HYDROLOGICAL PROCESSES
Hydrol. Process. **27**, 2048–2060 (2013)

(wileyonlinelibrary.com) DOI: 10.1002/hyp.9312

A conceptual model of water yield effects from beetle-induced tree death in snow-dominated lodgepole pine forests

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Abstract:

In regions of western North America with snow-dominated hydrology, the presence of forested watersheds can significantly influence streamflow compared to areas with other vegetation cover types. Widespread tree death in these watersheds can thus dramatically alter many ecohydrologic processes including transpiration, canopy solar transmission and snow interception, subcanopy wind regimes, soil infiltration, forest energy storage and snow surface albedo. One of the more important causes of conifer tree death is bark beetle infestation, which in some instances will kill nearly all of the canopy trees within forest stands. Since 1996, an ongoing outbreak of bark beetles (*Coleoptera: Scolytidae*) has caused widespread mortality across more than 600,000 km^2 of coniferous forests in western North America, including numerous Rocky Mountain headwaters catchments with high rates of lodgepole pine (*Pinus contorta*) mortality from mountain pin beetle (*Dendroctonous ponderosae*) infestations. Few empirical studies have documented the effects of MPB infestations on hydrologic processes, and little is known about the direction and magnitude of changes in water yield and timing of runoff due to insect-induced tree death. Here, we review and synthesize existing research and provide new results quantifying the effects of beetle infestations on canopy structure, snow interception and transmission to create a conceptual model of the hydrologic effects of MPB-induced lodgepole pine death during different stages of mortality. We identify the primary hydrologic processes operating in living forest stands, stands in multiple stages of death and long-dead stands undergoing regeneration and estimate the direction of change in new water yield. This conceptual model is intended to identify avenues for future research efforts. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS forest hydrology; bark beetle infestation; tree death; ecohydrology; snow accumulation and melt; water yield

Received 17 October 2011; Accepted 2 March 2012

OVERVIEW

Forest canopies affect snow accumulation and melt regimes at the forest floor by attenuating incoming sunlight and precipitation and by reducing wind speeds and regulating the subcanopy microclimate (Bernier, 1990; Marks *et al*., 1999; Pomeroy *et al*., 2009; Varhola *et al*., 2010). Across western North America, tree mortality from bark beetles has affected large areas of coniferous forest, resulting in thinned canopies in more than 600,000 km^2 of forested watershed since 1996 (Bentz *et al*., 2009). By causing changes to snow dynamics, evapotranspiration, soil moisture and other factors, this dramatic change in forest structure has potentially significant implications for water yield in affected watersheds (Boon, 2009, 2011; Pugh and Small, 2011).

Several recent peer-reviewed studies have investigated particular aspects of the effects of tree death on hydrology (Boon, 2007, 2009, 2011; Bewley *et al*., 2010; Winkler *et al*., 2010; Pugh and Small, 2011). However, effects of tree death on multiple hydrologic processes are still poorly understood, and many questions remain about how hydrologic processes and resultant flow regimes change throughout the duration of a bark beetle attack and the subsequent period of forest regeneration (Table I).

Earlier studies (e.g., Love, 1955; Bethlahmy, 1974, 1975; Potts, 1984; results summarized in Table II) used paired-watershed designs to infer quantitative changes in water yield because of bark beetle infestations. Although all of these studies found significant increases in water yield and other flow variables, Alila *et al*. (2009) questioned the wisdom of relying on paired-watershed analyses in understanding the influence of forest cover removal on water yield. They noted that the ANOVA and ANCOVA analyses used in these articles did not incorporate changes in the frequency of flooding and peak flow events and may be influenced by the difficulty in matching peak flows between the paired basins from individual storm events, especially in snow-dominated regions (Alila *et al*., 2009). In addition, these earlier studies did not quantify the level of mortality in study watersheds using consistent or precise methods and did not consider the fact that snow accumulation in mountainous regions with sharp relief may differ significantly over relatively short distances, making it difficult to find accurate control and treatment watersheds (Faria *et al*, 2000).

To begin addressing gaps in our understanding of hydrologic effects from bark beetle infestations, we consider what relevant literature says about the effects of widespread tree death and then present a conceptual model aimed at synthesizing current knowledge and identifying future research directions. We focus on understanding the temporal changes in hydrologic processes that occur

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Table I. Some outstanding questions about the hydrologic effects of bark beetle–induced tree death, as discussed during the Western Water Assessment–sponsored beetle–water symposia held in April 2010 and April 2011 (for more information, see http://wwa.colorado.edu/ecology/beetle/other.html)

Do bark beetle–infested forests yield more water overall, as is the case with harvested forests?
Does the cessation of evapotranspiration in dead trees lead to higher low flows during the growing season?
Does increased accumulation and shortwave radiation through more open canopies in dead forests increase peak flows during snowmelt?
How do the relevant processes controlling snow accumulation and melt change during the different stages of tree mortality?
How will fallen trees knocked over in major blowdown events affect snow accumulation and ablation?
How will regenerating forests affect water yield and peak and low flows?

Table II. Summary of historical findings from paired-watershed studies aimed at understanding water yield effects of bark beetle infestations

Study	Basin	Dominant tree species	Inferred change in water yield after infestation
Love (1955)	White River, CO	*Picea engelmannii*	+14% to +26%
Bethlahmy (1974, 1975)	White River, CO	*P. engelmannii*	+15%
	Yampa River, CO	*P. engelmannii*	+16%
Potts (1984)	Jack Creek, MT	*Pinus contorta*	+15%

throughout the course of successive postmortality stages resulting from a beetle infestation rather than treating bark beetle epidemics as static episodes. This contrasts with most of the literature on this topic, which treats affected stands as having binary states: “living” or “dead” (*e.g.*, Boon, 2009; Adams *et al.*, 2011). To provide additional empirical evidence supporting aspects of our conceptual model, we surveyed effective leaf area index (LAI′) and derived effects on canopy snow interception and canopy shortwave transmission in lodgepole pine (*Pinus contorta*) stands.

