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Helga Van Miegroet

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E. Matthew Hansen, Michael C. Amacher, Helga Van Miegroet, James N. Long, and Michael G. Ryan

Mountain pine beetle-caused tree mortality has substantially changed live tree biomass in lodgepole pine ecosystems in western North America since 2000. We studied how beetle-caused mortality altered ecosystem carbon (C) stocks and productivity using a central US Rockies age sequence of ecosystem recovery after infestation, augmented with growth-and-yield model simulations. Field measurements showed that total C stocks were reduced by beetle outbreaks, although differences compared with undisturbed stands were not easily distinguished. Simulations with outbreaks showed long-term C losses of 1–30%. Field data indicated that aboveground C productivity was reduced among plots infested within 25 years of measurements, but productivity levels of plots with older infestations were indistinguishable from those of undisturbed plots. Simulations indicated that outbreaks reduced C productivity for 20–60 years, but rates recovered such that 100-year postoutbreak averages were similar among infested and undisturbed stands. Simulations also showed that C dynamics are affected by outbreak severity and that C productivity might be stimulated by outbreaks relative to that of undisturbed stands. Outbreaks redistributed C from live (sinks) to dead pools (sources), but slow decomposition of snags combined with recovered tree growth resulted in resilience of aboveground C stocks.

Keywords: bark beetle, carbon productivity, carbon stocks, decomposition, carbon balance

Bark beetle outbreaks have been unusually widespread and severe over the past two decades throughout western North America (Bentz et al. 2009), resulting in more carbon (C) in beetle-killed trees than from fire-killed trees (Hicke et al. 2013). Tree mortality modifies forest structure, alters the course of forest development, and affects nutrient and carbon cycling at multiple scales (Shore et al. 2006, Edburg et al. 2011, 2012, Hicke et al. 2012, Rhoades et al. 2013, Hansen 2014). Widespread bark beetle-caused mortality may influence the atmospheric CO_2 concentration (Kurz et al. 2008), and knowledge of postoutbreak recovery will aid prediction of regional forest C balances and future atmospheric CO_2 concentration (Kashian et al. 2013).

Ecosystems inevitably undergo cycles of birth, growth, death, and renewal, and insect-related disturbance is one agent of ecosystem release (Holling 1992, Kay 2000). Lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) is a disturbance-adapted species that quickly recolonizes landscapes after stand-replacing wildfires, commonly forming pure, even-aged stands (Lotan et al. 1985). Stands older than 60–80 years are increasingly at risk for mountain pine beetle (*Dendroctonus ponderosae* Hopk., Coleoptera: Curculionidae, sf. Scolytinae) outbreaks because mountain pine beetle prefers large diameter hosts (Amman et al. 1977). Infested stands may thereafter be reinfested every 20–50 years (Cole and Amman 1980, Alfaro et al. 2004, Axelson et al. 2009). Typically, many stems survive infestation including varying amounts of overstory lodgepole pine, nearly all understory lodgepole pine, and non-pine species (Hansen 2014). Surviving stems accelerate growth after the death of neighboring stems. Seedling recruitment into canopy

Table 1. Carbon cycle terminology and definitions as used in this article.

Term	Definition
Productivity	The rate of stand-level C accumulation from live plants; the increment of new C biomass per unit time
Stocks	The amount of C biomass held in forest stands at a point in time, either in component pools (e.g., overstory trees, advance regeneration, forest floor) or aggregated pools representing the entire ecosystem
ANPP*	An estimate (denoted by the asterisk) of aboveground net primary productivity; the annual accretion of aboveground C biomass in live plants
Net C balance	The net rate of C accumulation or loss from the ecosystem[1]

[1] For empirical data, this was calculated as ANPP* minus decomposition of snags, downed woody materials, and forest floor; for simulated data, this included belowground pools excepting mineral soil and was calculated by comparing total ecosystem C at each 10-yr time step.

gaps is usually substantial after mountain pine beetle outbreaks, ranging from mostly lodgepole pine to mostly nonpine species, such as fir (*Abies* spp.) and spruce (*Picea* spp.) (Hansen 2014).

Stand-level C productivity (Table 1) is reduced immediately after mountain pine beetle outbreaks, but production rates recover to those of undisturbed stands after 5–56 years (Romme et al. 1986, Pfeifer et al. 2010, Edburg et al. 2011, Kashian et al. 2013). Empirical and theoretical evidence suggests that mountain pine beetle disturbances may not necessarily decrease *cumulative* C productivity (i.e., total productivity over multiple years to decades). In fact, intermediate-severity disturbances (e.g., bark beetle infestations) may accelerate, maximize, or, even regulate ecosystem cycling and production (Mattson and Addy 1975, Romme et al. 1986, Loreau 1995). First, consider the widely observed forest developmental phenomenon in even-aged stands, in which aboveground wood production reaches its maximum rate within a few decades after stand establishment and then declines over the life of the stand (Gower et al. 1996, Ryan et al. 1997, Smith and Resh 1999, Smith and Long 2001). Second, consider that lodgepole pine stands most susceptible to mountain pine beetle infestation (>80 years old) Amman et al. 1977, Cole and Amman 1980) have developed beyond culmination of current annual increment, which peaks at 24–60 years after stand establishment and declines thereafter to 16–48% of maximum values by age 200–350 years (Pearson et al. 1987, Ryan and Waring 1992, Smith and Resh 1999, Kashian et al. 2013). Thus, frequent moderate severity disturbances may stimulate C productivity among mature stands because the partial disturbance "resets" development to an earlier, possibly more productive, stage (Kimmins 1987).

The potential impact of mountain pine beetle outbreaks on ecosystem C stocks (i.e., total pool size, aggregated from various compartments such as soil, downed woody material, and live vegetation) (Table 1) is confounded by multiple processes affecting inputs and outputs. Live pool inputs (i.e., C productivity) will be reduced in the short term even if long-term rates are increased, and dead pool outputs should be increased due to the greater volume of material available for microbial decomposition. Output rates will vary by substrate type (foliage, bark, stemwood, and roots) and by alterations in stand structure that also modify microclimate and process rates. Most of the biomass of beetle-killed trees is held in the boles, however, and even boles in contact with the ground are slow to decay (Hansen 2014). Because postoutbreak rates of C accumulation and loss will vary with time, it is necessary to consider long-term patterns of C stocks (e.g., >100 years).

