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Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone

Daniel C. Donato [a,*], Martin Simard [b], William H. Romme [c], Brian J. Harvey [a], Monica G. Turner [a]

[a] Zoology Department, University of Wisconsin, Madison, WI 53706, USA

[b] Department of Geography and Centre for Northern Studies, Université Laval, Pavillon Abitibi Price, 2405 de la Terrasse, Québec City, Québec, Canada G1V 0A6

[c] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

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ABSTRACT

Large-scale bark beetle (Curculionidae: Scolytinae) outbreaks across western North America have prompted widespread concerns over changes to forest wildfire potentials. Management actions following outbreaks often include the harvest of beetle-killed trees and subsequent fuel treatments to mitigate expected changes to fuel profiles, but few data exist to inform these actions. In both lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests of the Greater Yellowstone Ecosystem, Wyoming, USA, we used the Forest Vegetation Simulator to evaluate how fuel profiles, stand structure, and biomass carbon storage are influenced by various post-outbreak fuel treatments (removal of beetle-killed trees ['salvage'] followed by either no treatment, prescribed burning, pile-and-burn, or whole-tree-removal). The model was initialized with field data from five unmanaged gray-stage stands in each forest type and projected over 50 years of post-treatment time. Across all treatment methods, the strongest projected effects relative to unharvested stands were reductions in coarse woody surface fuels (after 10–20 yr), fewer well-decayed standing snags (after 40 yr), and reduced biomass carbon storage (throughout all 50 years). The reduction in coarse woody surface fuels suggests reduced heat release and resistance to control in future fires. Projected effects on fine fuels, both in the canopy and surface layers, were surprisingly minor or short-lived; natural fall and decay of fine material in unharvested stands led to the convergence of most fuel variables between treated and untreated stands within about a decade, especially in Douglas-fir forests. Most follow-up treatment methods – whether unmerchantable tree parts were left in place, burned, piled, or removed entirely – had similar impacts on most aspects of fuel and stand structure in both lodgepole pine and Douglas-fir forests. However, the prescribed burning treatment was distinct and generally had the strongest effects, owing to greater consumption of forest floor mass and mortality of small trees, which had persistent influences on both the canopy and surface fuel layers. Treatment effectiveness in reducing fuels was mirrored by reductions in biomass carbon storage and recruitment of well-decayed snags, illustrating common trade-offs involved in fuel treatments. Harvest of beetle-killed trees and subsequent treatments altered the fuel profile and structure of outbreak-impacted stands, but overall effects were similar among treatments, suggesting flexibility in management options in post-outbreak forests.

1. Introduction

Bark beetles (Curculionidae: Scolytinae) are major native disturbance agents in most temperate coniferous forests, often impacting more land area than wildfire (Raffa et al., 2008). Epidemic eruptions of bark beetles occur periodically and result in up to 80% mortality of trees over scales of 10^3–10^6 hectares (Meddens et al., 2012). These outbreaks can result in significant changes to the structure, function, and composition of forest ecosystems (Romme et al., 1986; Veblen et al., 1991; Hicke et al., 2012a), the signature of which may be apparent for decades to centuries (Collins et al., 2011). Affected stands are often a focal concern for land and resource management, but thus far, scarce information exists on the effects of post-outbreak management interventions on future stand development.

One of the key concerns to arise from the recent bark beetle outbreaks across western North America (>10 million hectares since the late 1990s) is their potential influence on future wildfires

* Corresponding author. Present address: Washington State Department of Natural Resources, P.O. Box 47016, Olympia, WA 98504, USA. Tel.: +1 608 265 8001.
E-mail address: ddonato@wisc.edu (D.C. Donato).

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(Jenkins et al., 2008; Hicke et al., 2012b). The associated pulse of tree mortality is known to significantly alter fuel profiles (arrangement, quantity, and composition of biomass) across several forest types in western North America (Page and Jenkins, 2007a; DeRose and Long, 2009; Klutsch et al., 2011; Simard et al., 2011; Hoffman et al., 2012; Schoennagel et al., 2012; Donato et al., 2013). Primary impacts center on the deterioration and falling of beetle-killed trees, thinning of canopy biomass, subsequent surface fuel accumulations, and eventual growth of understory trees into the midstory (ladder fuels). Each of these changes is expected to influence the intensity and propagation of fire within and between the canopy and surface fuel layers (Hicke et al., 2012b) – albeit to varying degrees depending on forest type, being less evident in structurally variable systems in which outbreak effects have low 'signal-to-noise' relative to background variability (Donato et al., 2013). Empirical studies of fires burning through beetle-affected landscapes have reported equivocal results on outbreak effects on fire severity (the effects of fire to the ecosystem) (Bebi et al., 2003; Lynch et al., 2006; Kulakowski and Veblen, 2007; Bond et al., 2009; Kulakowski and Jarvis, 2011), which may also vary among ecosystems.

Management objectives in beetle-affected forests often include mitigating these alterations to fuel profiles and stand structure (e.g., Collins et al., 2012). In addition to recouping economic timber value, harvest of beetle-killed trees (i.e., 'salvage') may be prescribed to reduce the amount of dead material in the forest canopy (to reduce crown fire spread potential) and to decrease the surface accumulation of woody fuels from natural snag-fall over time (to reduce surface fire intensity and resistance to control). The extent of recent beetle outbreaks has led to broadening application of these treatments, but to date, few data are available to inform post-outbreak management actions (see Lewis, 2009; Collins et al., 2011, 2012; Griffin et al., 2013) – especially compared to that for post-wildfire and post-windstorm settings (e.g., Rumbaitis-del Rio, 2006; McIver and Ottmar, 2007; Peterson and Leach, 2008; McGinnis et al., 2010; Buma and Wessman, 2011; Fraver et al., 2011; Donato et al., in press). So far, studies have evaluated operations in which both beetle-killed trees and residual green trees are removed, including most of the regeneration layer (e.g., Collins et al., 2011, 2012). Although such operations are common in parts of the western US, they are similar to, and informed by the many studies of, traditional clearcut timber harvest (e.g., Snell and Brown, 1980; Weatherspoon and Skinner, 1995). Treatment prescriptions vary widely among regions, and less is known regarding other regionally common prescriptions that remove beetle-killed trees but retain much or all of the surviving trees for a future multi-cohort stand or as seed trees. Rather than initiating a new stand, such treatments perpetuate an existing stand that may take different pathways depending, in part, on post-outbreak management.

Of particular uncertainty is how different post-harvest fuel treatments in beetle-affected stands, such as prescribed burning and mechanical removal, affect fuel profile dynamics and other characteristics of stand structure over the ensuing decades. Variations in treatment of post-harvest slash (the unmerchantable components of felled trees including branches and tree tops) are an important determinant of future fire potentials after harvest of live trees (Weatherspoon and Skinner, 1995; Graham et al., 2004; Agee and Skinner, 2005; Stephens et al., 2009), but such variation has scarcely been evaluated for dead-tree felling in post-outbreak forests. In addition, there is broadening interest in how various wildland fuel treatments, and post-disturbance harvests specifically, influence other ecosystem features such as wildlife habitat (Fontaine and Kennedy, 2012) and carbon sequestration (Bradford et al., 2012; Powers et al., 2013). Informed ecosystem management will require balancing these multiple objectives rather than focusing solely on fuels, making it essential to simultaneously evaluate how post-outbreak management affects other land-use objectives (Bradford and D'Amato, 2012).

In this study we evaluated the short- and long-term (0–50-year) effects of common post-outbreak management treatments on fuel profiles and stand structures in two major forest types of the Greater Yellowstone Ecosystem (GYE). Using a forest growth and yield model, the Forest Vegetation Simulator (FVS; Dixon, 2002), we simulated the effects of removal of beetle-killed trees followed by various fuel treatments in both lodgepole pine (*Pinus contorta* var. *latifolia*) and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests affected by the mountain pine beetle (*Dendroctonus ponderosae*) and Douglas-fir beetle (*D. pseudotsugae*), respectively. We previously reported on how responses to beetle epidemics differ between these forest types, with the drier Douglas-fir type exhibiting lower and more variable post-outbreak fuel loads relative to lodgepole pine (Simard et al., 2011; Donato et al., 2013). Further, although there is considerable variability within each forest type, most studies in lodgepole pine report that abundant advance and new regeneration eventually develops into ladder fuel (vertical continuity) after outbreaks (Simard et al., 2011; Pelz and Smith, 2012), whereas much sparser regeneration in Douglas-fir stands can result in far slower re-development of vertical fuel continuity (Donato et al., 2013). In this study we asked: a) how different post-harvest fuel treatments compare in terms of fuel profile and stand structure development, and b) how these comparisons potentially differ by forest type. Responses of interest included canopy fuel metrics, surface fuel loads, snag and live-tree dynamics, and carbon storage in live and dead tree biomass. Understanding relationships among dynamics of fuel profiles and other aspects of stand structure can inform prescriptions and tradeoffs involved in post-outbreak management.