In the Influence of Forests on Hydrologic Processes in Snow-Dominated Regions section, we review the influences of an undisturbed forest on relevant subcanopy hydrologic and meteorologic processes and discuss the connection between forest hydrology and streamflow, using existing knowledge to set baseline parameters for our conceptual model. In the Harvesting and Other Forest Changes as Analogues for Bark Beetle Attacks section, we review literature on disturbances such as harvesting, fire and tree girdling and assess their relevance as analogues of insect infestation in their effects on hydrologic processes. In the Empirical Measurements of Effective Leaf Area Index section, we report the results of our canopy structure survey in lodgepole pine stands across northern Colorado. Then, by synthesizing these results along with findings from other literature on both bark beetle infestations and relevant analogue disturbances, we present in the Conceptual Model section a process-based, time-varying conceptual model of tree death effects to hydrology intended to help develop testable hypotheses to guide future research. Finally, we acknowledge the many mediating factors that create watershed-scale variability in the expression of hydrologic effects of tree death and conclude by discussing the implications of this variability for water management.

Because bark beetles are most common in high-elevation forests of the western USA, this article focuses on hydrologic effects in these snowmelt-dominated regions. We also limit our analysis to effects of bark-beetle-killed trees on major hydrologic processes including snow accumulation, melt timing and water yield. Further, given that affected lodgepole pine forests in western North America are well studied and often occur in the headwaters of rivers crucial to regional water resources, we present our conceptual model as a set of sequential stages of forest mortality in the manner observed in lodgepole pine ecosystems (Wulder *et al.*, 2006).

We do not assess the potential effects of beetle infestation on nutrient cycling and water quality. Although significant research has been devoted to understanding biogeochemical cycling in forested regions (*e.g.*, Fahey *et al.*, 1985; Parsons *et al.*, 1994; Yang *et al.*, 2010), only a few empirical analyses have assessed the effects of widespread tree mortality on those cycles (*e.g.*, Knight *et al.*, 1991; Griffin *et al.*, 2011). These and other initial results seem to demonstrate that bark beetle attacks are unlikely to result in significant increases in stream nitrate concentrations (Clow *et al.*, 2011; Cooper *et al.*, in prep). However, little work has been performed to try to observe significant changes in nutrient levels at the watershed scale.

In describing effects caused by tree death after beetle attack, we will refer to changes to individual trees and to stand structure as a series of stages in an idealized lodgepole pine stand. Stage 0 (undisturbed forest) is a conceptual baseline, describing hydrologic processes in a state of no major disturbance. After a successful bark beetle attack, trees die and evapotranspiration ceases within weeks or months, but needles often retain moisture and appear green for approximately 1 year, which is thus termed stage 1 (green phase) (Wulder *et al.*, 2006). After 1 year postattack, stands proceed into stage 2 (red phase), as needles turn red and brown and begin to fall to the ground. After approximately 2 to 3 years in the red phase, trees lose all of their needles and are considered to be in stage 3 (grey phase) (Wulder *et al.*, 2006). Eventually, a stand enters stage 4 (tree fall phase) when individual trees begin to fall to the ground, although the timing of these tree falls varies widely based on tree species and the occurrence of stochastic events such as weather events and soil moisture conditions (Veblen *et al.*, 1991; Lewis and Hartley, 2006; Wulder *et al.*, 2006; Klutsch *et al.*, 2009). During stage 5 (forest regeneration phase), hydrologic processes may shift back towards baseline levels as forested areas regenerate. Note that real-world watersheds usually feature a patchwork of stands in various stages, and even within individual stands, different clusters of trees may experience different stages at one time, making generalizations about hydrologic effects difficult. It is also important to recognize that conifer species other than lodgepole pine experience different timing of postinfestation mortality stages. For example, spruce trees (*Picea spp.*) do not experience a true red phase, as their needles fall to the ground much more rapidly than pine needles.

INFLUENCE OF FORESTS ON HYDROLOGIC PROCESSES IN SNOW-DOMINATED REGIONS

Before describing effects of bark beetle–induced tree death on specific hydrologic processes, it is important to note that the relationship between forest hydrology and streamflow in snow-dominated regions is complicated by a variety of factors. Once frozen precipitation enters a watershed, it can accumulate as snowpack, melt into groundwater storage or exit through surface runoff, hyporheic exchange or evapotranspiration. Thus, streamflow generated from forested watersheds is controlled by a combination of surface and groundwater processes (Bonell, 1993).

Our conceptual model, described in the Conceptual Model section, traces several of these processes throughout the course of tree death after bark beetle infestation, along with predicted changes in major streamflow variables. Here we set the context for the baseline levels for the model by describing the influence of intact, living forest canopies on hydrologic processes in snow-dominated regions (Figure 1).

Water yield from a forested watershed is controlled by both the water budget and the energy budget in the watershed. The water budget, in turn, is largely governed by the amount of incoming precipitation that actually reaches the forest floor. Up to 60% of incoming snowfall is intercepted by the forest canopy and of that, as much as 40% is sublimated back to the atmosphere (Pomeroy and Schmidt, 1993; Pomeroy and Gray, 1995; Hedstrom and Pomeroy, 1998) without adding to snowpack, groundwater or runoff. During the winter, most precipitation that does reach the forest floor remains in frozen form as part of the snowpack. With the onset of warmer spring temperatures, the snowpack begins to melt, and exiting water either infiltrates through the soil into groundwater storage or flows out of the watershed as surface runoff. Water in subsurface storage can be drawn by trees and exit the system through evapotranspiration, which varies in magnitude by tree species (Rutter, 1968) and is significantly affected by the length of the growing season (Molotch *et al.*, 2009). In addition, water may exit the watershed because of evaporation and/or sublimation, a turbulent flux that increases with faster wind speeds. Sublimation at the forest floor is decreased relative to a clearing through the reduction of wind speeds by the canopy (Bergen, 1971; Bernier, 1990).