Our goals were to measure and model the influence of mountain pine beetle infestation on lodgepole pine ecosystem carbon productivity and stocks and to test the hypothesis that mountain pine beetle outbreaks significantly increase average C productivity over long time scales (e.g., 100-year postoutbreak average) compared with that of undisturbed stands. Although other investigators have examined various aspects of this topic (Romme et al. 1986, Pfeifer et al. 2010, Edburg et al. 2011, Kashian et al. 2013), ours is the broadest attempt to combine empirical data and simulations to investigate short- and long-term responses in C dynamics among undisturbed and infested lodgepole pine stands. We investigated beetle-influenced C dynamics by quantifying C stocks, estimating C productivity levels, and measuring the decomposition rates of litter and fine woody debris from central US Rockies field plots in undisturbed and previously infested mature lodgepole pine stands. In addition to undisturbed stands, sampled stands included those infested once since stand initiation (measured ~25, ~35, and ~80 years postoutbreak) and others infested twice since stand initiation (measured ~3–10 years since the second outbreak). Because of difficulty identifying areas with co-occurring infested and undisturbed mature stands (e.g., within 25–50 km of each other) and because of limited resources for installing and measuring plots, we augmented our empirical results with growth-and-yield model simulations to provide complete chronosequences of stand-level C dynamics with and without repeated mountain pine beetle disturbance. Model simulations had the further benefit of holding stand conditions (e.g., site quality, basal area, and stem density) constant while varying time among simulations with and without mountain pine beetle disturbance. For the sake of simplicity, we did not consider climate disruption influences on bark beetle activity (Seidl et al. 2008, Bentz et al. 2010) and host species distributions (Rehfeldt et al. 2012).

Methods
Plot Selection and Sampling Methods

Potential plot locations were considered from lodgepole pine type throughout the US Rocky Mountains, and selections were intended to represent mature lodgepole pine stands with and without mountain pine beetle disturbance and, for infested stands, a range of time since infestation. After consultation with US Department of Agriculture (USDA) Forest Service Forest Health Protection entomologists, many areas with recent mountain pine beetle infestations (e.g., since 2000) were not used because of the lack of nearby undisturbed stands. Because we knew of no single forest or mountain range that encompassed a full range of lodgepole pine mountain pine beetle history, three landscapes were chosen such that they, in aggregate, represented a wide spectrum of conditions (Table 2; Figure 1). Each landscape had an uninfested, mature class of plots ranging from 118 to 145 years old with no evidence of infestation or other disturbance subsequent to stand initiation ("undisturbed"), and one landscape (Uinta Mountains) had an uninfested, old-growth class of plots ranging from 266 to 387 years old ("old-growth"). Nearby infested plots represented a range of time since infestation (3–80 years). At two landscapes (Henry's Lake Mountains and Uinta Mountains), infested plots had stand ages similar to those of undisturbed plots and infested plots showed evidence of a single infestation since stand initiation. At the third landscape (central Idaho), infested plots were older than nearby undisturbed plots and infested plots showed evidence of one or two mountain pine beetle outbreaks since stand initiation. We did not

Table 2. Plot characteristics.

Disturbance class (replicate)	Stand age (yr)[1]	Infested BA[2] (% LPP[3])	Live BA (% LPP)	US density[4] (% LPP)	Seedling density[4] (% LPP)
		.....................(m² ha⁻¹).......................		.........................(stems ha⁻¹)...........................	
Central Idaho[5]					
Undisturbed (1)	120	NA	33.2 (100)	0 (NA)	0 (NA)
Undisturbed (2)	119	NA	29.9 (100)	600 (100)	7,620 (100)
Undisturbed (3)	118	NA	43.8 (100)	0 (NA)	0 (NA)
MPB ca. 2006 (1)	138	17.8	23.5 (90)	2,400 (100)	22,580 (99)
MPB ca. 2006 (2)	212	8.8	18.2 (84)	2,100 (100)	22,700 (96)
MPB ca. 2006 (3)	163	14.5	8.8 (89)	300 (100)	29,644 (95)
MPB ca. 2006 (4)	139	3.4	13.8 (100)	300 (100)	45,975 (100)
MPB ca. 2002 (1)	197	23.2	10.4 (100)	2,100 (100)	9,190 (100)
MPB ca. 2002 (2)	112	21.2	18.8 (100)	0 (NA)	16,510 (92)
MPB ca. 2002 (3)	155	15.6	11.1 (100)	600 (100)	36,656 (93)
MPB ca. 2002 (4)	155	15.1	18.2 (100)	4,200 (100)	19,794 (100)
MPB ca. 1999 (1)	150	19.7	6.7 (90)	900 (100)	13,288 (100)
MPB ca. 1999 (2)	192	16.4	10.3 (95)	300 (100)	12,019 (100)
MPB ca. 1999 (3)	139	22.1	11.6 (100)	0 (NA)	0 (NA)
MPB ca. 1930 (1)	154	NA	37.0 (99)	1,200 (25)	7,550 (88)
MPB ca. 1930 (2)	150	NA	39.2 (100)	600 (100)	5,540 (100)
MPB ca. 1930 (3)	130	NA	18.7(100)	4,500 (100)	11,072 (97)
Henry's Lake Mountains, Idaho/Montana					
Undisturbed (1)	135	NA	29.1 (100)	0 (NA)	0 (NA)
Undisturbed (2)	145	NA	41.8 (100)	300 (100)	15,240 (50)
Undisturbed (3)	130	NA	54.4 (100)	0 (NA)	1,270 (0)
MPB ca. 1974 (1)	135	4.4	18.6 (100)	1,500 (100)	600 (100)
MPB ca. 1974 (2)	163	13.7	17.8 (94)	2,700 (78)	13,160 (84)
MPB ca. 1974 (3)	128	9.3	17.5 (93)	500 (100)	300 (100)
Uinta Mountains, Utah					
Undisturbed (1)	128	NA	55.9 (94)	0 (NA)	0 (NA)
Undisturbed (2)	127	NA	56.3 (100)	0 (NA)	0 (NA)
Undisturbed (3)	127	NA	39.0 (100)	1,200 (100)	0 (NA)
Undisturbed (4)	118	NA	54.8 (100)	600 (100)	0 (NA)
MPB ca. 1984 (1)	131	24.6	7.6 (100)	300 (100)	3,370 (100)
MPB ca. 1984 (2)	127	23.2	36.2 (100)	0 (NA)	4,110 (0)
MPB ca. 1984 (3)	121	35.1	16.9 (96)	300 (NA)	8,680 (100)
MPB ca. 1984 (4)	121	30.3	6.0 (100)	1,200 (100)	40,820 (39)
MPB ca. 1984 (5)	125	51.7	9.5 (98)	300 (0)	8,820 (79)
Old-growth (1)	387	NA	34.6 (85)	0 (NA)	2,270 (0)
Old-growth (2)	287	NA	59.3 (97)	0 (NA)	1,670 (0)
Old-growth (3)	266	NA	31.3 (98)	0 (NA)	600 (100)
Old-growth (4)	285	NA	40.5 (74)	500 (60)	2,770 (0)

MPB, mountain pine beetle; NA, not applicable.

[1] Stand age is breast height age of the oldest sampled tree in the plot plus 15 years.

[2] Infested trees at central Idaho plots mostly had bark on, whereas those at Henry's Lake Mountains and Uinta Mountains plots did not. Thus, infested basal area (BA) is probably underestimated at Henry's Lake Mountains and Uinta Mountains plots.

[3] Non-lodgepole pine (LPP) tree species were subalpine fir (all landscapes), Douglas-fir (central Idaho), whitebark pine (Henry's Lake Mountains), and Engelmann spruce (Uinta Mountains).

[4] Understory (US) size class: 1.3 cm rcd to 7.5 cm dbh; seedling size class: <1.3 cm rcd.