2. Methods

2.1. Study area

The Greater Yellowstone Ecosystem is an 80,000-km^2 portion of the Rocky Mountains spanning parts of Wyoming, Montana, and Idaho, USA (approximate center: latitude/longitude 44°12′N, 110°21′W). Two of the most common vegetation types in the region are subalpine forests dominated by lodgepole pine and mid-elevation forests dominated by interior Douglas-fir. Lodgepole pine forests occupy infertile volcanic (rhyolitic) soils across the Yellowstone Plateau, while Douglas-fir forests occupy moderately fertile (non-rhyolitic, sedimentary) soils on adjacent sloping terrain. The climate of the GYE is continental with cold, snowy winters and warm, dry summers. Mean July high temperatures are 21 °C on the plateau and 24 °C at mid-elevations, and mean January lows are ~ -15 °C across the region; mean annual precipitation ranges from 600 to 1100 mm on the plateau and 350–650 mm at mid-elevations (www.prismclimate.org). Study sites were at elevations of 2000–2600 m on a full range of aspects, and slopes ranged from nearly flat to 30° (mean 17°).

Lodgepole pine and Douglas-fir account for about two-thirds of the forested area of Greater Yellowstone and occur in either pure or mixed stands, along with associates Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) on moist/high-elevation sites, or limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*) on dry/low-elevation sites. Lodgepole pine forests are characterized by a stand-replacing crown fire regime with intervals of ~150–300 years and often contain an even-aged overstory pine cohort (Romme and Despain, 1989). Douglas-fir forests sustain a mixed-severity fire regime with surface and crown fires at intervals of ~20–200 years, and are often multi-aged (Barrett, 1994; Baker, 2009). Mountain pine beetles and Douglas-fir beetles are also important disturbance agents in lodgepole pine and Douglas-fir forests, respectively, reaching epidemic levels and killing trees across large areas of the region on ~20–50-year cycles (Raffa et al., 2008). Stand-level mortality rates from beetle outbreaks are typically 40–80% by basal area (Simard et al., 2011; Donato et al., 2013).

2.2. Data collection

Field data on post-outbreak canopy, surface, and ground fuels were collected in five stands within each forest type (Simard et al., 2011; Donato et al., 2013). Five stands were >90% lodgepole pine and five were >90% Douglas-fir by basal area, and both samples sustained a mean of 56–60% basal area beetle-killed (range ~40–80% in each type). All stands were in the early-gray stage following beetle outbreak, defined as after mortality has ceased and >95% of needles have fallen off trees, usually beginning ~3 years after disturbance (Hicke et al., 2012b). Stands at this post-outbreak stage are the most likely to receive management treatments that include harvest of dead trees, after accounting for common regulatory procedures on public forest lands, such as environmental impact review (e.g., Collins et al., 2012; Griffin et al., 2013). Further, given the relative synchrony of the recent *Dendroctonus* outbreaks across western North America beginning in the early 2000s (Raffa et al., 2008), the gray stage now constitutes the majority of the beetle-affected landscapes and will continue as such for the next decade or more.

Our field sampling methods, as well as validation of initial conditions and outbreak severities, are reported in detail by Simard et al. (2011) and Donato et al. (2013). Briefly, within a 0.25-ha plot in each stand, all live and dead trees >1.4 m height were measured for species, diameter at 1.4 m height (dbh), total height, and crown dimensions in three parallel transects spaced 25 m apart (2×50 m in lodgepole pine, 6×50 m in Douglas-fir). Live and dead trees <1.4 m height were measured for species, height, and crown dimensions in two subtransects at opposite corners of the plot. Surface fuels were measured along ten planar intercept transects (Brown, 1974) within each plot and recorded by size class (i.e., timelag class: 1-h, 0–0.64 cm diameter; 10-h, 0.64–2.54 cm; 100-h, 2.54–7.62 cm; 1000-h, >7.62 cm). Depths of the litter, duff, and fuelbed strata were recorded at 20–30 systematic locations, and cover of understory vegetation was recorded in 20 systematically placed 0.25-m^2 microplots, within each plot. Initial fuel loadings (pre-simulation) were computed using standard methods consistent with those used by FVS, described by Brown (1974, 1978, 1981), Reinhardt and Crookston (2003), and Reinhardt et al. (2006), as augmented and described in detail by Simard et al. (2011) and Donato et al. (2013).

2.3. Model projections

To project the ten stands into the future with and without management treatments, we entered our field data into the Forest Vegetation Simulator, a semi-distance-independent individual-tree growth and yield model (Dixon, 2002). The FVS estimates tree growth, mortality, and snag and surface fuel fragmentation/decay using region-specific parameters. For our data we applied the Teton (TT) model variant (Keyser and Dixon, 2008). In concert with the Fire and Fuels Extension (FFE), the model estimates fuel profile dynamics for both the canopy and surface layers, including canopy bulk density (CBD – the amount of fuel per unit volume of canopy, a determinant of mass flow rate and spread potential of crown fire), canopy base height (CBH –vertical gap beneath base of tree crowns, which affects the ability of fire to move vertically from the surface to the canopy), and surface fuel loads by size class (which affect fireline intensity, spread, and transition to crowns) (Van Wagner, 1977; Rothermel, 1983; Cruz et al., 2003; Reinhardt and Crookston, 2003; Reinhardt et al., 2006). The FVS-FFE tracks dynamic transfers between canopy fuels (e.g. snags, foliage) and the surface layer (woody fuels and litter), as well as subsequent losses to decay. In this study we focus on projected changes in fuel profiles and other stand attributes (e.g., snag densities, live trees, biomass carbon storage) rather than modeled fire behavior, because the fire models implemented within FVS-FFE have known shortcomings in heterogeneous post-outbreak stands that are as yet unresolved (Jenkins et al., 2008; Cruz and Alexander, 2010; Klutsch et al., 2011; Hicke et al., 2012b). We further explore these issues in Section 4.

2.3.1. Model corroboration

We first evaluated the model by comparing 25-year projections of the ten gray stands, without management, to empirical data from stands of similar post-outbreak age (26–30 years) (Appendix A). The latter data came from field measurements of eight lodgepole pine and five Douglas-fir stands in the same region, which were previously validated to have otherwise similar pre-outbreak structure to the gray stands analyzed in this study (Simard et al., 2011; Donato et al., 2013). Model projections of most variables fell within the 95% confidence intervals for our empirical samples (Appendix A). Snag densities were underpredicted at 25 years, but adjustments to snag fall/decay rates adversely affected the majority of variables that otherwise calibrated well (surface woody fuels, most canopy fuels, forest floor mass, basal area, stem density); therefore we left the native parameter values for these rates intact. Thus, snag results were interpreted as relative differences among forest types and treatments, rather than absolute values. For lodgepole pine, it was necessary to reduce tree diameter growth rates and canopy bulk density estimates, and also to implement abundant natural regeneration to match the stem densities and regeneration dynamics observed in actual forest stands (our sample stands exhibited <20% serotiny and therefore had ongoing natural regeneration; see Appendix A). Post-outbreak regeneration is minimal in Douglas-fir stands (Donato et al., 2013) so we did not add this component to the projections. Finally, as part of the above exercise, we verified that results of the study were not qualitatively dependent on the few adjustments that were made by performing a sensitivity analysis on parameters that were calibrated (Appendix A).

2.3.2. Simulation experiments

We simulated a series of common management alternatives in beetle-affected stands (Table 1), comparing their effects over a 50-year projection period (years 2010–2060). All management scenarios except for the control began with the harvest of 90% of beetle-killed trees, with residual live overstory trees (survivors of outbreak) and the advance regeneration layer retained. Harvest therefore affected only the dead-tree component of each stand (Table 2). This prescription pertains to treatments commonly implemented in multiple national forests across Greater Yellowstone (T. Silvey, Caribou-Targhee National Forest; E. Jungck, Shoshone National Forest; and D. Abendroth, S. Ainsley, K. Beurmeyer, and E. Davy, Bridger-Teton National Forest, pers. comm.). Snag retention ranges from 5 to 30 ha^{-1}. Residual overstory trees are often retained as part of the future stand and for seed tree function. Exceptions occur (a) when significant loss of residual trees is anticipated via ongoing beetle outbreak or exposure to windthrow, and (b) when residual live basal area is above 18 m^2 ha^{-1} or severely infected with mistletoe. Our study stands did not show evidence of continued outbreak or severe mistletoe infestation, and virtually all were below the residual basal area threshold already (Table 2); thus, the stands were unlikely to

Table 1.
Management treatments simulated in beetle-impacted 'gray stage' Douglas-fir and lodgepole pine forests within the Forest Vegetation Simulator (FVS).

Treatment name	Treatment description[a]
Control	No trees harvested; no fuel treatments implemented
Slash in place	Beetle-killed trees harvested; branches and unmerchantable tops (slash) cut from boles and left in place, not piled
Prescribed burn	Beetle-killed trees harvested; branches and unmerchantable tops cut from boles, then burned over most of harvest unit area
Pile and burn	Beetle-killed trees harvested; branches and unmerchantable tops cut from boles, aggregated into piles and burned
Whole tree removal	Beetle-killed trees harvested; entire trees including branches and unmerchantable tops removed from site

[a] For treatments with harvest of beetle-killed trees (slash-in-place, prescribed-burn, pile-and-burn, whole-tree-removal), cutting prescription included retention of 10% of snags left standing, and assumed a 15% cull rate (stems cut but left on site due to breakage/defect; adapted from Snell and Brown (1980)).

experience live-tree removal. Advance regeneration is also protected and utilized wherever possible, especially in the drier Douglas-fir type where regeneration is often limited or difficult to establish. Otherwise, commonly described prescriptions were similar between lodgepole pine and Douglas-fir forests. Slash treatments comprise a wide range of actions, including leave-in-place (lop-and-scatter), burning (with or without prior piling, usually in the autumn ~1 year after harvest), or yarding off-site to landings.