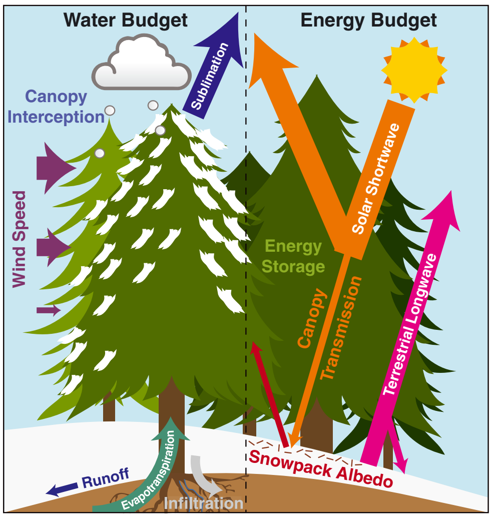

Figure 1. Relevant meteorologic and hydrologic processes in a snow-dominated forest system

The rate at which any of these water balance processes occurs is in turn governed by the energy balance within the forest. The amount of incoming solar radiation transmitted to the forest floor is primarily controlled by the attenuation of shortwave radiation by the canopy (Sampson and Smith, 1993), a process that changes significantly during tree death after a bark beetle attack. This transmitted solar radiation is the most significant energy input into the snowpack, and its ability to melt snow is affected by the snow surface albedo, which in turn is affected by the presence of forest litter or other impurities (Melloh *et al.*, 2001, 2002). Subcanopy long-wave reemission, the release of heat energy from the trees themselves (Rouse, 1984; Ni and Woodcock, 2000), comprises an additional component of overall energy available for melt, which controls the rate at which snow accumulated on the forest floor changes to liquid water. Thus, relative to clearings, areas under forest cover exhibit major differences in snow accumulation, melt timing and water yielding. In Table III, we highlight relevant findings from the literature on the quantifiable effect of forest cover on various hydrologic processes in a snow-dominated environment.

It is important to note that the processes affecting melt timing and water yield from a forested watershed often have opposing effects that are difficult to parse during natural disturbances. For example, although canopy interception reduces the amount of snowfall that reaches the forest floor, intact forest stand structure also reduces

Table III. Effect of canopy cover on hydrologic processes in snow-dominated watersheds, as compared with a clearing

Process	Effect of forest cover relative to clearing	References
Evapotranspiration	After snowmelt, forests lose soil water to tree transpiration. Lower wind speeds reduce the variability of subcanopy humidity and temperatures, which allows for an increase in tree transpiration	Rutter (1968), Kaufmann (1985), Raynor (1971), Link and Marks (1999) and Dixon and Grace (1984)
Soil infiltration	Tree roots create macropores in forest soils, allowing for increased hydraulic conductivity between soil horizons	Noguchi *et al.* (1997) and Brooks *et al.* (2010)
Solar transmission	Tree canopies attenuate incoming shortwave radiation and trap it in the subcanopy	Pomeroy and Dion (1996) and Sampson and Smith (1993)
Needle fall	Needle fall creates a snowpack litter layer, which reduces snowpack albedo and causes earlier snowpack depletion. The accumulation of litter on the forest floor increases soil infiltration	Pomeroy and Dion (1996), Hardy *et al.* (1998), Melloh *et al.* (2001, 2002) and Pugh and Small (2011)
Wind speed	Forests exhibit slower average wind speeds, which vary with height in canopy. This wind screen effect reduces subcanopy air temperature variability	Bernier (1990) and Raynor (1971)
Canopy energy storage	Water in trees stores heat energy from sunlight and ambient air. The reemission of this heat helps lower variability in subcanopy air temperatures and humidity	Rouse (1984) and Pomeroy *et al.* (2009)
Canopy snow interception and sublimation	Forest canopies intercept up to 60% of incoming snowfall. Of that, up to 40% is sublimated back to the atmosphere. Clearings experience more sublimation due to faster wind speeds and steeper vapor pressure gradients	Pomeroy and Schmidt (1993), Pomeroy and Gray (1995), Hedstrom and Pomeroy (1998), Molotch *et al.* (2009) and Varhola *et al.* (2010)
Snow accumulation	Forests accumulate less snow due to canopy snow interception and subsequent sublimation	Golding and Swanson (1978), Veatch *et al.* (2009) and Molotch *et al.* (2009)
Snowmelt timing	Forests retain snow later into the melt season. Melt timing advances as canopy cover decreases	Gary and Troendle (1982), Molotch *et al.* (2009) and Varhola *et al.* (2010)
Water yield	Water yield increases as forest canopy density decreases due to forest treatments, although a minimum threshold is necessary	Knight *et al.* (1991), Brown *et al.* (2005) and Bosch and Hewlett (1982)

ablation because of direct sunlight and wind, making forest cover the strongest predictor of timing and magnitude of both snow accumulation and ablation (Varhola *et al.*, 2010). Overall, forests generally not only reduce snow accumulation but also cause snow to melt more slowly than would be the case in a clearing. Although the effect of various forest disturbances on hydrologic processes is highly variable, most results suggest that anthropogenic disturbances (*e.g.*, varying levels of harvesting) increase water yield (Bosch and Hewlett, 1982), with clear-cutting resulting in as much as a 277% increase in water yield in one study (Knight *et al.*, 1991). The findings of increased water yield from harvested stands imply that canopy density is the dominant forest influence affecting water yield. To date, however, studies looking at the effects of natural forest die-off portray much more varied changes to water yield (Adams *et al.*, 2011; Guardiola-Claramonte *et al.*, 2011).

As a given stand moves through the various stages of beetle-induced tree mortality (introduced in the Overview section), many of the parameters affecting water yield will change. Our conceptual model traces likely changes in the processes outlined above through the stages that follow beetle-induced tree death and attempts to synthesize resulting effects on water yield variables while noting the numerous complexities of forest hydrology that make predictions difficult.

HARVESTING AND OTHER FOREST CHANGES AS ANALOGUES FOR BARK BEETLE ATTACKS

As briefly discussed by Adams *et al.* (2011), the hydrologic effects of potential analogues to forest die-off (*i.e.*, tree harvesting and fire) are important to consider. However, these analogues do not address the critical temporal element of beetle attacks. More specifically, beetle attacks cause forest stands to change over the course of several years, whereas both harvesting and fire cause nearly immediate changes to a watershed. A more appropriate analogue for beetle infestations is tree girdling, although only one hydrologic study has used it for that purpose, finding a 92% increase in water yield compared with an undisturbed stand, one third of the increase produced in a clear-cut stand (Knight *et al.*, 1991). Thus, we focus on using relevant aspects of the literature as appropriate to inform the conceptual model without relying on any particular analogue.

