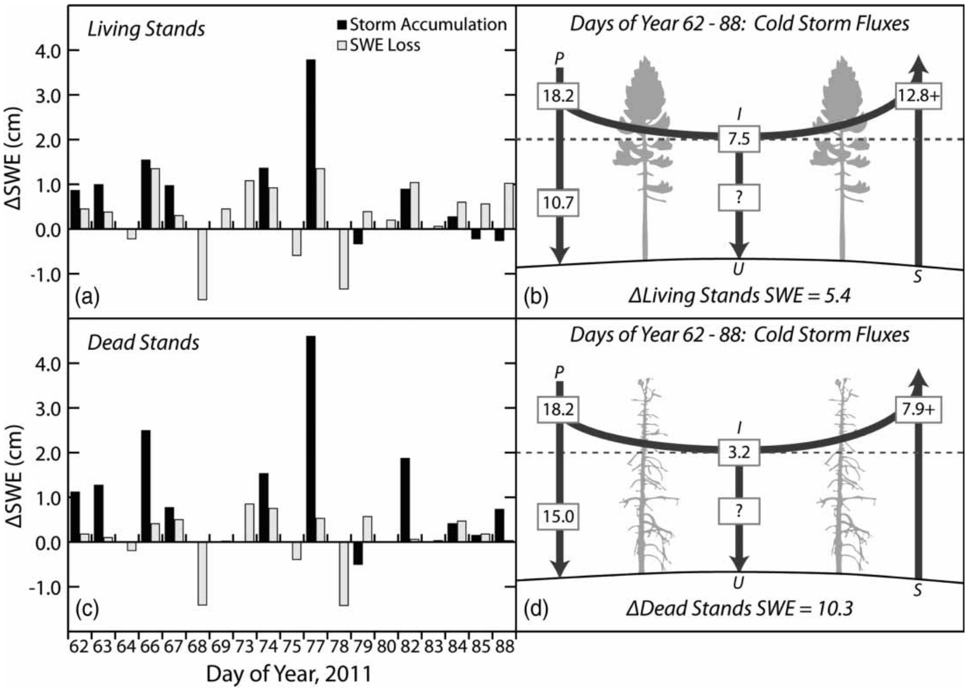

Figure 5 | Water fluxes during the interval DoY 62–88. (a) Storm accumulation and *SWE Loss* in living stands. (b) Water mass balance in living stands, represented as cm SWE. (c) Storm accumulation and *SWE Loss* in dead stands. (d) Water mass balance in dead stands, represented as cm SWE. *P* indicates precipitation, *I* indicates interception, *U* indicates unloading and *S* indicates sublimation.

indirect and are only suggestive, based on SWE changes measured on the ground. These values need to be confirmed via more direct measurements from eddy covariance or similar methods. Because *SWE Loss* was largely coincident with precipitation, we estimate that the majority of the sublimation taking place in the living stands occurred from intercepted canopy snow. This assessment agrees with the findings of studies conducted in both maritime and continental climates, which suggest the majority of snow sublimation from conifer forests occurs from the canopy rather than from the ground (Storck *et al.* 2002; Molotch *et al.* 2007).

Our analyses are dependent on assumptions that introduce uncertainty to these results. We assumed that the observed differences in snow accumulation were the result of tree death, not simply an artefact of differences that existed between the stands prior to MPB infestation (Pugh & Small 2012). Given the limited topographic variations across the study area, differences in slope, aspect and microclimate are negligible between the sites. However, the dead stands studied did have larger diameter trees and lower stem densities (Table 1), consistent with the preference of MPB for infesting larger trees (Negrón & Popp 2004). Therefore, some of the measured differences in snow accumulation are likely due to stand structure and canopy characteristics that existed prior to tree death (Woods *et al.* 2006). We would have likely observed even greater differences in snow accumulation between living and grey phase stands if (1) all of the trees in our living stands had been alive (i.e., no red phase trees) or (2) the living stands had had similar diameters and stem densities as the dead stands. Finally, if we had chosen a different clearing to be our reference clearing, our calculated amounts of intercepted snow would have been different (Table 3). For example, if we had used the 1.76*H* clearing as our reference, intercepted snow amounts would have been larger. However, the difference in calculated interception between living and dead stands would not have varied greatly (<7%).