The five harvest scenarios differed in the subsequent treatment of slash material, which was either (a) left in place as in lop-and-scatter treatments (referred to hereafter as slash-in-place); (b) left in place then burned over a broad area (prescribed-burn); (c) aggregated into piles which are then burned (pile-and-burn); or (d) removed from the site entirely along with the merchantable portions of trees (whole tree removal) (Table 1). For the two burn treatments, we retained the model's default parameters for: weather conditions (fuel moisture condition 2 "dry" such that fine fuels have 8–10% moisture and duff has 50% moisture, wind speed 5 km h^{-1} at 6 m above vegetation, temperature 21 °C, autumn burn); ground area/fuel amount affected (70% for prescribed-burn, while pile-and-burn collects fuels from 70% of the area, then burns them in piles encompassing just 10% of ground area); and mortality functions for small trees (dependent on stand structure). The burn treatments consume litter, duff, fine woody fuels, and some coarse woody fuels over the surface area affected, thus creating lower loading and continuity of surface fuels; slash-in-place should result in greater loading and continuity of surface fuels; and whole-tree removal is designed not to increase or decrease surface fuels.

Table 2
Stand structure (mean, S.E.) before harvest of beetle-killed trees (pre-harvest) and immediately after harvest but before subsequent fuel treatments (post-harvest).[a]

Structural attribute	Lodgepole pine		Douglas-fir	
	Pre-harvest	Post-harvest	Pre-harvest	Post-harvest
Basal area (m^2 ha^{-1})				
Live	16.0 (3.1)	16.0 (3.1)	14.4 (2.3)	14.4 (2.3)
Dead	21.5 (3.9)	2.2 (0.4)	25.1 (5.0)	2.5 (0.5)
Stem density (trees ha^{-1})				
Live (>1.4 m height)	850 (160)	850 (160)	425 (122)	425 (122)
Live (<1.4 m height)	8080 (1612)	8080 (1612)	232 (100)	232 (100)
Dead	275 (52)	26 (4.9)	236 (48)	23 (4.5)
Quadratic mean diameter of live trees (cm)	5.1 (0.9)	5.1 (0.9)	21.4 (5.8)	21.4 (5.8)
Mean% composition by basal area[b] (lodgepole pine/Douglas-fir)	95%/0%	95%/0%	1%/97%	1%/97%

[a] Pre-treatment data are from stands reported by Simard et al. (2011) and Donato et al. (2013).
[b] Live trees only, after outbreak but before harvesting. Remainder to 100% included primarily Engelmann spruce (*Picea engelmannii*), whitebark pine (*Pinus albicaulis*), and subalpine fir (*Abies lasiocarpa*).

Response variables included canopy fuel metrics (CBD, CBH), surface fuel loads by size class, snag densities, live tree basal area and mean size, and biomass carbon storage. In addition to displaying continuous 50-year trajectories of each variable, we evaluated differences in scenarios over time by comparing 95% confidence intervals (CI) for each response variable at major time points of 1, 10, 25, and 50 years after treatment. Parametric hypothesis tests such as repeated measures ANOVA were not employed because (a) confidence interval comparisons contain more information than null hypothesis tests (e.g., Brandstätter, 1999) and (b) the simulation outputs represent projections of assumptions for the same stands from a single measurement in time, rather than actual data re-measured through time. Confidence intervals mutually excluding other treatments' means indicate strong differences (Ramsey and Schafer, 2002).

3. Results

3.1. Stand structure

After the removal of 90% of beetle-killed trees, the discrepancy in snag densities between treated and unharvested stands was estimated to last much longer in Douglas-fir forests (~50 years) than in lodgepole pine (~20 years), due to slower natural snag-fall rates for Douglas-fir (Fig. 1A and B). Douglas-fir snags were estimated to remain standing long enough to decay into soft snags (well-decayed, defined by FVS-FFE and references therein) after several decades, whereas lodgepole pine stands did not recruit soft snags regardless of management (Fig. 1C and D). Most treatments had no effect on the live-tree component of stand structure, with the exception of the prescribed burn which was estimated to reduce live basal area by 25–45%, and increase quadratic mean tree diameter by 19–33%, via mortality of small saplings and poles (Fig. 1E–H). The effect of the prescribed-burn treatment on quadratic mean diameter was much smaller and short-lived in lodgepole pine due to rapid infilling with new regeneration cohorts (Fig. 1G and H).

3.2. Canopy fuels

Most treatments were estimated to have no effect on canopy bulk density relative to the unharvested condition (Figs. 2A and B, 3A, 4A), in part because live trees were not included in the cutting prescriptions, and in part because CBD computations in FVS-FFE do not include the fine dead fuels on snags, which were the component felled from the canopy. However, the prescribed burn slash treatment was estimated to reduce CBD by 30–40% due to small-tree mortality, with the effect lasting >25 years in lodgepole pine stands, and throughout the 50-year simulation in Douglas-fir stands (Figs. 2A and B, 3A and 4A). Similarly, canopy base height was only affected by the prescribed burn slash treatment, in which mortality of small trees was estimated to lift the canopy base by 1.5–3.5 m relative to the control and all other treatments (Fig. 2C and D). This effect was ephemeral (<10 yr) in lodgepole pine stands due to subsequent rapid infilling by new regeneration, and, while apparently more persistent in Douglas-fir, was not significant

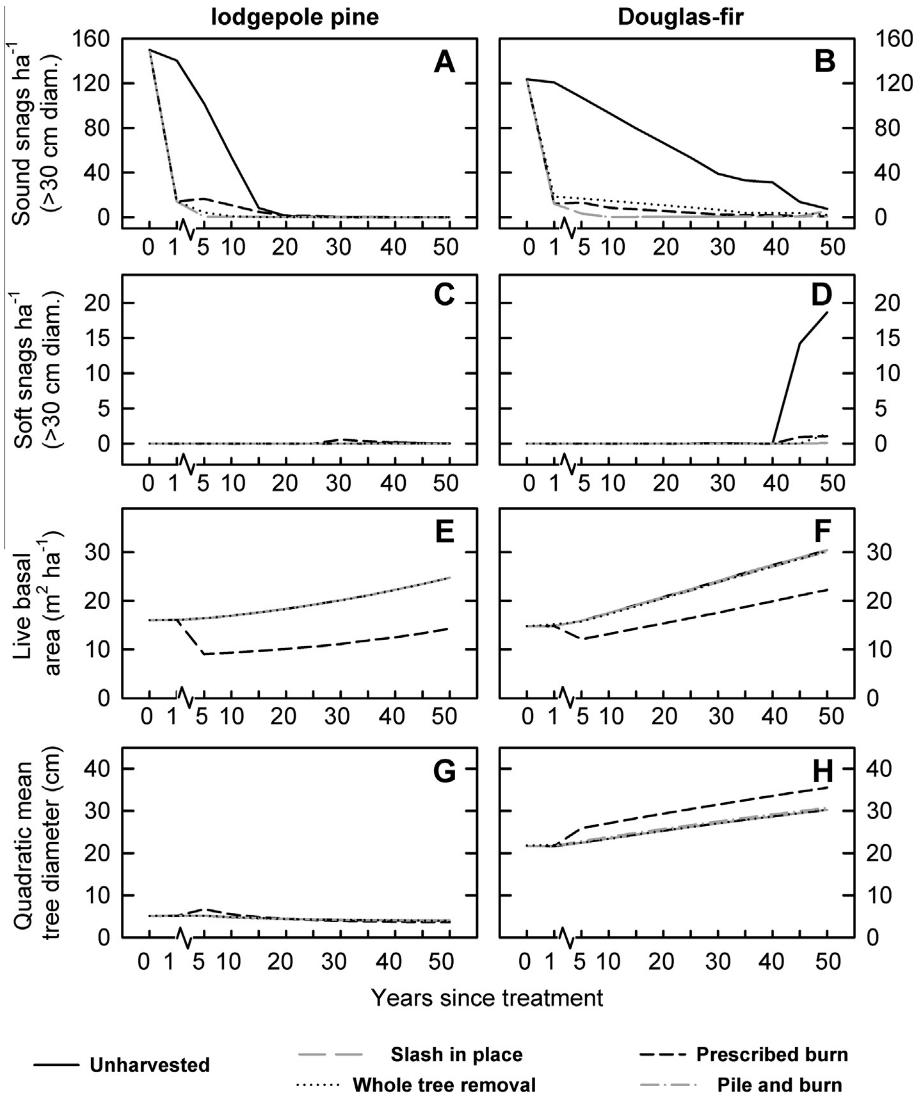

Fig. 1. Projections of stand structure over 50 years of post-treatment time. Each line is the mean of 5 replicates under a given treatment. Snag densities are for large (>30 cm dbh) snags only.

relative to wide background variation at any time point (Figs. 2C and D, 3B and 4B).

The reduction of standing (aerial) coarse fuel mass in all treatments (initially reduced by 45–75 Mg ha^{-1}, or 66–98%) was estimated to last ~10 years in lodgepole pine stands and throughout the 50-year simulation period in Douglas-fir (Figs. 2E and F, 3C and 4C). Aerial fine dead fuels were estimated to be significantly lower immediately after treatment in all managed stands relative to the unharvested control (initially by 12–20 Mg ha^{-1}, or 57–95%); however, by 10 years this effect was slight or undetectable in both forest types (Figs. 3D and D) because the model projected fine fuels to drop from the canopy rapidly with or without treatment (Fig. 2G and H). Projections of aerial foliage mass were only influenced by the prescribed burn slash treatment, the only treatment to kill a significant amount of live trees (Figs. 2J and K, 3E and 4E).