[5] Other than those in the undisturbed class, all central Idaho plots had evidence of a mountain pine beetle outbreak ca. 1930. Infested BA is only for recently killed trees. All plots affected by the ca. 1930 outbreak may be substantially older than the "stand age" listed in this table. These stands were probably at least 60–80 years old in 1930 (Amman et al. 1977); thus, all infested central Idaho stands were probably initiated a minimum 140–160 years before plot measurements.

seek out predetermined outbreak severity levels, rather we simply sought mature, lodgepole pine-dominated stands that were affected by mountain pine beetle. Although overstory mortality can approach 100% in some stands, extreme mortality rates are uncommon at the landscape level (Hansen 2014). Thus, our infested stands represent a typical range of mortality; in some stands, most lodgepole pine were killed, whereas, in others, most survived (Table 2). Soils and climate information for each landscape can be found in Appendix A.

Within each landscape, plot locations were randomly chosen among potential areas restricted by elevation (300 m range), aspect (135° window), and slope (10% window) in an effort to minimize environmental differences. Because of these constraints and because we did not randomly select from among all possible landscapes, our plots may not necessarily represent all central US Rockies lodgepole pine type. Geographic information system (GIS) maps were produced with these topographical masks and overlaid with aerial detection survey maps with locations of infested trees by year of infestation.[1] Final stand selections were made after ground reconnaissance that confirmed the local dominance of lodgepole pine, the presence/absence of mountain pine beetle-caused mortality, and no other disturbance such as logging. Plot centers were determined using random distances and azimuths from a reference point. In an effort to achieve spatial independence, plots were separated by at least 1 km (Turner et al. 2004).

Sampling methods were based on "Phase 3" USDA Forest Service Forest Inventory and Analysis (FIA) protocols (USDA Forest Service 2008). Base FIA plots are designed to measure over- and understory trees, whereas Phase 3 adds measurements of downed woody material (Woodall and Monleon 2008), vegetation, and soils (O'Neill et al. 2005) among other metrics. Many protocols were modified to fit the needs of the present study (details given below).

Figure 1. Plot locations (circles), precipitation stations (asterisks; see Appendix A), and lodgepole pine distribution (polygons) in the central US Rocky Mountains.

Additional measurements were added to estimate litterfall and decomposition rates. Plots were established in 2008 and 2009.

Vegetation Measurements

Overstory C pools were calculated from plot data using allometric equations to obtain biomass and multiplied by component-specific C concentrations to get total C pool sizes. Each selected stand was sampled with a single fixed-radius plot, which varied in size from 100 to 400 m² such that >20 overstory trees were included. Centered on the overstory plot, a 33.3 m² subplot was established to measure advance regeneration (trees <7.6 cm dbh but ≥1.3 cm root collar diameter [rcd]). Each stem was measured for diameter and height. Live stems were measured for crown height and percent live crown with a subsample cored for age. Dead stems were classified into one of five decay classes (USDA Forest Service 2008). Species- and size-specific allometric equations were applied to determine aboveground component-specific biomass for each tree (Ter-Mikaelian and Korzukhin 1997; Table 4 in Lambert et al. 2005). Components were totaled and rescaled to a ha^{-1} basis. Component-specific C concentrations (percent mass) were obtained by analyzing tissue samples from off-plot trees (see Appendix B). Three off-plot lodgepole pine from a subset of plots at each landscape were sampled for bark, stemwood, and foliage tissues (central Idaho, 10 plots; Henry's Lake Mountains, 5 plots; Uinta Mountains, 6 plots). Nonpines were also sampled for foliage; bark and stemwood C of nonpines were assumed to be 50% of biomass. Foliage sampling protocols followed the guidelines of Heilman (1971). Component-specific C concentrations were measured using dry combustion analyzer methods (O'Neill et al. 2005).

Twelve 0.66-m² subplots at each plot were established to estimate biomass of shrubs, forbs, and grasses as well as tree stems <1.3 cm rcd. From each plot center, these subplots were spaced at 2-m intervals with three subplots along each cardinal direction. Within these subplots, percent cover was ocularly estimated for forbs, grasses, and *Vaccinium* spp., a low, spreading woody shrub with multiple small diameter stems, using a template of known dimension for scale (Moore et al. 2007). Estimates for nontree species were rounded to the nearest 5%; species with <2.5% cover were not tallied. Stems of tree species were tallied by species and 0.25-cm rcd class. Forbs and shrubs were identified to genus, whereas sedges and grasses were lumped as "grass."

Allometric equations for these plants were determined by destructive sampling from nearby, off-plot locations. Destructively sampled specimens were measured as described above (i.e., percent cover or rcd), with all plants clipped at the root collar. Sampled vegetation was oven-dried, weighed, and analyzed for C content using the dry combustion method (O'Neill et al. 2005). Least squares regression (PROC REG; SAS Institute, Inc., Cary, NC) was used to model the relationships between cover and genus-specific C mass; "landscape" was coded as a dummy variable. Annual C productivity for *Vaccinium* was estimated from published biomass accumulation ratios (~2) (Whittaker and Niering 1965, Whittaker and Woodwell 1968), whereas annual C productivity for forbs and grasses was assumed to be equivalent to total aboveground C biomass (Moore et al. 2007). An allometric relationship between rcd and C mass for seedlings was developed using a generalized mixed model (PROC GLIMMIX; SAS Institute, Inc., Cary, NC). These intermediate C content results are presented in Appendix B. Mosses and lichens were not sampled because the forest floor could not practically be separated from plant material.

Plot-level C productivity levels were estimated by comparing the C of live plot trees to the same trees remeasured 3 years after the original surveys ("Approach 1" in Clark et al. 2001). Annual C productivity was calculated by dividing C accretion by the number of years between surveys and adding annual litterfall (described below). Carbon productivity in our study pertains only to aboveground components (over- and understory trees and nontree vegetation) as we made no attempt to measure root growth, exudates, or carbohydrate transport to root symbionts. Moreover, we did not attempt to measure losses to consumers, volatilization, or leaching (Clark et al. 2001). Thus, we will hereafter use "ANPP*" to denote that our measurements are *estimates* of aboveground net primary productivity, ANPP (*sensu* Clark et al. 2001; Table 1).

Soil and Litterfall Sampling

Forest floor (O-horizon) and mineral soil sampling was based on FIA protocols (O'Neill et al. 2005) with three sampling locations along the perimeter of the overstory plot (0, 120, and 240° azimuth relative to the plot center). The forest floor was sampled by collecting all organic material <0.6 cm within a 30-cm diameter sampling frame. The upper 20 cm of the mineral matrix was sampled using two 10-cm-long liners within the core head of an impact driver. All standard FIA analyses of soil physical and chemical properties (O'Neill et al. 2005) were performed at the Logan, Utah, Forestry Sciences Laboratory. Carbon input to the forest floor was estimated using litterfall traps. Fifteen-gallon nursery containers (0.11-m² opening) were installed near the three forest floor sample locations

along the perimeter of each plot. The contents of these were collected at ~1-year intervals over 2 years. Litterfall was analyzed for C content using the dry combustion method (O'Neill et al. 2005).