Conventional wisdom regarding the effect of bark beetle attacks on hydrologic processes is largely based on studies investigating other changes to forest cover, especially harvesting (Lukas and Gordon, 2010). For example, a long history of harvesting experiments in forested watersheds has helped demonstrate a relationship between reduction in forest cover and increase in water yield (e.g. Hibbert, 1967; Bosch and Hewlett, 1982; Stednick, 1996; for a review, see NRC, 2008). As discussed in the Influence of Forests on Hydrologic Processes in Snow-Dominated Regions section, reducing forest cover increases snow accumulation through a reduction in interception and redistribution of snowpack and also increases wind speeds, leading to larger evaporative losses from sublimation (Stegman, 1996). Overall, tree harvesting can dramatically increase snow accumulation; for example, researchers in Colorado found an increase in peak snow water equivalent of more than 90% after removing 1 ha of forest (Stottlemeyer and Troendle, 2001), and a review of studies in the Pacific Northwest found water yield increases of approximately 6 mm per percentage of canopy cover removed (Moore and Wondzell, 2005). These findings have bolstered the conventional wisdom that widespread tree mortality from bark beetle infestation necessarily results in increased water yield.

Harvesting, however, does not provide a good analogy for bark beetle attacks in many respects. Even in “dead” stands in the grey phase of a beetle attack, 20% to 30% of the trees are still living (Romme *et al.*, 1986; Klutsch *et al.*, 2009), often younger trees that exhibit higher ET rates than the mature trees that dominated the canopy before beetle attack. Knight *et al.* (1991) found that water outflow increases were three times higher in a clear-cut stand (100% of trees removed, 100% reduction in leaf area) than that in a stand with 60% of trees killed and a 43% reduction in leaf area, which would be more typical of a beetle-infested stand. Also, snow accumulation only increases until reaching a threshold of harvested area before ablation offsets the reduction in interception. One review found optimum snow accumulation in subalpine forests when harvested patches were limited to eight times the height of a neighbouring stand (Leaf, 1975). Finally, harvesting using mechanical equipment often results in soil compaction, greatly reducing infiltration rates and increasing overland flow (NRC, 2008). Harvesting thus likely overrepresents the increases in water yield and other effects that might occur with bark beetle attacks.

Fires, both wildfires and prescribed fires, can also significantly reduce leaf area and forest cover, in some cases shifting an entire stand into the equivalent of late grey phase conditions within minutes to hours. High-severity fires, or those that kill many canopy trees, generally increase water yield, peak flows and low flows (NRC, 2008) by reducing canopy interception and ET, similar to the observed effects of tree harvesting. The remaining standing dead trees can attenuate shortwave radiation, temperature, accumulation and wind speed relative to a clear-cut plot (Burles and Boon, 2011). However, fires also have the potential to reduce infiltration and increase water repellency in soils, especially in coniferous forests (NRC, 2008). High-severity fires change several chemical and physical properties of soils. For example, fires can create a hydrophobic layer at the soil surface (Certini, 2005), increasing the amount of overland water flowing directly into streams and potentially increasing peak flows during snowmelt and runoff. In addition, soil sealing can reduce infiltration, slowing the rate at which water reaches tree roots or groundwater (NRC, 2008). Soil water repellency has been found, in one area, to become nondetectable 1 year after fire (MacDonald and Huffman, 2004), but some high-severity fires can result in long-term changes to certain soil properties (Certini, 2005). In addition, fire can also result in major reductions in understory biomass (Adams *et al.*, 2011).

Thus, forest fire is generally not a useful analogue for the effects of bark beetle on hydrologic processes. The period of time from predisturbance to significant canopy removal is much shorter in the fire analogy, leading to much more immediate effects but potentially faster forest regeneration, depending on fire severity, tree species and predisturbance site conditions such as precipitation and elevation. Moreover, as discussed, fire can change the movement of water into soil, which likely will result in different net effects on water yield and peak and low flows compared with a bark beetle attack, which may affect different soil properties (*e.g.*, loss of fine roots, increased bulk density of soil and lower porosity).

A small number of experiments have used girdling, or cutting through the living cambial tissue around the circumference of a tree to induce tree death, to study the effects of tree death in isolation. By causing tree death without affecting soil properties or drastically changing stand structure and composition, girdling studies generally avoid many of the issues that make harvesting and fire poor analogues. Knight *et al.* (1991), mentioned previously, used girdling to mimic bark beetle attacks and found a 92% increase in modelled water outflow in a conifer stand with 60% mortality from girdling. A comparable clear-cut plot showed a 277% increase in outflow, demonstrating the clear difference in magnitude between clear-cutting and other disturbances that do not entail the removal of woody biomass and widespread soil compaction. Overall, however, girdling in coniferous stands is more commonly used to assess biogeochemical cycling (*e.g.*, Hogberg *et al.*, 2001; Yarwood *et al.*, 2009) rather than water yield, possibly due to the labour-intensive nature of girdling large plots to effectively study the latter. The paucity of girdling experiments, combined with the difficulty of using other forest disturbances as analogues for bark beetle attacks, leaves us with few empirical findings regarding water yield directly applicable to bark beetle infestations.

EMPIRICAL MEASUREMENTS OF EFFECTIVE LEAF AREA INDEX

To provide additional empirical results to bolster specific aspects of our conceptual model, we make stand-scale estimates of effective LAI′ and use the results to model the effects of tree death on canopy processes such as snow interception and solar transmission. LAI′ is defined as the product of a clumping factor (Nilson, 1971) and the leaf area index (Black *et al.*, 1991). When derived from hemispherical photography, values of LAI′ reflect total plant area (*i.e.*, include estimates of canopy woody material). Because LAI′ derived from hemispherical photography captures trunk, branch and twig area in addition to leaf area, it is a good metric for tracking diminished total canopy area during tree death. Models of canopy snow interception and light transmission often use LAI′ in lieu of leaf area index because canopy woody material also contributes to the interception of precipitation and sunlight (see next section).

Our LAI′ estimates are derived from 468 hemispherical photographs taken in 39 living and beetle-killed dead lodgepole pine stands during July 2009 and August 2011. To incorporate structural variations in forest with geography, these stands were located at 15 sites across north-central Colorado (Figure 2). Study stands, ranging in elevation from 2614 to 2933 m, are each 2500 m^2 in size and topographically flat. All stands were more than 95% lodgepole pine, and the stand canopies ranged in height from 18 to 25 m. Images were taken 1 m above the ground using a Nikon D700 camera and Sigma EX 8 mm Fisheye lens. Once acquired, images were processed using Gap Light Analyzer software (Frazer *et al.*, 1999), and LAI′ was integrated over the zenith angles 0° to 60° (Stenberg *et al.*, 1994). Stand-scale LAI′ values are calculated from 12 individual hemispherical photographs collected in each stand using the methods described by Pugh and Small (2011).