3.3. Surface fuels

Surface coarse wood mass was estimated to be lower in all treated stands relative to the unharvested control, with the difference becoming significant at 10 years in lodgepole pine stands and between 25 and 50 years in Douglas-fir stands (Figs. 5A and B, 6A and B). The pile-and-burn treatment showed the largest reduction and was also significantly lower than other treated stands throughout the 50-year simulation period, in both forest types (Fig. 6A and B). Maximum differences over time between treated versus untreated stands were an 80% reduction in surface coarse fuels for the pile-and-burn treatment, and a ~50–60% reduction for other treatments.

Surface fine fuels (woody component) were also affected by treatments, but much differently than for coarse fuels. Initially, fine fuel mass was estimated to be 1.5–2 times greater in all treated stands relative to unharvested controls, with the exception of whole-tree-removal, which maintained similar fine fuel levels as control stands. By 10 years post-treatment and beyond, treatment effects were projected to be mostly minor and non-significant (especially for Douglas-fir stands), with the main exception of whole-tree-removal which showed the lowest fine fuel loads (Fig. 6C and D). Treatment effects on the forest floor (litter and duff) were largely non-significant, except for the prescribed burn treatment, which was estimated to reduce forest floor mass by ~50% in both forest types – a difference that persisted throughout the 50-year projection.

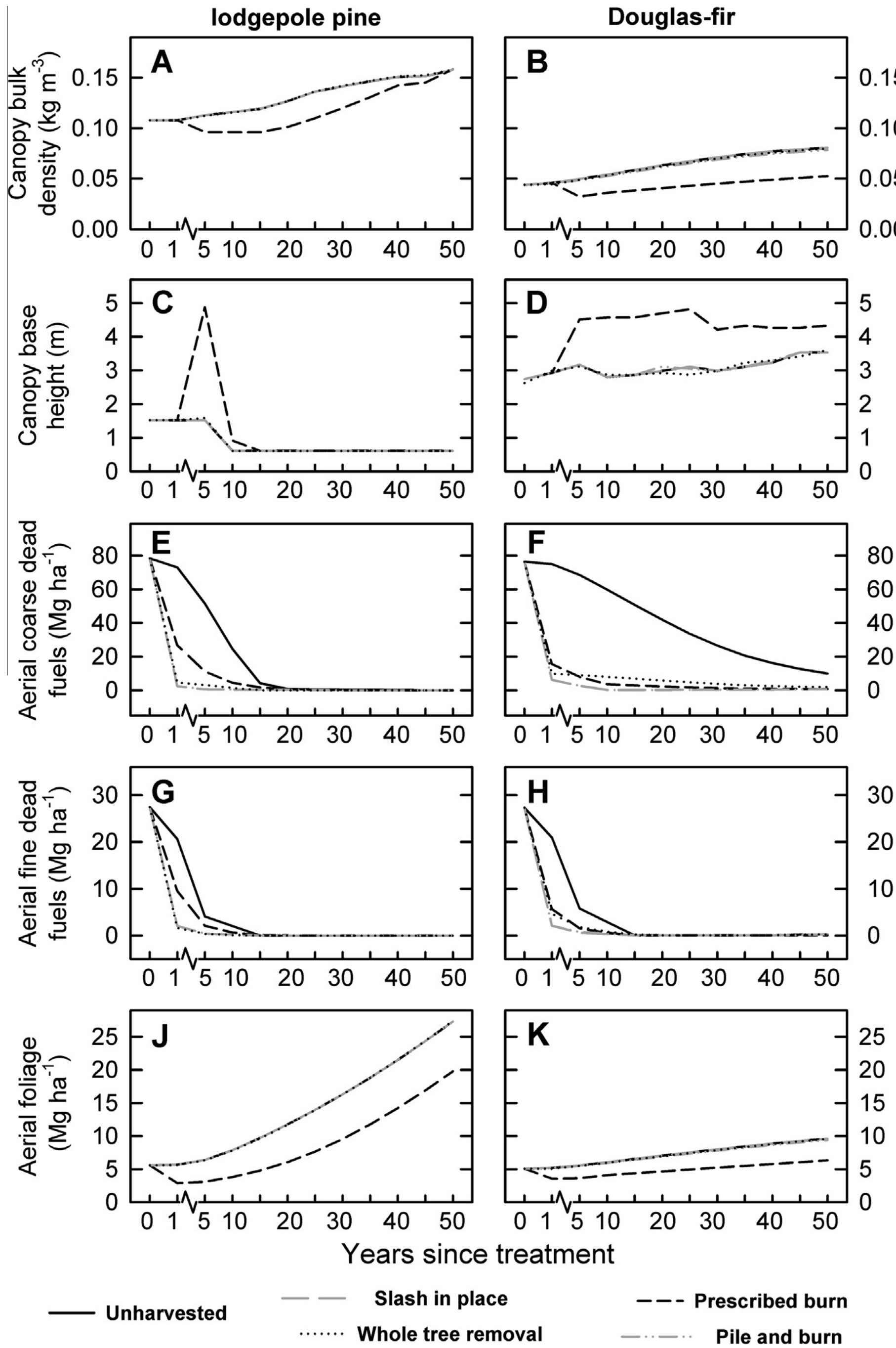

Fig. 2. Projections of canopy fuel metrics over 50 years of post-treatment time. Each line is the mean of 5 replicates under a given treatment. For statistical comparisons, see Figs. 3 and 4.

3.4. Biomass carbon storage

Across both forest types, all post-outbreak treatments were estimated to significantly reduce on-site carbon storage (live + dead biomass) relative to unharvested stands, by 30–45 Mg ha^{-1} or 22–33% (Figs. 7 and 8). There were few significant differences among treated stands; the lone significant difference was at 25–50 years in lodgepole pine stands and 50 years in Douglas-fir stands, in which the prescribed burn treatment had lower biomass carbon storage than other treated stands (Fig. 8A). In unharvested stands, the biomass carbon storage curve was projected as relatively flat over time, dipping just 9–14 Mg ha^{-1} (6–10%) below its starting value in pre-treatment stands, with the minimum occurring at ~20 years in both forest types (Figs. 7 and 8). This temporal curve was similar in all treated stands as well (Fig. 7).

4. Discussion

Harvest of beetle-killed trees and subsequent follow-up treatments altered several aspects of the fuel profile and stand structure of outbreak-impacted stands. The strongest projected effects were reductions in long-term recruitment of well-decayed standing snags, less accumulation of coarse woody surface fuels, and

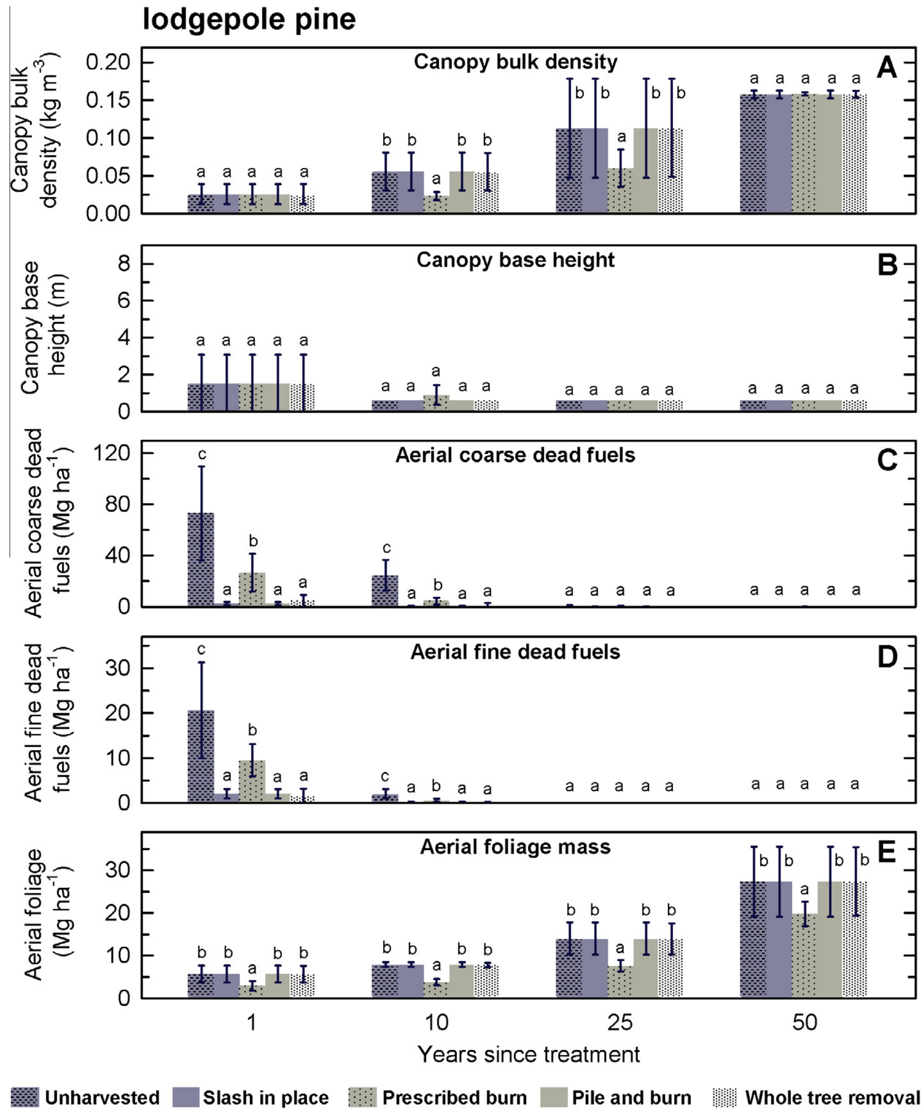

Fig. 3. Mean (±95% confidence interval) canopy fuel loads in lodgepole pine stands at major time points following post-outbreak fuel treatments. Bars were obtained by taking vertical slices through the line graphs (see Fig. 2) at time points of 1, 10, 25, and 50 years post-treatment. Superscript letters provide visual reference as to whether confidence intervals exclude other group means at a given time point.

reduced biomass carbon storage. Projected effects on fine fuels, both in the canopy and surface strata, were relatively minor or short-lived. Surprisingly, most follow-up treatment methods – whether slash was left in place, burned, piled, or removed entirely – had similar impacts on most fuel and stand structure metrics in both lodgepole pine and Douglas-fir forests. However, the prescribed burning treatment was distinct and generally had the strongest effects, owing to greater consumption of forest floor mass and mortality of small trees, which had persistent influences on both the canopy and surface fuel layers.