Downed Woody Materials Measurements

Downed woody materials were measured using FIA-based line transect sampling (Woodall and Monleon 2008). From each plot center, three 7.3-m line transects were extended radially at 30, 150, and 270°. Materials >7.5-cm diameter were sampled for diameter and decay class along the entire length of each transect, whereas materials 2.5–7.5 cm were sampled at the distal 3 m of each transect and materials 0.7–2.5 cm were sampled at the distal 1.8 m. Materials <0.7 cm were sampled with the forest floor (described above). Off-plot samples of downed woody materials, by decay and diameter class, were analyzed for dry weight and C content. Downed woody materials volume ha^{-1} was calculated (Equation 3.4.2 in Woodall and Monleon 2008) and converted to mass using the decay class-specific densities reported by Harmon et al. (2008). Carbon mass ha^{-1} was calculated using our C content results (shown in Appendix B).

Infestation Severity

To calculate the density and basal area of mountain pine beetle-killed trees on a ha^{-1} basis, snags and downed trees whose stumps were within the overstory plot radius were examined for evidence of mountain pine beetle infestation. Among the central Idaho plots, this was done only for boles killed during the ca. 2000 outbreak; although most boles killed during the ca. 1930 outbreak had visible mountain pine beetle galleries, some boles were too decomposed to unequivocally determine mountain pine beetle evidence. Moreover, diameters of these trees could not be accurately measured.

Decomposition Estimates

Decomposition rates of the forest floor were estimated by calculating mean residence time (MRT)

$$\text{Forest floor C mass/litterfall C mass year}^{-1} \qquad (1)$$

We assumed that forest floor/litterfall dynamics were steady state, a requirement for MRT estimates, although we acknowledge that this might not be valid for recently infested plots. In addition, this estimate does not account for inputs from fine roots, although these were not conspicuous in our sampling. MRT estimates were inversely-scaled (1/MRT) to facilitate comparisons to short-term decomposition rate constants.

Short-term decomposition rates were estimated by measuring 1-year mass loss of litterbags and tongue depressors (Remsburg and Turner 2006). Litterbags were made of fiberglass screen (2-mm opening) and filled with ~15 g of fresh, oven-dried lodgepole pine needles. Birch tongue depressors (Puritan Medical, Guilford, ME) were a proxy for fine woody debris and were selected for maximum consistency of material and size. Therefore, decomposition data from the tongue depressors were intended as a metric of decomposition potential and may or may not reflect decay rates of native fine woody debris. Eight each of litterbags and tongue depressors were deployed at each plot, 6 m from the plot center in each cardinal direction. At each location, one litterbag/tongue depressor pair was placed on top of the forest floor and one pair at the forest floor-mineral soil interface. This material was retrieved after about 1 year to determine mass loss. All materials were oven dried for 24 hours

Table 3. Input data sources for FVS simulations, simulation duration, and location of results.

Input data	Duration (yr)	Result locations
Empirical plot data	<100	Table 5; Figure 6
Bare-ground (seedlings, snags, and down woody materials)	200	Figures 5 and 7

before measurements. An exponential decomposition rate constant, k, was calculated using the before and after dry weights (Equation 8.1 in Karberg et al. 2008).

Net ecosystem C balance (aboveground compartments only) (Table 1) was estimated by subtracting estimated decomposition of snags, downed woody materials, and forest floor from ANPP*. We estimated a snag k of 0.0017 using data in Fahey (1983) and Harvey (1986) and used a downed woody materials k of 0.022, the mean of values reported by Busse (1994) and Fahey (1983). For forest floor decomposition, we used inverse MRT.

Growth-and-Yield Simulations

Sampling lodgepole pine stands with and without beetle-caused mortality is confounded by difficulty in matching stand conditions and environmental factors. Mountain pine beetle outbreaks are landscape-scale events, and few stands with suitable host type remain uninfested if nearby areas support an outbreak. Thus, our labor-intensive field sampling scheme had limitations including (1) minimal replication, (2) incomplete postoutbreak age sequences, (3) lack of control over preoutbreak stand conditions (*sensu* Pickett 1989), and (4) variability of infestation severity. To supplement the field data, we also simulated stand development with and without beetle infestation using the Forest Vegetation Simulator (FVS) (Dixon 2002). These simulations have at least two advantages over field measurements: complete chronosequences can be simulated and preoutbreak stand conditions can be specified, overcoming the limitations of space-for-time substitutions.

FVS is an empirically based growth-and-yield model with more than 20 regionally specific variants (FVS version 0979; version date July 15, 2013). FVS has been in development for about 40 years, and its algorithms are founded on robust USDA Forest Service inventories such as FIA data. Simulation input data sources were our empirical plot data as well as "bare-ground" simulations (Table 3). Stands in the bare-ground simulations are initiated with seedlings, and, therefore, C dynamics from stand initiation through disturbance and recovery can be examined (these stands simulate a postfire environment, with complete replacement of the live vegetation but including snags, downed woody materials, and a diminished forest floor). For simulations based on our field observations, we directly input tree data (i.e., individual stems) into FVS, whereas downed woody materials and forest floor data were first summarized and then were entered on a per plot basis. FVS default values were accepted for vegetation mass (i.e., shrubs and herbs). FVS does not track mineral soil C. Bare-ground (i.e., no live trees at time equals zero) simulations were initiated with starting lodgepole pine seedling densities of 3,100 stems ha^{-1}, the median value reported by Turner et al. (2004) after the 1988 Yellowstone National Park wildfires. For the bare-ground simulations, initial snag, downed woody materials, and forest floor biomass values were averaged from those of two central Idaho plots burned by a stand-replacing fire in 2006 (Hansen and Amacher, USDA Forest Service, Rocky Mountain Research Station, unpubl. data, July 2, 2012).

We used the Tetons variant (Keyser and Dixon 2008a) for central Idaho and Henry's Lake Mountains plot data and the Utah variant (Keyser and Dixon 2008b) for Uinta Mountains plot data. These variants grow lodgepole pine stands at different rates, a reflection of the empirical data used to parameterize each variant; stands simulated with the Tetons variant are notably more vigorous (input data included stand-specific site index). For each input empirical plot, two 100-year developmental trajectories were simulated: no mountain pine beetle disturbance and a cycle of mountain pine beetle disturbance every 40 years. This interval was chosen because 40 years is in the typical range for many lodgepole pine landscapes (Cole and Amman 1980, Alfaro et al. 2004, Axelson et al. 2009). For plots with recent mountain pine beetle history, the first simulated outbreak was scheduled for 40 years after the most recent outbreak, whereas uninfested plots had the initial outbreak scheduled for the first model cycle (FVS output is in 10-year cycles or time-steps). Mountain pine beetle-caused mortality was modeled with the Mountain Pine Beetle extension within FVS (Dixon 2002). Simulated outbreaks were scheduled manually, and all default settings were accepted. The FVS algorithm for simulating mountain pine beetle-caused mortality is derived from empirical data on the relationship between infestation probability and host diameter (Cole and McGregor 1983). The bare-ground simulations were made with each variant over a 200-year interval. Because the rate-of-loss model may overestimate mountain pine beetle-caused mortality (Cole and McGregor 1983) and because outbreak severity affects C dynamics (Edburg et al. 2011), we added a third developmental trajectory for the bare-ground simulations with reduced mortality rates. This was accomplished using the MaxYears keyword to arbitrarily reduce the duration of the outbreak from 10 to 6 years and the QValues keyword to increase the probability of survival, especially among smaller size classes.