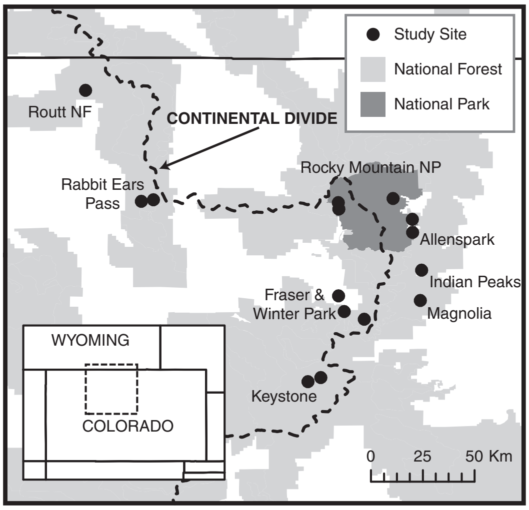

Figure 2. Location of 15 study sites in north-central Colorado. The sites contain 39 stands where hemispherical photographs were collected for forest canopy structure analysis

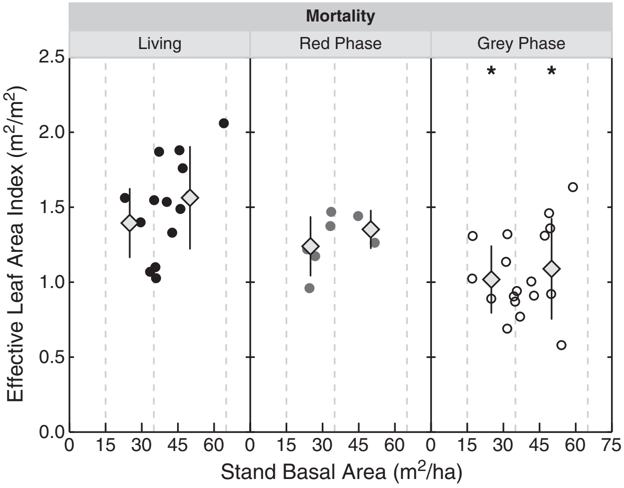

Figure 3. Stand-scale estimates of effective leaf area index (LAI′). Circles represent one stand-scale LAI′ value. Diamonds represent basal area bin means, with lines representing one standard deviation from the mean. *Significant difference from living stands of comparable basal area ($p < 0.05$, Student's *t*-test)

Because stand-scale LAI′ values will increase with increasing basal area, we break study stands into two classes, low (15–35 $m^2\,ha^{-1}$) and high (35–65 $m^2\,ha^{-1}$) basal areas. For basal areas ranging from 15 to 35, stands had mean LAI′ values of 1.39 ± 0.22, 1.24 ± 0.20 and 1.02 ± 0.20 for living, red phase and grey phase mortality, respectively (Figure 3). Stands in the high basal area class had mean LAI′ values of 1.56 ± 0.34, 1.35 ± 0.13 and 1.09 ± 0.30 for living, red phase and grey phase mortality, respectively. Grey phase stands had significantly lower LAI′ values than living stands in both basal area ranges ($p < 0.05$, Student's *t*-test).

Canopy snow interception

Hedstrom and Pomeroy (1998) developed a canopy snow interception model that predicts interception using LAI′, species-specific intercepted load properties, falling snow density and storm size. This model is widely used (*e.g.*, Gelfan *et al.*, 2004) and has been incorporated into several land surface and hydrologic models (Essery *et al.*, 2009; Rutter *et al.*, 2009). A key feature of the Hedstrom and Pomeroy model is interception efficiency that decreases with storm size and approaches an asymptote at a maximum intercepted load. Their model relates intercepted snow mass to LAI′, tree species load capacity, canopy density, air temperature, wind speed and snowfall (see Hedstrom and Pomeroy, 1998). Here we assume an initially snow-free canopy, a maximum plan area value of 1 for snow-leaf contact per unit area of ground (Hedstrom and Pomeroy, 1998), a falling snow density of 70 $kg\,m^{-3}$ (Gelfan *et al.*, 2004) and a lodgepole pine species snow-loading coefficient of 6.6 $kg\,m^{-2}$ (Schmidt and Gluns, 1991). The species snow-loading value used here may be an overestimate of actual conditions in dead pine stands because of changing branch orientation, reduced branch flexibility and needle loss (Pugh and Small, in review). Nonetheless, this model provides a quick assessment of the likely magnitude of interception changes.

We investigate changes to the percentage of intercepted snow in living and dead lodgepole pines by calculating interception using our estimates of stand-scale LAI′ for precipitation events of two magnitudes: 5 and 30 mm (Table IV). Low (15–35 $m^2\,ha^{-1}$) and high (35–65 $m^2\,ha^{-1}$) basal area stands are considered separately. Using this model, high basal area lodgepole pine stands in the grey

Table IV. Percentage of canopy snow interception in various mortality stages for small and large precipitation events and percentage of canopy shortwave transmission in various mortality stages

Interception	Low basal area			High basal area		
Snowfall SWE	Living	Red phase	Grey phase	Living	Red phase	Grey phase
5 mm	75.6%	73.2% (−2.4%)	68.8% (−6.8%)	77.8%	75.0% (−2.8%)	70.4% (−7.4%)
30 mm	27.5%	24.8% (−2.7%)	20.6% (−6.9%)	30.4%	26.8% (−3.6%)	22.0% (−8.4%)
Transmission						
	37.2%	41.5% (4.3%)	48.5% (11.3%)	33.0%	38.3% (5.3%)	46.2% (13.2%)

Values are modelled using LAI′ derived from hemispherical photos of lodgepole pine (*Pinus contorta*) in northern Colorado. Results are given for two basal area classes, low (15–35 $m^2 ha^{-1}$) and high basal (35–65 $m^2 ha^{-1}$) area. Differences from living stand interception/transmission are given in parentheses for red and grey phase stands. For modelling methods, see the Empirical Measurements of Effective Leaf Area Index section.

phase intercept 7.4% and 8.4% less snow than living stands during small and large precipitation events, respectively. Similar stands in the red phase intercept only moderately less snow than living stands (2.4% and 3.6% reductions). Assuming that 60% of intercepted snow sublimates back to the atmosphere, these reductions in canopy snow interception in high basal area grey phase stands could result in additional subcanopy snow accumulation of 8.3% and 6.1% for small and large precipitation events, respectively. These modelled increases in subcanopy accumulation agree in magnitude with recent field observations (Boon, 2011; Pugh and Small, 2011), although they are slightly lower than other model results (Mikkelson *et al*., 2011).