4.1. Changes in stand structure

Management of dead wood in fire-prone forests often seeks to balance its importance to ecosystem function with that of fire potentials (Brown et al., 2003). In addition to their contribution to fuel profiles, standing snags are an important component of structural complexity and habitat in forest stands (Harmon et al., 1986; Saab et al., 2007; Lewis, 2009). Large-diameter, well-decayed 'soft' snags are particularly important in this regard (Bull et al., 1997). The FVS projections for unharvested stands suggest that large, decayed snags begin to appear in Douglas-fir forests in a few decades after outbreak, while lodgepole pine snags fall much faster and are down before they matriculate into the decayed class (Fig. 1C and D). Our empirical studies in older (>25 yr) post-outbreak forests support these projections, with relatively few lodgepole pine snags remaining due to complete boles toppling from the base (Simard et al., 2011), compared to Douglas-fir which tends to break in pieces and remain standing as broken-topped snags (Donato et al., 2013). In the short term, retention of new sound snags during management actions is important for providing post-disturbance wildlife habitat (Saab et al., 2007). In the longer term, because few soft snags are recruited in lodgepole pine stands regardless of management (Fig. 1C), prescriptions attempting to maintain snag structures well into the future may be most relevant to tree species that stand longer as snags, such as Douglas-fir. Maintaining a long-term snag component in such forests would require at least moderate levels of snag retention during post-outbreak harvest to minimize this potential tradeoff between fuel management and wildlife habitat (Lewis, 2009).

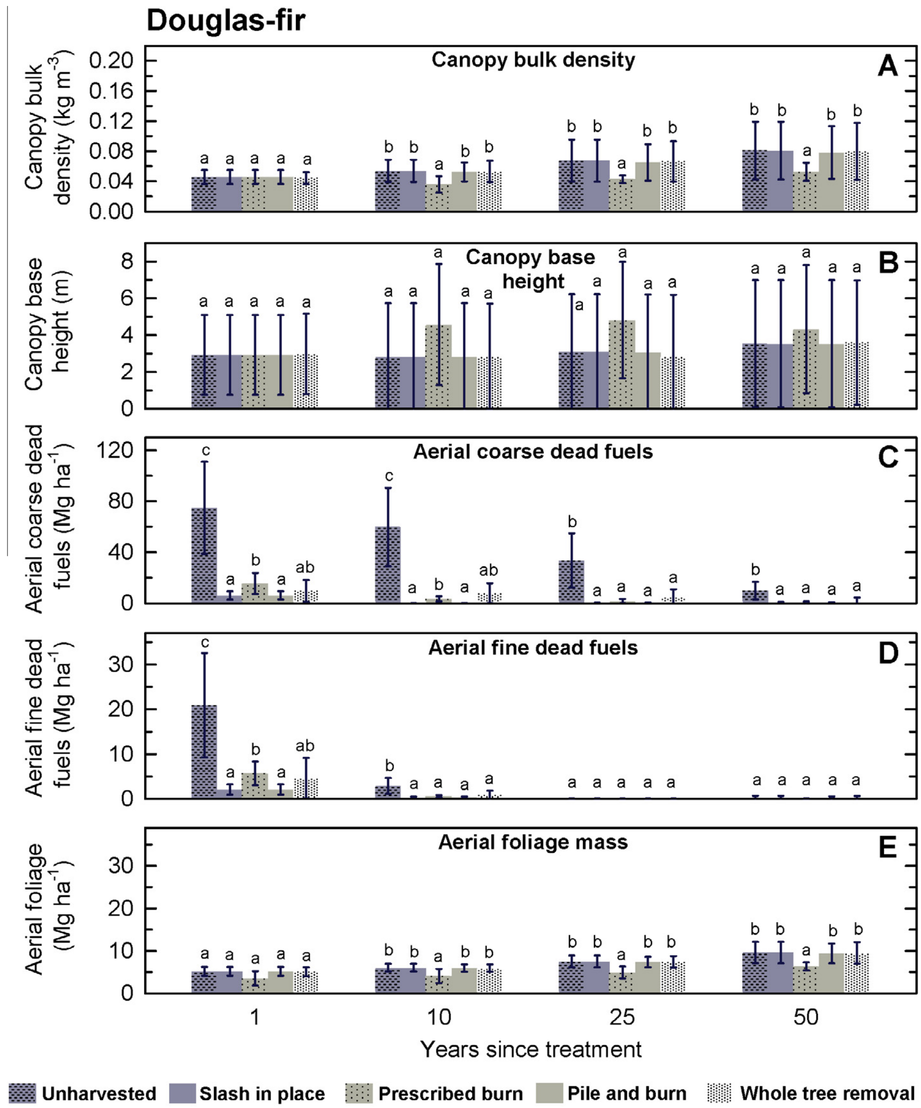

Fig. 4. Mean (±95% confidence interval) canopy fuel loads in Douglas-fir stands at major time points following post-outbreak fuel treatments. Bars were obtained by taking vertical slices through the line graphs (see Fig. 2) at time points of 1, 10, 25, and 50 years post-treatment. Superscript letters provide visual reference as to whether confidence intervals exclude other group means at a given time point.

4.2. Changes in canopy fuels

Model simulations suggested minimal effects of harvesting beetle-killed trees on the canopy fuel metrics that drive crown fire behavior, and also few differences among post-harvest treatments (Figs. 3 and 4). This finding stems from a harvest prescription of only dead trees, and differs substantially from operations that include concurrent removal of live trees (Collins et al., 2012). By the gray stage, beetle-killed trees carry no needles – the primary contributor to canopy bulk density and base height (Cruz et al., 2003; Reinhardt and Crookston, 2003; Reinhardt et al., 2006). Multiple studies have reported that crown fire potentials are already reduced in gray-stage forests, without management, due to needle drop that thins out canopy biomass relative to undisturbed stands (DeRose and Long, 2009; Klutsch et al., 2011; Simard et al., 2011; Schoennagel et al., 2012). Since available canopy fuel (particularly foliage) on dead trees has already dropped, it follows that removal of gray-stage beetle-killed trees should make little additional difference to canopy bulk density or base height. Similarly, Griffin et al. (2013) reported that harvest of beetle-killed trees reduced canopy bulk density in stands where dead needles were still in the crowns, but would be unlikely to make a difference in later years. In our study of gray-stage stands, the only post-harvest prescription to influence modeled CBD was the prescribed-burn treatment, as it was the only method that resulted in significant mortality of live trees (Figs. 3A and 4A). Other options to more strongly influence canopy fuels would be to remove live trees (Agee and Skinner, 2005; Stephens et al., 2009); however such treatments are not unique to post-disturbance environments and apply to thinning in most any forest condition.