All simulations included regeneration at each 10-year time step, comprising 12.5 lodgepole pine and 7.5 subalpine fir ha^{-1}. Added to these were 2.5 stems ha^{-1} of Engelmann spruce for Uinta Mountains plots, Douglas-fir for central Idaho plots, and whitebark pine for Henry's Lake Mountains plots. These numbers were chosen based on our experience, although they may be unrealistically high for undisturbed stands and low for partially disturbed stands. In preliminary trials, however, we confirmed that FVS-simulated C stocks and production are essentially insensitive to the amount of regeneration simulated, assuming that the stand is fully stocked. This is due to the mortality algorithm of FVS (we accepted default parameters) in which increasingly greater amounts of simulated regeneration merely translate to increased seedling mortality and/or slower growth per stem, neither of which substantially affect stand-level C productivity or C stocks. In addition, recruitment of 1,000 lodgepole pine stems ha^{-1} was simulated one 10-year time step after any mountain pine beetle outbreak. Among our infested empirical plots, lodgepole pine seedling (<1.3 cm rcd) density averaged 12,496 stems ha^{-1} (Table 2); thus, 1,000 lodgepole pine stems ha^{-1} is a conservative estimate of postoutbreak lodgepole pine recruitment.

Total C stocks at each time step were calculated by summing the aboveground C in the trees with additional compartments computed by FVS. We used the CarbRept keyword, in the Fire and Fuels Extension of FVS (Rebain 2010) to generate estimates of C stocks among belowground tree components (live and dead), snags, downed woody materials, forest floor, and shrubs/herbs. With the CarbCalc keyword, we requested the allometric equations of Jenkins et al. (2003) (these equations are not specific to lodgepole pine).

This affected the C estimates for belowground components and snags, whereas we calculated aboveground C stocks using species-specific allometric equations (Ter-Mikaelian and Korzukhin 1997, Lambert et al. 2005) and our component-specific C concentrations. We accepted default values for shrubs/herbs and decomposition rates. The SnagFall keyword was used to apply a rate of fall correction factor (0.75) such that ~50% of snag biomass remained standing 10 years after infestation (Mitchell and Preisler 1998). Net ecosystem C balance was calculated by comparing total C stocks at each 10-year time step with the value one time step earlier. Total C stocks larger than that 10 years earlier were considered to have a positive C balance (sink), whereas those smaller than earlier values were considered to have a negative C balance (source).

ANPP* was derived by dividing time step C productivity by the number of years in the time step. FVS uses "tripling" to add stochastic effects to simulated forest development, adding two duplicate tree records for each stem in the input file (Dixon 2002). To allow tracking of individual stems per the Clark et al. (2001) equation, we used the NoTriple keyword to disable this feature.

Statistical Analyses

Generalized linear mixed models (PROC GLIMMIX) (Littell et al. 2006) were used to detect differences in C stocks and productivity among the disturbance history classes for the empirical and FVS-simulated data. Additional analyses were conducted for the empirical data by comparing combined infested disturbance history classes (i.e., infested ca. 1930, infested ca. 1974, infested ca. 1984, and so on) with combined undisturbed history classes (i.e., undisturbed and old-growth). Tested covariates included basal area of mountain pine beetle-killed trees, stand age, and years since mountain pine beetle disturbance, plus their interactions. We analyzed these data in a single model, aware that regional differences were possible. Because the undisturbed plots among the three landscapes are of similar age (Table 2), it was reasonable to expect similarity in C stocks and productivity if differences in environmental conditions are negligible. In a preliminary model that tested for landscape differences of the undisturbed plots, C stocks were not significantly different among the landscapes whether considering total C ($F_{2, 7} = 0.65$, $P = 0.551$) or live overstory C ($F_{2, 7} = 1.00$, $P = 0.416$). Likewise, ANPP* was not significantly different whether considering total ($F_{2, 7} = 0.22$, $P = 0.805$) or overstory ANPP* ($F_{2, 7} = 0.94$, $P = 0.436$).

Although the landscapes were not randomly selected from a population of lodgepole pine landscapes, "landscape" was modeled as a random variable because we needed to account for this potential source of variance yet we were not interested, per se, in its effects. Denominator degrees of freedom were specified as Kenward-Roger type. Ratios of generalized χ^2 to degrees of freedom were used to check for overdispersion. We specified Gaussian or log-normal error distribution, an a posteriori decision based on residuals. For data with multiple subplot samples (e.g., nontree/seedling, soil, forest floor, and litterbags), subplot location was modeled as a random variable.

Because of the small sample sizes within each disturbance history class, regarding plot-level carbon stocks and productivity data, and because we considered the risk of Type I and II errors to be equally important, we relaxed the significance level (α) of statistical tests to 0.10 (Franks and Huck 1986). When a test statistic was $P < 0.10$, we conducted a Tukey-Kramer multiple range test for all pairwise comparisons among disturbance history classes. For analyses using subplot data (forest floor, mineral soil, litterfall, and decomposition), we used $\alpha = 0.05$.

Table 4. Total ecosystem C mass and C mass by compartment among disturbance history classes.

Disturbance class	Ecosystem total[1]	Live overstory[1]	Advance regeneration[2]	Nontrees/seedlings[2]	Snags/DWM[1]	Forest floor[1]	Soil (0–20 cm)[1]
				(Mg C ha^{-1})			
Undisturbed	160 (8.6)ab	93.0 (8.6)a	0.6 (0.4)a	0.2 (0.1)a	13.7 (3.2)b	23.7 (2.8)a	28.9 (4.5)ab
Old-growth	178 (13.6)a	85.6 (17.0)ab	0.5 (0.6)a	0.2 (0.1)a	33.7 (5.0)a	17.7 (5.7)a	36.1 (8.1)a
MPB ca. 2006	135 (13.6)ab	41.7 (17.0)cd	2.0 (0.6)a	0.2 (0.1)a	41.1 (5.0)a	20.3 (5.7)a	30.3 (8.3)ab
MPB ca. 2002	121 (13.6)b	37.3 (17.0)cd	1.2 (0.6)a	0.3 (0.1)a	43.1 (5.0)a	20.9 (5.7)a	19.6 (8.3)b
MPB ca. 1999	125 (15.7)ab	24.4 (18.1)d	0.2 (0.7)a	0.3 (0.1)a	57.0 (5.8)a	22.0 (6.0)a	21.8 (8.7)ab
MPB ca. 1984	145 (12.2)ab	25.4 (16.3)d	0.9 (0.5)a	0.2 (0.1)a	53.5 (4.7)a	26.3 (5.4)a	34.3 (7.8)ab
MPB ca. 1974	127 (15.7)ab	40.6 (18.1)bcd	1.6 (0.7)a	0.3 (0.1)a	26.1 (5.8)ab	23.3 (6.0)a	38.5 (8.7)ab
MPB ca. 1930	147 (15.7)ab	73.9 (18.1)abc	2.4 (0.7)a	0.2 (0.1)a	15.5 (5.8)ab	20.7 (6.0)a	35.8 (8.7)a

Plots were measured during 2008–2009. Within each compartment (column), means followed by the same letter are not significantly different at $P > 0.10$ using tests of pairwise differences (Tukey-Kramer). Data are means (SE).
[1] The data for this compartment are presented in original scale, whereas the test results were from a model using a log-normal scale.
[2] Combined infested classes had significantly more C in this compartment than combined undisturbed and old-growth classes.