Canopy shortwave transmission

Hellström (2000) modified the Beer–Lambert model for light flux to account for conifer-specific variations in canopy architecture. His model relates under-canopy radiation to above-canopy radiation, LAI′ and an extinction coefficient. This model incorporates variation in transmission with solar zenith angle (Strasser *et al*., 2011). Liston and Elder (2006) tested Hellström's transmission scheme in mixed conifer forest at the USDA Fraser Experimental Forest, which is approximately at the centre of our study region, and arrived at a best-fit extinction coefficient value of 0.71. We used this extinction coefficient value in our calculations. Using Hellström's light penetration model, we investigated changes to the percentage of solar radiation being transmitted through living and dead lodgepole pine canopies. This is accomplished by calculating the percentage of above-canopy radiation that reaches the subcanopy using our estimates of stand-scale LAI′ (Table IV). Using this model, grey phase lodgepole pine stands transmit 11.3% and 13.2% more sunlight than living stands for low and high basal areas, respectively. Red phase stands transmit only moderately more sunlight than living stands (4.3% and 5.3% increases). Pugh and Small (2011) hypothesized that this modest increase in light transmission during the red phase of tree death results from both needle removal and changes in canopy whorl orientation.

In the next section, we describe our conceptual model of the effects that bark beetle–induced tree death can have on several hydrologic variables (Figure 4). The results of the analysis of our LAI′ measurements, along with data related to other variables from recent studies, provide additional empirical evidence for specific aspects of the model.

CONCEPTUAL MODEL

Given the thin empirical literature on the effects of bark beetle to hydrologic processes and the problems with "analogous" disturbances, a conceptual model can help identify priorities for future empirical studies. In Figure 4, we present the hydrologic effects of forest mortality as a temporal sequence divided into stages (described in the Overview section) of bark beetle–induced tree death, canopy changes and forest regrowth. While considering the following conceptual model, it is important to keep in mind that this is a process-driven, rather than a scale-driven, model. Actual hydrologic modelling needs to build on the ideas presented here to understand point-, stand-, watershed- or basin-scale changes.

Stage 0: undisturbed forest

As described in the Influence of Forests on Hydrologic Processes in Snow-Dominated Regions section, forests create sheltered environments relative to clearings. By partially blocking incoming sunlight and storing energy for later reemission, as well as by reducing wind speeds, forest subcanopies exhibit microclimates that are less variable than those of clearings. These processes lead to later snowpack depletion under canopies, although warmer wintertime temperatures in forested stands may lead to an earlier onset of isothermal snowpack. Finally, because of canopy interception and evapotranspiration, forest systems have less available water than clearings, producing less infiltration and runoff. Figure 1 provides a conceptual diagram of these processes in a healthy forest, which are considered baseline levels in Figure 4.

Stage 1: green phase

In the green phase of tree mortality, trees die but retain green needles after death. This phase has been shown in lodgepole pine to last up to 1 year after initial bark beetle