A potentially important crown fuel component not addressed in the model, however, is the contribution of fine dead twigs on beetle-killed trees. While foliage is the primary contributor to available canopy fuel, a fraction of the aerial fine twig biomass is also considered an important fuel, even in undisturbed forests (Reinhardt et al., 2006). The fine twig component may increase in importance in beetle-affected forests as some fine twigs change from live to dead, with lower moisture content and ignition thresholds (Jenkins et al., 2008; Jolly et al., 2012). Although no field data exist as to whether fine twigs on gray-stage trees are actually an

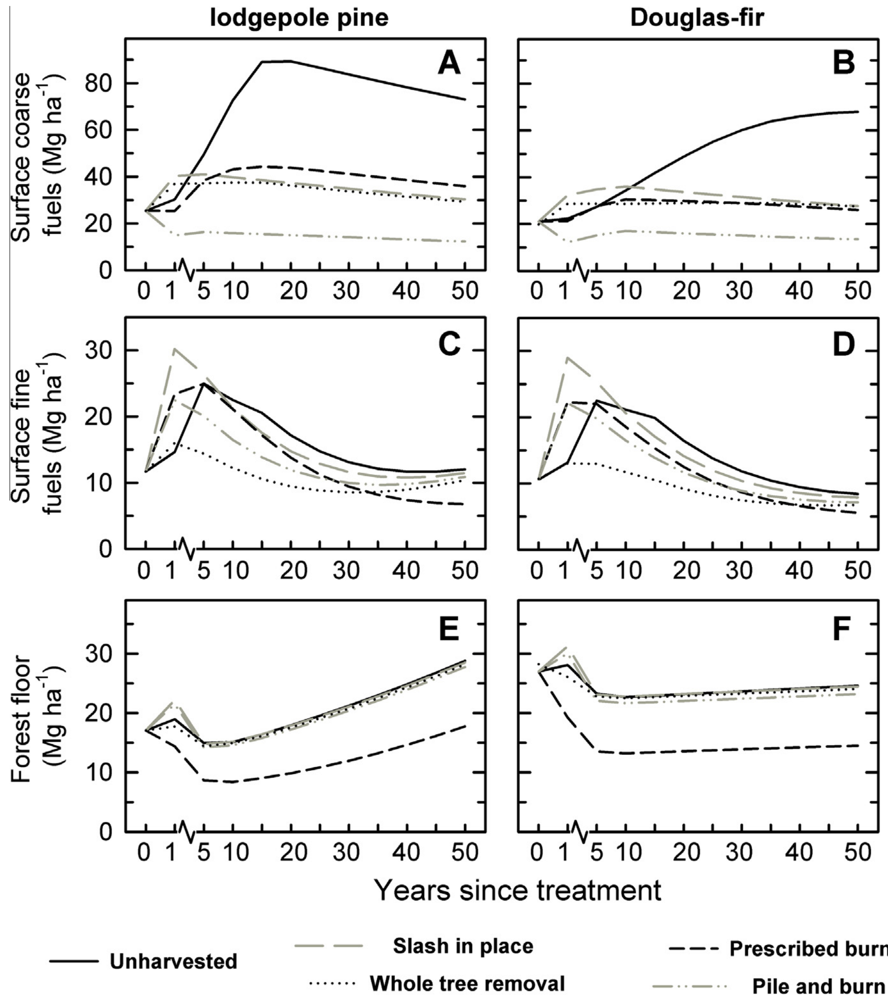

Fig. 5. Projections of surface fuel metrics over 50 years of post-treatment time. Each line is the mean of 5 replicates under a given treatment. For statistical comparisons, see Fig. 6.

important canopy fuel, to the extent they are a management concern it is important to note that FVS-FFE and related models, as commonly implemented, do not include fine branch fuels on dead trees when computing CBD and CBH. Dead branches within live tree crowns are considered within the model, but are ignored in the canopy once trees die – an omission that will likely be addressed in future FVS versions (USFS FVS support staff, pers. comm.). The current omission explains why the model's CBD and CBH estimates track mainly the foliage biomass in our study stands (compare panel A to panel E in Figs. 3 and 4). Conversely, CBD and CBH appear unaffected by aerial fine dead fuels in these stands (compare panel A to panel D in Figs. 3 and 4). Further, the poorly understood role of standing snags in fire behavior, such as producing embers, is not addressed in common fire models and warrants future research. These points suggest that, compared to modeled fire behavior simulations, reporting detailed fuel profiles can actually carry more complete information on how fire potentials may be affected by beetle outbreaks.

Our model projections suggest that aerial fine dead fuels were initially reduced by the harvest of beetle-killed trees, but the effect was short-lived (Figs. 3D, 4D). By 5–10 years, only a small fraction of fine dead fuels remained in the canopy in the absence of management, so treatment differences were already minimal. This effect was consistent among all of the modeled treatments. Although post-outbreak management objectives are often focused primarily on reducing surface coarse fuels, where canopy fuel metrics are also a concern these findings suggest that prompt post-outbreak management is important in maximizing the window of efficacy (see also Griffin et al., 2013). Harvest of dead trees conducted after this time period may have little relevance to reducing crown fire potentials.

4.3. Changes in surface fuels

Mitigating the surface accumulation of fine and coarse woody fuels is often a primary goal of post-disturbance tree harvest (e.g., Brown et al., 2003; McGinnis et al., 2010; Collins et al., 2012; Donato et al., in press). Our model simulations suggest that reduced accumulation of coarse surface fuels (at $\geqslant$10 years in lodgepole pine and $\geqslant$20 years in Douglas-fir) was the strongest effect of the harvest treatments relative to unharvested stands (Figs. 5A and B and 6A and B). Although coarse fuels are not the primary carriers of fire, the 50–80% reductions in coarse fuel load relative to the maxima projected for unharvested stands suggest the potential for less smoldering, smoke production, and total heat release, as well as reduced resistance to control for fire operations (Pyne et al., 1996). These findings are consistent with other studies of post-disturbance logging in other forest types (McIver and Ottmar, 2007; Monsanto and Agee, 2008; Collins et al., 2012; but see McGinnis et al., 2010). Our projections of coarse surface fuel increases over time without management, and the related decreases in treated stands, are of less magnitude than that reported by

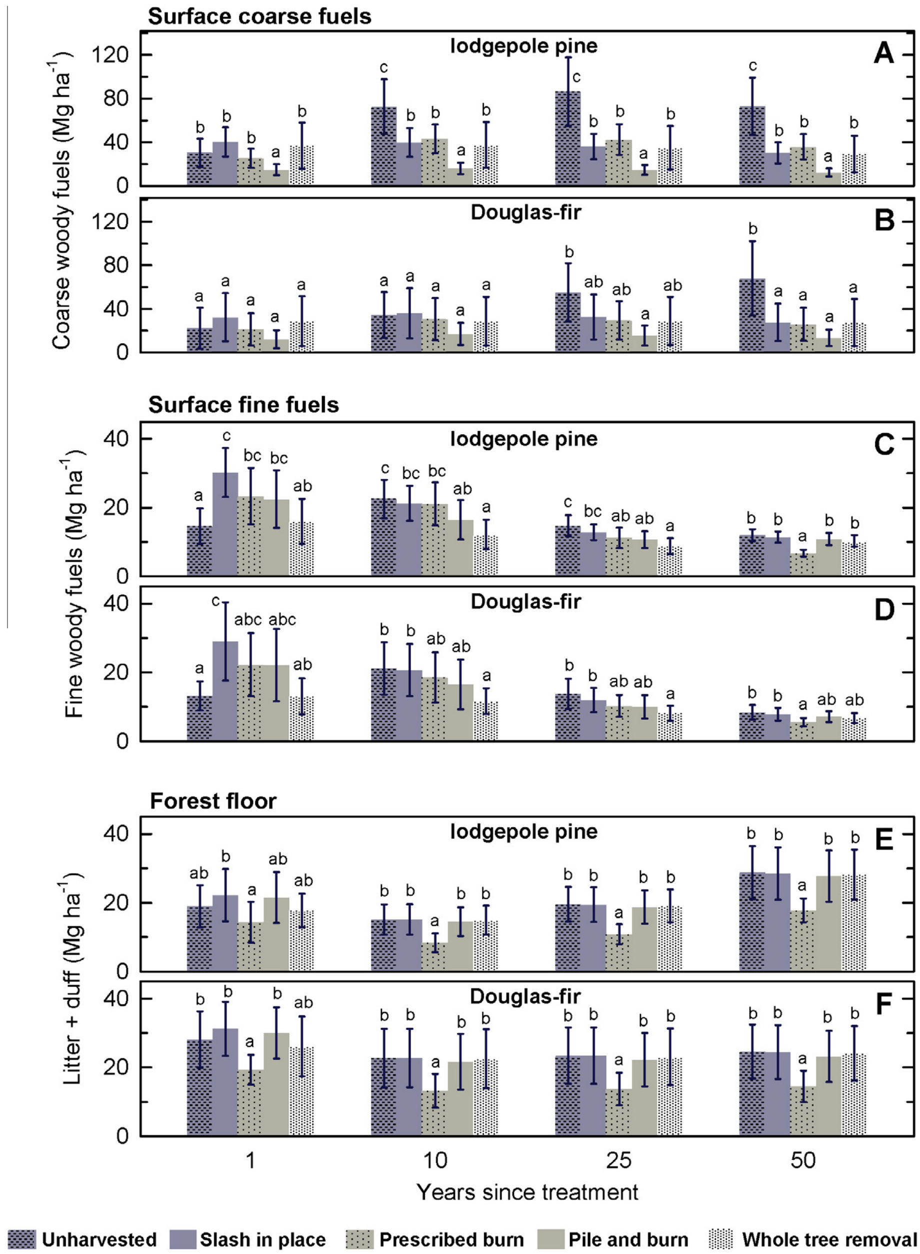

Fig. 6. Mean (±95% confidence interval) surface fuel loads in lodgepole pine stands at major time points following post-outbreak fuel treatments. Bars were obtained by taking vertical slices through the line graphs (see Fig. 5) at time points of 1, 10, 25, and 50 years post-treatment. Superscript letters provide visual reference as to whether confidence intervals exclude other group means at a given time point.

Collins et al. (2012); perhaps because of different mortality levels or initial stand densities between our study regions. Among the different post-harvest treatments, long-term projections of coarse fuels were mostly similar; however, the pile-and-burn treatment was estimated to be significantly more effective at reducing surface coarse fuel loads than other treatments (Figs. 5A and B and 6A and B), because it consumed even the large boles associated with the 15% cull rate. As such, pile-and-burn may be the treatment of choice if reducing coarse fuels is the primary objective.