Results

Carbon Stocks

Total system C stocks were significantly greater among old-growth plots compared with those infested a second time ca. 2002 ($F_{7, 28} = 2.37$, $P = 0.049$) (Table 4). No other pairwise comparisons were significantly different, and none of the covariates or their interactions were significant. Total C stocks among *combined* infested classes, however, had significantly less (~19%) total C than the combined undisturbed and old-growth classes ($F_{1, 33.04} = 7.53$; $P = 0.010$). Carbon stocks by *compartment* were substantially different among the disturbance history classes. For example, C stocks in live overstory trees were significantly greater among undisturbed plots than among infested classes except those infested ca. 1930 ($F_{7, 28} = 10.49$; $P < 0.001$); combined plots infested within the previous ~25 years averaged about 35% of live overstory C stocks compared with that for combined uninfested plots (undisturbed and old-growth). Although C stocks in the advance regeneration compartment did not significantly differ among the disturbance history classes ($F_{7, 28} = 1.75$; $P = 0.138$), combined infested classes had significantly greater mean C in this compartment than undisturbed and old-growth classes combined (undisturbed mean: 0.53 Mg C ha^{-1}; infested mean: 1.36 Mg C ha^{-1}; $F_{1, 34} = 4.13$; $P = 0.050$). Similarly, C stocks in the nontree/seedlings compartment were not significantly different among the disturbance history classes ($F_{7, 26.75} = 1.92$; $P = 0.106$), but combined infested classes had significantly more C in this compartment than the combined undisturbed and old-growth classes ($F_{1, 32.24} = 9.49$; $P = 0.004$), albeit this pool contributes very little to ecosystem totals. Undisturbed plots had significantly less C in snags and downed woody materials than all other classes except those infested ca. 1974 and ca. 1930 for which much of this material would have decomposed ($F_{7, 25.99} = 11.14$; $P < 0.001$). Forest floor C stocks did not significantly vary among the disturbance history classes ($F_{7, 1} = 0.72$; $P = 0.722$) or among combined undisturbed and infested class plots ($F_{1, 33.93} = 0.21$; $P = 0.649$). Mineral soil C stocks were significantly greater among old-growth plots and plots infested ca. 1930 compared with plots infested a second time ca. 2002 ($F_{7, 24.06} = 2.91$; $P = 0.023$) although combined undisturbed and infested class plots did not significantly differ ($F_{1, 34} = 0.00$; $P = 0.988$). Mineral soil C stocks were the only compartment in which a tested covariate was significant; mineral soil C stocks were positively related to mountain pine beetle-killed basal area ($F_{1, 25} = 9.54$; $P = 0.005$).

Carbon Productivity

ANPP* was significantly greater among undisturbed plots than among old-growth plots (note the old-growth class plots were only in the Uinta Mountains landscape), whereas all other pairwise comparisons were not significantly different ($F_{7, 28} = 2.78$; $P = 0.025$) (Figure 2, top panel). Combined infested class plots, however, had significantly less ANPP* (~19%) compared with combined undisturbed class plots. None of the covariates were significant (e.g., basal area of infested trees). We also analyzed the ANPP* data by landscape, after reorganizing the recently infested central Idaho data into a single class (i.e., combined ca. 1999, ca. 2002, and ca. 2006 classes; i.e., all plots infested a second time since stand initiation). Among the Henry's Lake Mountains and Uinta Mountains landscapes, the mountain pine beetle-infested plots had stand ages similar to those of the undisturbed plots (Table 2), allowing for direct, intralandscape comparisons. Although infested plot means were lower, the differences were not significant compared with those for undisturbed plots (Henry's Lake Mountains: $F_{1, 4} = 0.07$; $P = 0.808$), whereas ANPP* among old-growth plots was significantly lower than that of the younger, undisturbed plots (Uinta Mountains: $F_{2, 10} = 3.43$; $P = 0.074$) (Figure 2, bottom panel). Among central Idaho plots, comparisons of similarly-aged infested and undisturbed plots were not possible because the infested plots are at least 20–70 years older than the undisturbed plots (see Table 2, footnote 5). Nevertheless, it is notable that ANPP* of plots infested ca. 1930 was not significantly different from that of undisturbed plots despite the former being several decades older than the latter. ANPP* of plots infested a second time ca. 2000 was about 60% of the value among the undisturbed plots ($F_{2, 14} = 4.86$; $P = 0.025$), although direct comparison is confounded by the infested plots being in older stands.