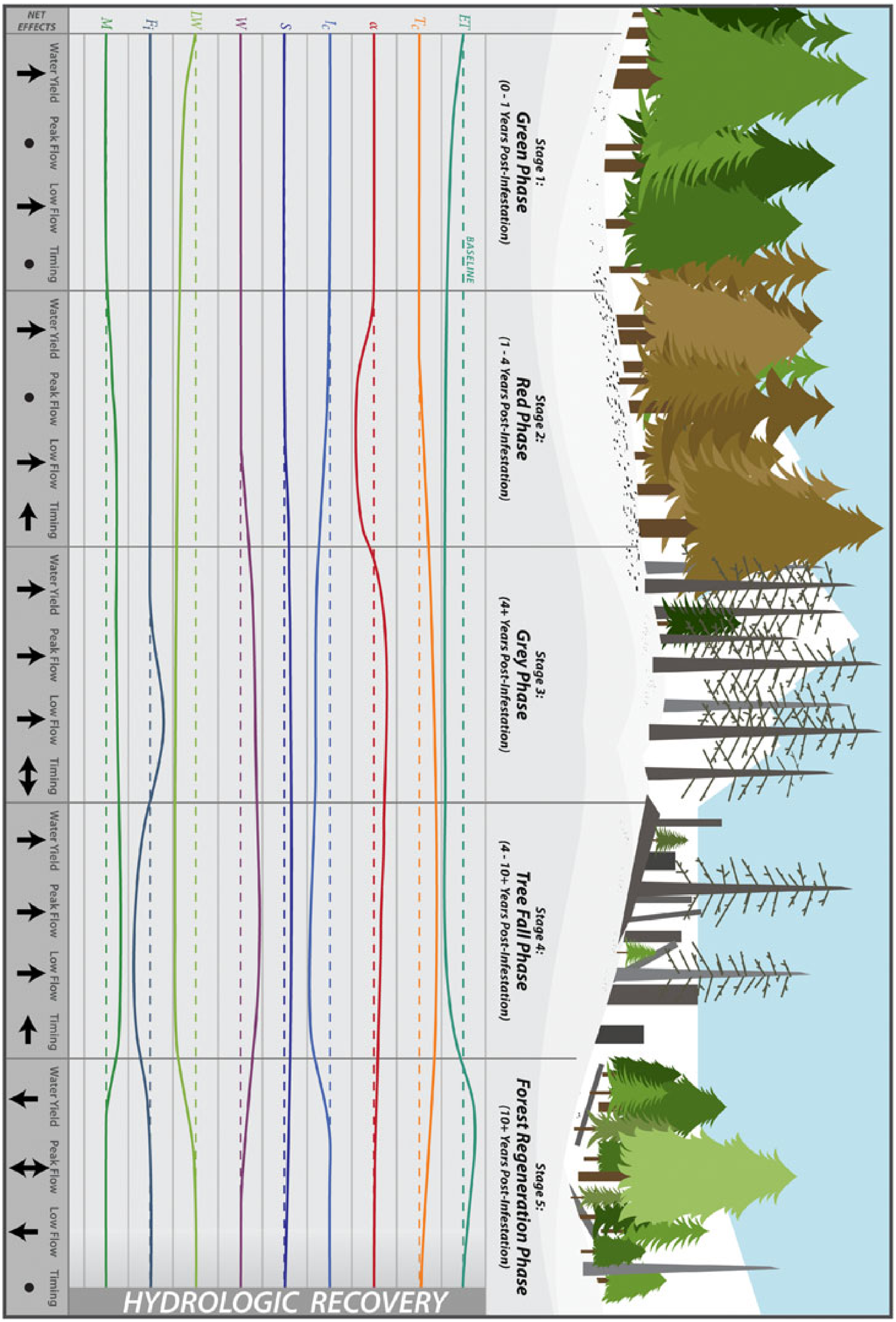

Figure 4. Predicted changes to individual forest processes relative to an undisturbed baseline (dashed line) as a hypothetical forest progresses through the successive stages of death (left to right). Process abbreviations are as follows: evapotranspiration (ET), canopy solar transmission (T_c), snow surface albedo (α), canopy snow interception (I_c), snow sublimation (S), wind speed (W), canopy long-wave reemission (LW), soil infiltration (F_i) and overall melt energy (M). Vertical net effect arrows represent increases and decreases, whereas horizontal arrows indicate advancing or retarding net effects. Double arrows mean the effect could go either way, and black dots represent little or no net change.

infestation (Wulder *et al.*, 2006). The canopy and root systems are undisturbed, maintaining canopy transmission, canopy interception, snow surface albedo, snow sublimation, subcanopy wind speeds, subcanopy melt rates and soil infiltration at close to baseline levels. As the trees die, however, they begin to take up less water through their root systems, quickly reducing ET rates. This reduction in water uptake results in more water staying in the soil. Knight *et al.* (1991) modelled a 92% increase in water outflow in a lodgepole pine stand with 60% mortality from a simulated bark beetle infestation. Subcanopy temperatures, although controlled by incoming shortwave radiation, are regulated in living stands by heat storage in the water within trees. Stored heat is then released upward and downward from the tree canopy as long-wave radiation (Rouse, 1984). As ET is reduced and tree moisture decreases, heat storage in dead trees is less regulated by water's high heat capacity, causing more fluctuation in subcanopy temperatures (Boon, 2009). Overall water yield would be expected to increase relative to undisturbed stands as dead trees no longer take up water. However, given that stand structure and thus canopy interception of snow and solar shading remain essentially the same as before the attack, peak flows resulting from snowmelt are not expected to change, and any observable increases in water yield would likely occur during late summer low flows because of reduced uptake.

Stage 2: red phase

Within approximately 1 year of initial infestation, needles begin to turn red and then brown. These dead needles remain on trees for 2 to 3 years (Wulder *et al.*, 2006). During the early part of the red phase, ET has ceased entirely, and desiccated needles begin to fall to the snow surface, significantly reducing albedo (Winkler *et al.*, 2010; Pugh and Small, 2011). The rate of needle loss in dead conifers is much more rapid than for live trees; for example, lodgepole pine trees naturally retain their needles between 9 and 13 years, depending on forest elevation (Schoettle, 1990, 1994; Vose *et al.*, 1994). Thus, bark beetle attacks cause tree canopies to lose needles and other woody material approximately five times more rapidly than those in living stands (Klutsch *et al.*, 2009; Bigler and Veblen, 2011). Compared with the green phase, the red phase exhibits further reduction in ET rates, reduced snow albedo and increased overall snow melt rate. Although the LAI′ measurements discussed in the previous section did not show a significant difference between the red phase and the undisturbed stands, trees in the red phase show reduced canopy density and are expected to transmit more light (Pugh and Small, 2011). As the canopy thins over low-albedo snow, augmented shortwave (Pugh and Small, 2011) and long-wave (Sicart *et al.*, 2004) energy fluxes will increase subcanopy melt rates. Increased litter accumulation resulting from canopy denudation will likely lead to greater soil infiltration (Martin and Moody, 2001), but it may not be possible to detect such an increase. Overall water yield may increase above green phase as interception rates decline, potentially causing peak flow to increase. Snowmelt timing will also likely shift earlier, with the rising limb of the hydrograph advancing by as much as 1 week (Pugh and Small, 2011).

Stage 3: grey phase

Eventually, the dead trees lose all of their needles and enter the grey phase, appearing to be "skeletons" with only trunks and branches. At 4 years post-infestation, Klutsch *et al.* (2009) found no remaining needles on lodgepole pines in their plots, and our results shown above demonstrate that LAI′ is approximately 30% lower in grey phase stands than living (stage 0) stands. Because canopy density is inversely correlated with snow accumulation (Gary and Troendle, 1982), this loss of canopy greatly reduces interception and canopy snow sublimation (Boon, 2011; Pugh and Small, 2011, in review), leading to increased snow accumulation on the ground. Canopy loss also causes both canopy shortwave transmission to the snow surface and wind speeds to increase (Pollet and Omi, 2002; Page and Jenkins, 2007; Boon, 2009; Pugh and Small, 2011). Wind speeds also change with reduced canopy density; Bergen (1971) observed 30% greater wind speeds through dead branches as opposed to living canopy in lodgepole pine stands. Increased snow surface albedo, due to the cessation of needle drop from the canopy, will mitigate some of the effect of increased transmission (Pugh and Small, 2011). In addition, tree roots, which normally comprise a large proportion of macropores in forest soils (Noguchi *et al.*, 1997), may begin to rot. This transition will leave larger soil macropores in spaces that roots once occupied, increasing soil hydraulic conductivity. Overall runoff is likely still greater than during the red phase because of additional snow accumulation. Peak and low flows remain elevated, and the hydrograph may either remain advanced over baseline or retard because of changes to snowmelt timing associated with the greater ablation energy required to melt augmented snow volumes (Boon, 2009; Pugh and Small, 2011).