Decreased interception in dead stands is likely the result of both reductions in the amount of canopy material and changes in the branch-scale mechanisms of interception and subsequent sloughing. At the stand scale, the magnitude of subcanopy snow accumulation is inversely related to canopy cover (Varhola *et al.* 2010), presumably due to the effects of canopy material on snow interception. It follows that a reduction in canopy material in dead pine stands should yield reduced interception and greater snow accumulation on the ground. LAI′ in the grey phase stands is 0.81 whereas LAI′ in the living stands is 1.20. Therefore, approximately one-third of the canopy material that could intercept snow has been shed from grey phase stands. If the amount of canopy material was the only control on interception, we would expect that interception was lower in dead stands by a similar magnitude. However, over the 10 snow-only events during the analysis period, the total amount of interception was 7.5 cm SWE in living stands and 3.2 cm SWE in dead stands (Figure 5). This is a larger change than one would predict from changes in LAI′ alone.

Table 3 | The percentages of precipitation intercepted in living and dead stands between DoY 62 and DoY 88 calculated using the three different clearings as reference

Clearing (*size*)	**Site 1 (*0.86H*) (%)**	**Site 2 (*1.73H*) (%)**	**Site 3[a] (*3.76H*) (%)**
Living interception	37	52	41
Dead interception	8	30	18
Difference (living – dead)	29	*22*	*23*

[a] As described in the text, Site 3 was used as reference clearing in all other calculations of interception.

A reduction in overall tree canopy cover does not completely represent the changes in canopy conditions in dead pine stands. Branches on dead pines can hold smaller snow loads than living branches because of mortality-driven transformations in flexibility, shape and needle-cover. By the time dead lodgepole pines enter the grey phase, branches are less flexible than living branches, leading to accelerated sloughing of snow from twigs and branches (Klutsch *et al.* 2009; Teste *et al.* 2011). A substantial portion of this sloughing occurs during storms. Therefore, snow could be intercepted and temporarily held by the canopy, but fall to the ground prior to our post-storm measurements. Branches that do remain on grey phase trees are bent downward (Figure 6). This increases the bedding angle of intercepted snow, which enhances sloughing even more. The removal of needles and twigs on branches will increase the mean branch diameter. This reduces snow bridging and decreases snow load holding capability (Schmidt & Pomeroy 1990; Schmidt & Gluns 1991; Pfister & Schneebeli 1999).

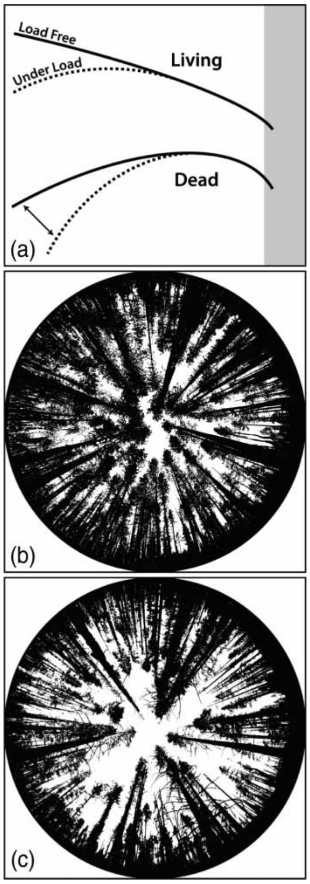

Figure 6 | (a) Branch shape and deflection commonly observed in living and grey phase dead lodgepole pine found in north-central Colorado. Hemispherical photographs of two lodgepole pine stands with similar basal area. (b) A living stand with an LAI′ value of 1.29 and (c) a grey phase dead stand with an LAI′ value of 0.73.