Optimum levels of surface coarse wood, defined as those that balance fuel-related and other objectives (e.g., habitat, soil function), are described as ranging from 23 to 68 Mg ha^{-1} for cooler fire-prone forests (Brown et al., 2003). Typical levels found in undisturbed lodgepole pine and Douglas-fir forests of the GYE range from 10 to 80 and 1 to 51 Mg ha^{-1}, respectively (Romme, 1982; Simard et al., 2011; Donato et al., 2013). The FVS model projections suggest that, in the absence of management, coarse wood biomass exceeds all of these ranges in lodgepole pine stands beginning at ~10 years, while in Douglas-fir stands the coarse wood biomass does not exceed the undisturbed range until ~20 years post-outbreak, and does not exceed the optimum range described by Brown et al. (2003) at any time during the 50-year simulation (Fig. 5). In treated stands, coarse wood loads were within typical or accepted ranges during the 50-year simulation, save for the pile-and-burn treatment which resulted in levels below the optimal range (Fig. 5); thus that treatment may be less desirable when considering other, non-fire objectives for coarse wood.

Treatment effects on fine surface fuels were markedly different than for coarse fuels. The initial pulse of fine material from harvest slash resulted in significantly higher surface fine fuel loads in most treatments relative to unharvested stands (especially in lodgepole pine stands), except for the whole-tree-removal treatment

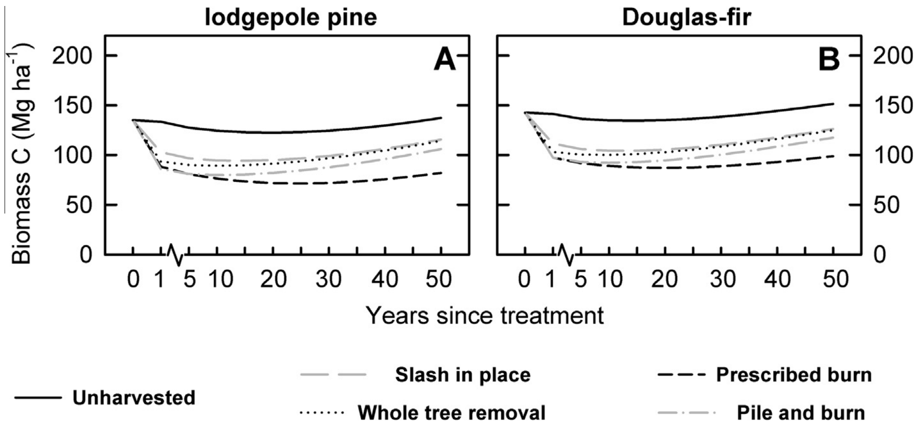

Fig. 7. Projections of on-site carbon storage (live plus dead biomass) over 50 years of post-treatment time. Each line is the mean of 5 replicates under a given treatment. For statistical comparisons, see Fig. 8.

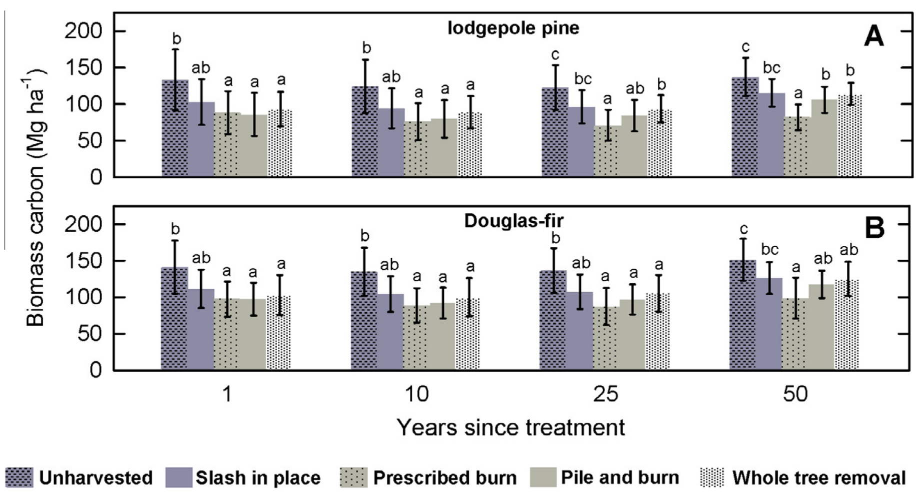

Fig. 8. Mean (±95% confidence interval) on-site carbon storage (live plus dead biomass) at major time points following post-outbreak fuel treatments. Superscript letters provide visual reference as to whether confidence intervals exclude other group means at a given time point.

(Figs. 5C and D and 6C and D). This finding is consistent with several other studies of post-disturbance harvest (Donato et al., 2006a,b; McIver and Ottmar, 2007; McGinnis et al., 2010; Collins et al., 2012; Donato et al., 2013,in press; Griffin et al., 2013). The effect lasted for only ~5 years, after which decomposition led to surprisingly few differences between treated stands relative to each other or to unharvested stands (Figs. 5C and D and 6C and D). Other than the whole-tree removal prescription, treatment effect sizes and biological significance at 10, 25, and 50 years were slight – particularly for Douglas-fir (Fig. 6C and D). Thus, the primary effect of most treatments was to shift the fine fuel accumulation curve toward earlier in time in both forest types, but otherwise the general shape and maximum remained similar (Fig. 5C and D). In addition, other than the prescribed-burn treatment, there were few detectable treatment effects on forest floor mass (litter and duff), a key carrier of most wildfires (Figs. 5E and F and 6E and F). These results for fine woody and forest floor mass, coupled with other studies reporting minimal or inconsistent increases in fine surface fuels after beetle outbreaks in general (Page and Jenkins, 2007a, 2007b; Simard et al., 2011; Jorgensen and Jenkins, 2011; Klutsch et al., 2011; Schoennagel et al., 2012; Donato et al., 2013), suggest that surface fine fuel accumulations may become a less important driver of post-outbreak management prescriptions.

4.4. Changes in biomass carbon storage

All the simulated treatments reduced carbon storage (on-site live + dead tree biomass) relative to unharvested stands in both forest types, and these reductions were larger than those associated with the beetle outbreak itself (Figs. 7 and 8). The relative flatness of the carbon storage curve over time in unharvested stands was the result of the dynamic balance between decay of beetle-killed trees and growth of surviving and regenerating trees. Several studies show that the rate at which forest carbon balance recovers following beetle outbreaks depends strongly on the amount of residual live trees remaining after the disturbance (Brown et al., 2010; Pfeifer et al., 2011; Edburg et al., 2011; Bowler et al., 2012; Hicke et al., 2012a). Often this residual live component is substantial and increases in productivity following the opening of the stand (Romme et al., 1986; Brown et al., 2010), leading to a return to carbon sink status within one to several decades (Hicke et al., 2012a). Our stands experienced 40–80% basal area mortality, leaving a significant component of both large and small live trees, which continued growing after the outbreak.

Ecosystem carbon storage is increasingly a policy and management objective on forest lands (e.g., IPCC, 2007; Stephens et al., 2011). That post-outbreak fuel treatments reduced on-site carbon storage is not surprising, since the objective was to remove biomass. Not all of the difference between unharvested and treated stands is emitted to the atmosphere immediately; the FVS model estimates that, of the total carbon removed from site, about half was stored in forest products initially, declining to about one-third by 50 years. Nevertheless, harvest of beetle-killed trees followed by any of the simulated post-harvest treatments resulted in a net reduction in total carbon storage (whether on- or off-site), quantitatively illustrating a tradeoff common to many fuel reduction activities (e.g., Campbell et al., 2011).

4.5. Forest type differences

Most simulated treatment effects were very similar across lodgepole pine and Douglas-fir forests. The main forest type differences were: (a) surface coarse wood, for which treatment effects were strongest in lodgepole pine because more rapid natural snag-fall in that type led to the highest coarse fuel loads in unharvested stands; (b) recruitment of advanced-decay snags in later years, which was absent in lodgepole pine but present in Douglas-fir; (c) greater variability in fuels in Douglas-fir, leading to less significant treatment effects; and (d) canopy base height and bulk density, which were respectively lower and higher (i.e., more conducive to crown fire) in lodgepole pine relative to Douglas-fir – in large part because of a dense regeneration layer in lodgepole pine forests that is often sparse or absent in Douglas-fir (Table 2; Simard et al., 2011; Donato et al., 2013). Such a difference may be most relevant for lodgepole pine forests with low serotiny levels, in which regeneration can be an ongoing process in the absence of fire. The model projections suggest that known differences in regeneration abundance between the forest types still persist after, and affect the outcomes of, post-outbreak treatments. The modest effect that the prescribed-burn treatment had on canopy base heights was especially short-lived in lodgepole pine stands (Fig. 2), as new regeneration quickly filled in the lower canopy layer. Otherwise, the effects of harvesting beetle-killed trees were largely the same between forest types for surface and canopy fuels, stand structure, and biomass carbon storage.

4.6. Key uncertainties

Models such as FVS are not predictions, but rather projections of a set of assumptions and of current understanding. Although we calibrated our projections by comparing to field data from older post-outbreak stands (Appendix A), like any modeling exercise, this analysis carries several key uncertainties. Perhaps the most important uncertainty relates to FVS' treatment of spatial heterogeneity in stand and fuel structure, a crucial factor in any discontinuous forest environment (Pimont et al., 2009), and particularly in post-outbreak forests (Donato et al., 2013). The model is aspatial, meaning that alterations to fuel continuity introduced by various treatments are not well addressed. The model outputs do not address localized gaps and accumulations of fuels ('jackpots') associated with clumped outbreak mortality, or clumped tree harvest and slash burning. As such, the potentially critical difference between, e.g., burning slash fuels in piles versus a broader prescribed burn, is not captured in terms of its effects on future fire spread. Surface continuity of forest floor fuels is typically much lower following the latter, which should further reduce the likelihood of surface fire spread for future fires, even given similar per-hectare fuel loads.