Litterfall and Forest Floor Decomposition Rates

Mean litterfall C fluxes were similar among disturbance classes, with significant differences only between undisturbed plots and plots infested ca. 1974 ($F_{7, 93} = 3.42$, $P = 0.003$) (Figure 3). Combined infested class plots had significantly less (~27%) litterfall than combined undisturbed class plots ($F_{1, 99} = 9.34$, $P = 0.003$). Although model results for inverse MRTs were significant ($F_{7, 24.46} = 2.55$, $P = 0.041$), no differences were detected in pairwise comparisons. Combined infested class plots, however, had significantly lower inverse MRTs than combined undisturbed and old-growth plots ($F_{1, 73.07} = 10.28$, $P = 0.002$). Litterbag exponential decay
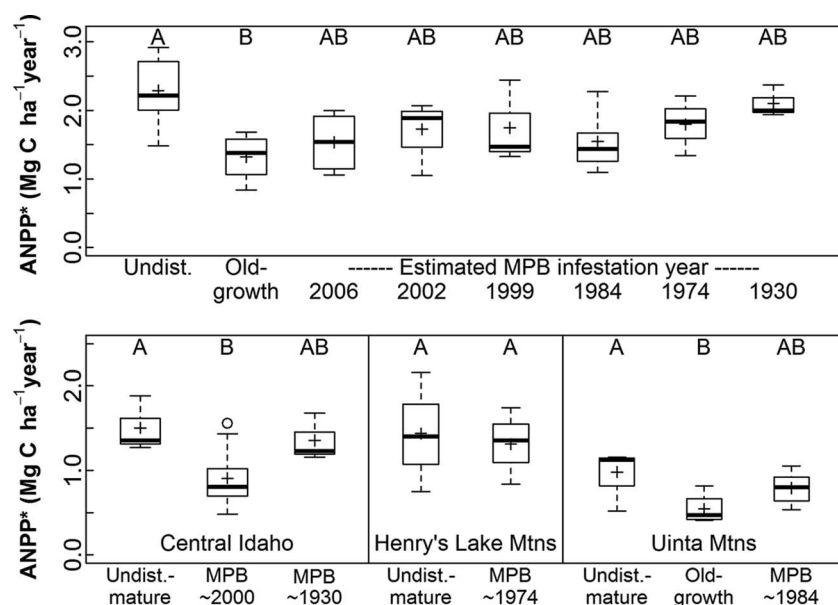
Figure 2. Boxplots of ANPP* by disturbance history class for all landscapes (top panel) and boxplots of ANPP* grouped by landscape (bottom panel). The data in the bottom panel are the same as in the top but reorganized for increased clarity in understanding the impact of mountain pine beetle (MPB) infestation on ANPP*. Within each box, means followed by the same letter are not significantly different at $P > 0.10$ using tests of pairwise differences (Tukey-Kramer). The "MPB ca. 2000" class is aggregated from three disturbance history classes (MPB ca. 1999, MPB ca. 2002, MPB ca. 2006). Note that stand ages are similar among undisturbed-mature and infested class Henry's Lake and Uinta Mountains plots whereas, among central Idaho plots, infested class stands are several decades older than undisturbed-mature stands.
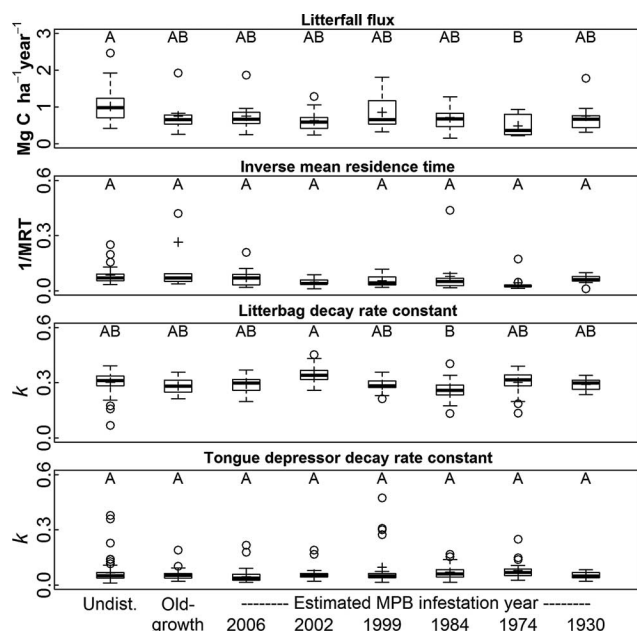
Figure 3. Boxplots of forest floor C inputs and rates of output (tongue depressors are a proxy for fine woody debris). Within each category, means followed by the same letter are not significantly different at $P > 0.05$ using tests of pairwise differences (Tukey-Kramer). MPB, mountain pine beetle.

rate constants (k) were significantly greater among plots infested a second time ca. 2002 than among plots infested ca. 1984 ($F_{7, 26.5} = 2.99$, $P = 0.019$); no other pairwise comparisons were significantly different. Litterbags decay rates were not significantly different among combined infested class plots compared with those among combined undisturbed and old-growth plots ($F_{1, 33.05} = 0.00$, $P =$
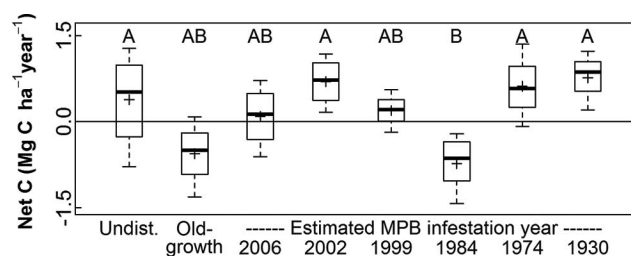

Figure 4. Boxplots of aboveground net C balance (ANPP* minus estimated losses due to decomposition of snags, downed woody materials, and forest floor). Across all disturbance history classes, means followed by the same letter are not significantly different at $P > 0.10$ using tests of pairwise differences (Tukey-Kramer). MPB, mountain pine beetle.

0.998). We observed no significant differences in the tongue depressor exponential decay rate constants (k) among the disturbance history classes ($F_{7, 28.23} = 1.61$, $P = 0.174$) or combined infested classes compared with combined undisturbed and old-growth classes ($F_{1, 33.25} = 0.09$, $P = 0.768$).

Net C Balance

Aboveground net C balance was variable within and among disturbance history classes with the lowest (negative) values among the plots infested ca. 1984 and the highest (positive) values among plots infested ca. 1930, ca. 1974, and ca. 2002 (second infestation) and undisturbed plots ($F_{7, 28} = 3.78$, $P = 0.005$) (Figure 4). All other pairwise comparisons did not significantly differ. From our estimates, plots infested ca. 1984 and old-growth plots were net C sources, whereas all other classes were either near C neutral or net C sinks. Aboveground net C balance was not significantly different among combined infested class plots and combined undisturbed plots ($F_{1, 34} = 0.09$, $P = 0.770$).

Table 5. 100-year averaged annual C productivity levels (trees only) and total system C stocks (excepting mineral soil pools) from FVS simulations with and without mountain pine beetle disturbance using empirical field data, by FVS variant and disturbance history class.

Variant, class, and simulation	C productivity in trees (Mg C ha^{-1} yr^{-1})	C stocks (Mg C ha^{-1})
Tetons variant		
Undisturbed		
No disturbance	1.28 (0.06)a	157.2 (9.9)a
MPB every 40 yr	1.03 (0.06)b	109.3 (9.9)b
MPB ca. 2000[1]		
No disturbance	1.15 (0.10)b	119.7 (5.3)a
MPB every 40 yr	1.21 (0.10)a	117.7 (5.3)a
MPB ca. 1974		
No disturbance	1.31 (0.21)a	125.0 (2.4)a
MPB every 40 yr	1.36 (0.21)a	110.2 (2.4)b
MPB ca. 1930		
No disturbance	1.07 (0.14)a	136.4 (16.2)a
MPB every 40 yr	1.23 (0.14)a	117.8 (16.2)b
Utah variant		
Undisturbed		
No disturbance	0.88 (0.06)a	181.6 (11.9)a
MPB every 40 yr	0.99 (0.06)a	134.2 (11.9)b
Old-growth		
No disturbance	0.65 (0.08)a	171.6 (17.2)a
MPB every 40 yr	0.81 (0.08)a	136.9 (17.2)b
MPB ca. 1984		
No disturbance	0.86 (0.06)a	129.6 (6.7)a
MPB every 40 yr	0.88 (0.06)a	116.2 (6.7)a

Within each variant class, means (SD) followed by the same letter are not significantly different at $P > 0.10$ using tests of pairwise differences (Tukey-Kramer). Note that, for C stocks, the data are presented in original scale, whereas the pairwise test results are from GLIMMIX models using log-normal transformations.
[1] Central Idaho plots infested a second time (ca. 1999–2006) combined.