Stage 4: tree fall

Depending on the species composition of a given stand, dead trees may begin to fall several years after initial infestation. A study in Oregon showed that most lodgepole pines fell within 5–18 years of death, whereas ponderosa pines generally took longer to fall (Lewis and Hartley, 2006). Researchers in Colorado have noted dead spruce standing more than 40 years after beetle outbreaks (Veblen *et al.*, 1991). Tree fall rates also vary with many other factors including stand density, wind patterns, aspect and soil moisture (Keen, 1955). As trees fall, the complete loss of canopy woody material causes snow interception and solar shading to be reduced to zero, although it is possible that increased surface roughness from downed woody debris at the forest floor may mitigate ablation. Root displacement and subsequent removal of macropores by infilling and compaction will decrease soil hydraulic conductivity to lower than baseline levels, resulting in a larger runoff ratio. Elevated melt rates and higher runoff ratios in this stage are

Table V. Site-specific factors that can influence the changes in hydrologic processes associated with tree death

Forest characteristics	Watershed	Climate/weather	Mortality
Species composition	Elevation	Temperature	Rate of change
Stem density	Slope	Precipitation	Total extent of mortality
Canopy leaf area	Aspect	Humidity	Extent of each mortality phase
Canopy geometry	Basin area	Wind speed	
Tree height	Forested area	Cloudiness	
Regenerating species composition			

expected to lead to higher peak flows, whereas low flows remain elevated pending forest regeneration. Reduced solar shading during this stage will likely lead to advanced snowmelt and result in earlier peak flows.

Stage 5: forest regeneration

Forest regeneration depends on multiple factors, including predisturbance site conditions and species composition. Although we present forest regeneration as a discrete phase in this idealized progression of bark beetle infestation, in the real world, new trees will likely begin to establish, and remaining live young trees will begin to grow more rapidly during stage 3 or 4 (Collins *et al.*, 2011). As the overstory canopy is removed, seedlings or saplings in the understory are released from their energy-limited setting and grow quickly, mitigating reductions in ET (Yang, 1998). These trees eventually create a new canopy, increasing interception and sublimation while reducing shortwave transmission, wind speeds and overall melt rate. The reestablished tree root networks also reintroduce macropores to the subcanopy forest soils, mitigating reductions in soil hydraulic conductivity. The time it takes to reach total hydrologic recovery, when hydrologic processes stabilize near baseline levels, will depend on initial forest composition, post-disturbance seedling recruitment and other factors. Actual timing of recovery is difficult to estimate; in fact, certain stands never return to baseline process levels due to dramatic changes in forest composition (Collins *et al.*, 2011).

Summary

The conceptual model's key predictions are that due to a reduction in canopy density, additional precipitation and shortwave radiation will reach the forest floor in the first few years after a beetle attack. These process changes will likely result in increased overall water yield and earlier snowmelt. Eventually, however, the growth of the understory will result in significantly increased water uptake and increased interception, mitigating the hydrologic effects of the infestation and returning the stand close to baseline levels once the forest has fully regrown.

MEDIATING FACTORS

The mortality stages described earlier are not truly discrete; instead, they should be considered as snapshots of different forest conditions that shift fluidly from one to the other over time. The exact timing of each of these stages and, more critically, the magnitude of process changes, depend on a multitude of variables, including forest structure and species composition, rate of tree death, topography, soil type and precipitation. For example, pure lodgepole pine stands will likely conform more to this conceptual model than mixed conifer stands where tree death is less uniform. Previous studies also demonstrate that the effects of vegetation change on water yield are more pronounced in more humid climates (Bosch and Hewlett, 1982). Finally, differences in rates at which mitigating vegetative processes (*e.g.*, understory regenerative release) occur will change the net effects in different stages. A list of potentially mediating site-specific factors relevant to our conceptual model is presented in Table V.

CONCLUSIONS

Given that previous empirical research on major anthropogenic forest disturbances (*e.g.*, as reviewed in Brown *et al.*, 2005) generally points to increased water yield after disturbance, there is a widespread assumption that bark beetle–induced tree mortality will likewise increase overall yield. The conceptual model presented in this article, however, indicates that reality is likely to be more complex. At a watershed scale, the actual changes in hydrologic processes will result from the interaction of many factors, including the scale of beetle infestation, the proportion of dead trees in a given area, the soil type, the topography and the watershed size. In addition, hydrologic response will vary depending on the postinfestation phase occurring in a given watershed, and any given forested area may be experiencing multiple phases at once. Without assessing site-specific factors, water managers should avoid assuming that watershed-scale increases in water yield will occur. As discussed in the following paragraphs, basin-scale research efforts may help overcome some of these mediating factors and help managers understand larger-scale effects of the beetle infestation on overall flow.

Greater understanding of both the main ecohydrologic processes at work and the factors influencing them will likely require both stand-level process studies and larger-scale modelling work. Bewley *et al.* (2010), for example, measured snow-water equivalent and energy balance components in the field to calibrate the DHVSM hydrology model for a large catchment in interior British Columbia. Model outputs showed increases in both snow accumulation and melt rates over the course of the beetle attack. Depending on the meteorology used in the model, peak SWE values increased by 12% to 19% compared with preattack figures, whereas melt rates increased 10% to 15%. Other researchers are engaged in similar multistage studies on the effects of bark beetle on hydrologic processes and resulting water yield (P. Brooks, personal communication).

The conceptual model presented here is intended to spur future empirical research on the effects bark beetle–induced tree mortality has on major water yield variables. In addition to ongoing process-level studies, we propose two future research directions: (i) coupled forest and hydrologic modelling capable of producing modelled changes in runoff based on a variety of forest death scenarios and (ii) large-scale statistical analyses of the relationships between observed naturalized streamflow data, gridded observed climate data representing basin-wide precipitation inputs and the level of bark beetle–induced tree mortality in basins. One recent attempt to pursue the second research path was conducted by Somor (2010), who found catchment-scale water yield reductions after bark beetle infestation in central Colorado. More work of this type needs to be performed to quantify real-world water yield effects and to understand the processes responsible for observed changes.

Beyond bark beetle attacks, numerous stand-scale studies have produced empirical evidence on the effects of forest disturbance and management practices on hydrologic processes. However, little work has been performed to try to test these results at larger scales, such as entire watersheds (NRC, 2008). Our conceptual model can help develop new testable research hypotheses and guide efforts to scale investigations to a level more useful to water management.

ACKNOWLEDGEMENTS

The authors thank Noah Molotch for use of field equipment and Jeff Lukas, Jeff Deems, Chuck Rhoades and an anonymous reviewer for their helpful comments before submission. They also gratefully acknowledge funding from the NOAA Climate Program office through the Western Water Assessment RISA program at CIRES, University of Colorado Boulder.

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