Finally, the thinner canopies in grey phase stands should be subjected to higher wind speeds than canopies in living stands (Tarboton & Luce 1997; Hellström 2000). Unloading of intercepted snow should be more rapid in grey phase stands due to higher wind speed within the canopy.

The way that canopy processes are represented in commonly used interception models is likely insufficient to predict changes associated with beetle-induced conifer death. Simple models scale interception linearly with canopy cover (Hellström 2000). Our LAI′ and interception data show that this approach underestimates the changes in interception resulting from tree death. More complex models predict interception using LAI′ in conjunction with parameters that represent snow loading capacity and branch morphology. For example, the Hedstrom & Pomeroy (1998) model also uses a species-specific snow loading coefficient (B), canopy plan area (C_p) and an unloading coefficient (U). These types of models can more adequately represent changes associated with tree death, if data exist to constrain parameter values. The Hedstrom & Pomeroy (1998) model incorporates a term for branch snow load capacity, B, which represents the maximum snow load per unit of branch area for a given tree species. For this term, Schmidt & Gluns (1991) suggest a value of 6.6 kg m^{-2} for pines. Assuming this value is appropriate for the living stands observed here, we suggest lower values for B would accurately represent maximum dead-branch snow loads. The maximum value of dead canopy snow load we observed in 2011 (Figure 4(b)) was roughly half of that observed in living canopies.

Modifications should also be made to the model terms for canopy plan area (C_p) and unloading rate (U). If snow fell vertically on a forest, the canopy leaf area available for interception (C_p) would equal the area of the top of the forest canopy, which is roughly equivalent to canopy density. Hedstrom & Pomeroy (1998) suggested that mature forest stands with wind speeds greater than 1 m s^{-1} should have a C_p value of 100%. This is because horizontal wind speeds would provide falling snow with diagonal trajectories capable of reaching all potential canopy areas, including those areas below the upper canopy. However, in a grey phase stand, the probability of a snowflake hitting a branch should be lower, because most branches are devoid of needles and twigs. Thus, for a given wind speed, snowflake–branch contact is less likely in a dead stand than a living stand. Furthermore, a reduction in C_p also decreases the predictive ability of LAI′. For canopies with C_p values less than 100%, such as grey phase stands, LAI′ becomes a weaker predictor of interception efficiency (Hedstrom & Pomeroy 1998). The intercepted snow unloading coefficient (U) is another parameter that should be modified following tree death. As described above, U is likely larger and more rapid in grey phase stands due to faster average canopy wind speeds, downward-bending branches and the increased likelihood of branch-breakage under snow loads.

Had this study been conducted in British Columbia, Canada (lower elevation, higher latitude) instead of in the Rocky Mountains of Colorado, a number of key site characteristics would likely have been different. Lower solar zenith angles, wind speeds and temperatures during storms would have increased the ability of living stands to intercept and retain canopy snow as well as have reduced the prevalence of sublimating conditions. The net effect of more interception but reduced likelihood of sublimation (e.g., Hedstrom & Pomeroy 1998) is unclear.

CONCLUSIONS

Grey phase lodgepole pine stands intercept more than 50% less snow than living stands. Canopy interception is significantly correlated with storm magnitude in living stands, as predicted from earlier studies, but not in dead stands. In addition to reduced leaf area, this diminished capacity to intercept snow is likely due to a combination of other forest structure changes including modifications to branch morphology and flexibility. Because less snow is intercepted in dead canopies, substantially less snow is removed by snow sublimation. This decrease in sublimation losses led to 20% more subcanopy snow accumulation over the course of a season. We suggest that both the simple and more complex models commonly used to predict canopy snow interception are likely inadequate to model the interception of snow in dead stands like those studied here. Models that explicitly account for interactions between different scales of interception platform (e.g., needles, twigs, branches), branch orientation and flexibility, total plant area and the top-of-canopy energy balance may be necessary.

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