A second key uncertainty concerns the fate of live tree retention, and how this may relate to other prescriptions in different sites or regions. For lodgepole pine in particular, windthrow can be an important factor in the decades following outbreak, associated with greater exposure in newly opened stands. The model does not automatically adjust falling/breakage rates in this situation. Our projections validated well against field data from 30-year post-outbreak stands, suggesting this potential error was minimized; however wind exposure is site-specific and post-outbreak dynamics of remnant live trees may differ in other sites. This uncertainty is more important for prescriptions that retain live trees, and less so for common post-outbreak prescriptions in other regions that remove all stems, resembling a clearcut (e.g., Collins et al., 2012). For the fate of live trees and other ecosystem responses, elucidating the effects of a wide range of live-tree retention prescriptions is an important next step in studies of post-outbreak management.

5. Conclusion

Projections of forest growth and decay within the Forest Vegetation Simulator suggest that harvest of beetle-killed trees and subsequent follow-up treatments alter the fuel profile and stand structure of bark beetle-impacted lodgepole pine and Douglas-fir forests. Primary differences included reductions in surface coarse fuel accumulations (especially in lodgepole pine), less recruitment of well-decayed snags (especially in Douglas-fir), and reduced biomass carbon storage (in both forest types). Effects on fine fuels, whether in the canopy or on the surface, were mostly minor or short-lived. Differences among post-harvest fuel treatment methods were unexpectedly minor; all treatments had qualitatively similar impacts on short- and long-term fuel dynamics and biomass carbon storage. Exceptions to this similarity were response-specific and included (a) the prescribed-burning treatment, which killed understory trees and consumed surface fuels over a broad area, resulting in long-term reductions in aerial foliage mass, canopy bulk density, and forest floor mass in both forest types; (b) the pile-and-burn treatment, which was most effective at reducing surface coarse fuels over the long term; and (c) whole-tree removal, the only treatment to avoid an initial pulse of fine surface fuels from tree-felling. Treatment effectiveness in reducing fuels was mirrored by reductions in biomass carbon storage, illustrating a tradeoff involved in many fuel treatments.

From a fuel management perspective, the mostly minor or short-lived effect of the simulated treatments suggests flexibility in management approaches in beetle-affected stands. In essence, natural fall and decay of fine material in unharvested stands led to similar post-outbreak fuel structure to treated stands within about a decade, with the exception of coarse surface fuels. This finding represents a key difference from operations in which all live and dead trees are removed, in which the result is similar to a clearcut and thus wholly different from untreated stands that retain mature trees (Collins et al., 2012). The main change we observed in fuel profiles following treatment – reduction in coarse woody surface fuels after 10–20 years – may result in reduced heat release and resistance to control in future fires (e.g., Monsanto and Agee, 2008; Collins et al., 2012); field studies of actual fires in older beetle-killed stands with and without management will best elucidate the magnitude of this effect. The otherwise minor effects suggest that management of post-outbreak stands may consider a variety of objectives rather than primarily fuel considerations. Finally, while modeling exercises are valuable in exploring the likely efficacy and tradeoffs associated with post-outbreak management, the current limitations of fuel/fire models in heterogeneous post-disturbance environments indicate that field experiments tracked over the long term ultimately will provide the most robust information.

Acknowledgements

We thank the US Forest Service FVS help desk for consistent and timely assistance with the modeling. We received invaluable input

Table A.1
Calibration of FVS model based on comparisons of 25-year projections with field-measured stands of similar post-outbreak age (Simard et al., 2011; Donato et al., 2013).

Variable	Lodgepole pine at 25 years post-gray stage			Douglas-fir at 25 years post-gray stage		
	FVS projection (95% CI)	Empirical data (95% CI)	Adjustment[a]	FVS projection (95% CI)	Empirical data (95% CI)	Adjustment
Live trees (ha^{-1})	13,100–19,600	12,000–34,100	A	365–1245	597–1005	None
Basal area (m^2 ha^{-1})	14.8–25.6	12.3–22.7	B	19.3–25.1	6.2–22.8	None
Snags (ha^{-1})	0–0.7	29–121	None[b]	29–89	114–448	None[b]
Canopy bulk density (kg m^{-3})	0.065–0.161	0.029–0.084	C	0.050–0.082	0.027–0.075	None
Canopy base height (m)	0.61–0.61	0–1.1	None	0.68–5.30	2.2–4.9	None
Coarse surface wood (Mg ha^{-1})	61.9–106	26.3–79.3	None	35.8–74.4	24.2–66.4	None
Fine surface wood (Mg ha^{-1})	11.7–14.9	10.6–16.0	None	10.6–16.8	8.7–21.1	None
Forest floor mass (Mg ha^{-1})	17.8–25.8	10.4–15.2	None	17.5–29.3	11.8–36.6	None

[a] FVS model outputs are after the following adjustments: A – implemented natural regeneration of 1200 saplings ha^{-1} every 5-year cycle, with mortality disabled in the model, to better reflect actual stem densities and regeneration dynamics in field-measured beetle-affected stands. B – applied a multiplier of 0.2 to tree diameter growth rates to better match empirically observed rate of basal area increase. C – model's original CBD output of 0.225 kg m^{-3} (without added regeneration) or 0.248 kg m^{-3} (with regeneration added, see Adjustment A) was far higher than the empirically measured stands and was therefore reduced with a multiplier based on the ratio of the maximum observed CBD in real stands (0.113 kg m^{-3}) to that from the output (ratio = 0.113/0.248 = 0.46).
[b] Modeled value was outside empirical confidence interval, but adjustments adversely affected other response variables, so native snag fall/decay rates were retained. Snag results therefore emphasize relative differences among forest types and treatments rather than absolute values.

on common post-outbreak treatment prescriptions in the GYE from several silviculturalists, fire ecologists, and district rangers: T. Silvey (Caribou-Targhee National Forest), E. Jungck (Shoshone National Forest), and E. Davy, S. Ainsley, K. Beurmeyer, and D. Abendroth (Bridger-Teton National Forest). Field work was facilitated by collaboration with Yellowstone and Grand Teton National Parks and the Bridger-Teton National Forest; we especially thank R. Renkin, D. Abendroth, and A. Bouchard for their assistance. Housing and logistical assistance was facilitated by the University of Wyoming – National Park Service research station. An earlier draft of this manuscript was improved by comments from Chuck Rhoades, Kristen Pelz, and two anonymous reviewers. We thank our many field crews for help with data collection. Funding was provided by the Joint Fire Science Program, Grant #09-1-06-3.

Appendix A

A.1. FVS model calibration

Before implementing and comparing management treatments in FVS, we evaluated the model's handling of beetle-affected stands by comparing 25-year projections of the ten gray stands, without management, to empirical data from stands of similar post-outbreak age (26–30 years, or early-gray stage plus ~25 years). The latter data came from field measurements of eight lodgepole pine and five Douglas-fir stands in the same region, which were previously validated to have otherwise similar pre-outbreak structure to the gray stands analyzed in this study (Simard et al., 2011; Donato et al., 2013).

Most structure and fuel variables corresponded well with the 95% confidence intervals from our empirical samples (Table A.1). Exceptions were snag densities in both forest types, which were too low. For lodgepole pine only, there were discrepancies in live tree densities (too low), basal area (too high), and canopy bulk density (too high). For snag densities, attempted adjustments adversely influenced calibrations for other variables, so the model's native snag fall/decay rates were retained. It should be noted, therefore, that snag densities may be underestimated in the model outputs, and that comparisons should emphasize relative differences among forest types and treatments rather than absolute values. Live tree density in lodgepole pine was adjusted in FVS by adding a natural regeneration component of 1200 saplings per hectare at each 5-year cycle, with no mortality, which corresponds with actual regeneration dynamics occurring in post-outbreak lodgepole pine stands (Simard et al., 2011). Regeneration was composed of 40% lodgepole pine, 30% Engelmann spruce, and 30% subalpine fir. Basal area in lodgepole pine was calibrated by decreasing tree diameter growth rates, applying a multiplier of 0.2 to the default rates. For canopy bulk density, the model's estimates were substantially higher than in the field-measured stands – modeled values at 25 years were 0.225 kg m^{-3} before we added the natural regeneration component, and 0.248 kg m^{-3} with the regeneration component added. (These high values appeared to be due to model assumptions about the vertical distribution rather than amount of canopy fuel mass.) We therefore applied a conservative adjustment factor by multiplying all CBD values across all projections by the ratio of the maximum field-measured value to the modeled values, a ratio of 0.113/0.248 or 0.46. Finally, we conducted a sensitivity analysis to verify that the parameter space associated with these adjustments was not idiosyncratic or disproportionally influencing results. We verified that 10% variations to these adjusted parameters resulted in $\leqslant$10% changes to the overall response variables. We also ran the models without any adjustments to any growth, regeneration, or decay parameters and found that the final results varied only quantitatively but not qualitatively, yielding similar overall comparisons between treatments and forest types.

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