FVS Simulations: C Stocks and Net C Balance

Among simulations based on the empirical plot data, 100-year averaged C stocks (all compartments represented except mineral soil) were 1–30% lower with a cycle of mountain pine beetle every 40 years compared with undisturbed simulations (Table 5). These differences were significant among all disturbance history classes except for plots infested a second time ca. 2000 (Tetons variant; $F_{1, 10} = 2.45$, $P = 0.149$) and plots infested ca. 1984 (Utah variant; $F_{1, 4} = 2.34$, $P = 0.201$). For the bare-ground Tetons simulations, the undisturbed trajectory averaged 156.9 Mg C ha^{-1} over 200 years compared with 132.9 Mg C ha^{-1} for the repeated mountain pine beetle trajectory using the default rate-of-loss model and 146.3 Mg C ha^{-1} for the mountain pine beetle trajectory with reduced outbreak severity (Figure 5). Using the Utah variant in a bare-ground simulation, the undisturbed trajectory averaged 152.7 Mg C ha^{-1} over 200 years compared with 100.2 Mg C ha^{-1} for the repeated mountain pine beetle trajectory using the default rate-of-loss model and 134.6 Mg C ha^{-1} for the mountain pine beetle trajectory with reduced outbreak severity.

The simulated postoutbreak net C balances using the empirical data were variable but mostly positive despite repeated mountain pine beetle outbreaks (Figure 6). Simulations using data from the undisturbed central Idaho and Henry's Lake Mountains plots switched to becoming net C sources for 10–20 years after the initial mountain pine beetle disturbance before returning to net C sinks. Undisturbed Uinta Mountains plots became net C sources for 20–30 years before returning to net C sinks. Subsequent outbreaks (using undisturbed plot data) sometimes, but not always, also switched plots from net sinks to sources for 10–20 years. Among the
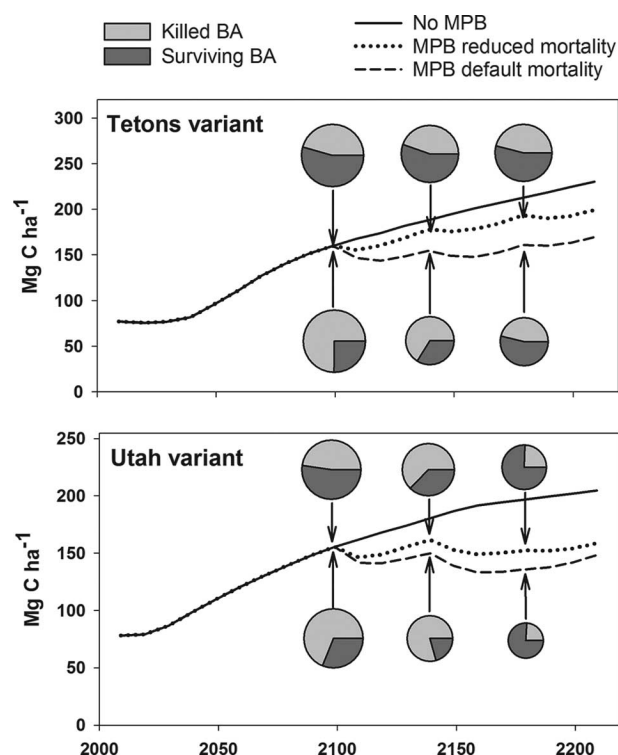

Figure 5. Total C stocks under developmental trajectories of no disturbance and cycles of mountain pine beetle (MPB) disturbance every 40 years using "bare-ground" Tetons and Utah variant FVS simulations. The "MPB default mortality" simulations used the default settings for beetle-caused mortality rates and the "MPB reduced mortality" simulations used the QValues keyword to reduce the probability of beetle-caused mortality (especially among smaller diameter classes) and the MaxYears keyword to reduce the outbreak duration from 10 to 6 years. The initial lodgepole pine density was 3,100 stems ha^{-1}, and the first mountain pine beetle outbreak was scheduled at age 100. All compartments are represented except mineral soil. Starting C stock values (snags, downed woody materials, and forest floor) were averaged from two central Idaho plots measured 3 years after a stand-replacing wildfire (Hansen and Amacher, USDA Forest Service, Rocky Mountain Research Station, unpubl. data, July 2, 2012). The circles represent surviving and beetle-killed basal area (BA) at the end of each outbreak and are proportional to the total basal area at the end of the initial outbreak in the time sequence.

17 combined infested class plots simulated with the Tetons variant, three remained net C sinks throughout the 100-year simulations despite the repeated outbreaks and another two did not become net C sinks until after the third simulated outbreak. Among the five infested ca. 1984 class plots simulated with the Utah variant, one remained a net C sink throughout the simulation, two recovered to become net C sinks after 20 years and remained such, and the other two oscillated between net C sinks and sources. On average, simulations using data from the infested ca. 1984 plots remained net C sinks throughout the 100-year simulations (Figure 6, bottom panel). The old-growth plots were the most severely impacted as they were net C sources for up to 60 years (average of 38 years for the four plots) after the first simulated outbreak, although subsequent outbreaks had little impact on net C balance. The Tetons variant bare-ground mountain pine beetle simulation using the default rate-of loss model switched the stand from net C sink to source for 10–30 years after each disturbance while the Utah variant simulation switched to a net C source for 20–30 years (downward trends in
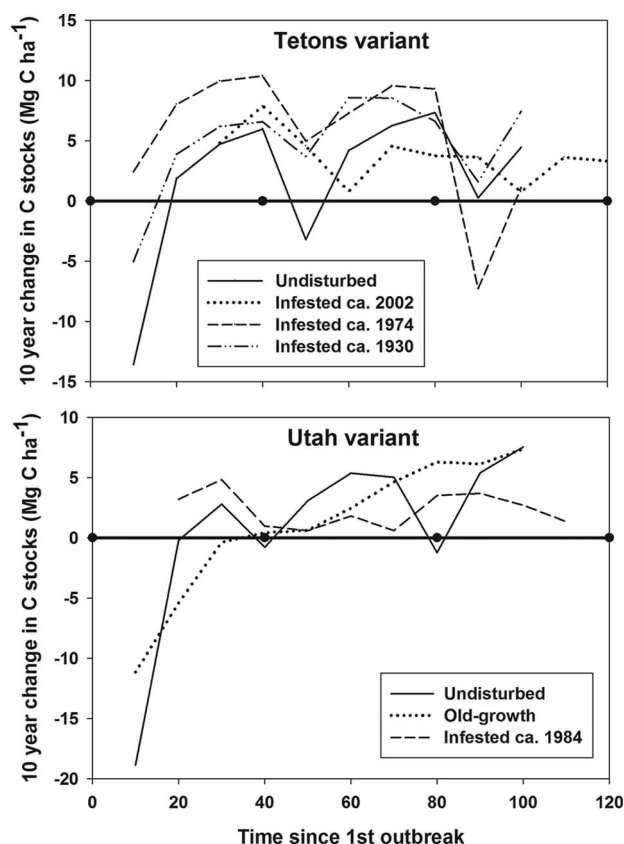
Figure 6. Net C balances (difference in total C stocks at each 10-year cycle) for FVS simulations, based on empirical plot data, with a cycle of mountain pine beetle outbreaks every 40 years (developmental trajectories without mountain pine beetle disturbance are not shown, but see Figure 5). Each trace is the averaged response among plots by variant disturbance history class. The bold solid trace is the C neutral line, and the circles represent the onset of a mountain pine beetle outbreak. "Time since 1st outbreak" refers to the first outbreak in the simulation, i.e., the first outbreak for undisturbed stands and the second or third outbreak for the previously infested plots.
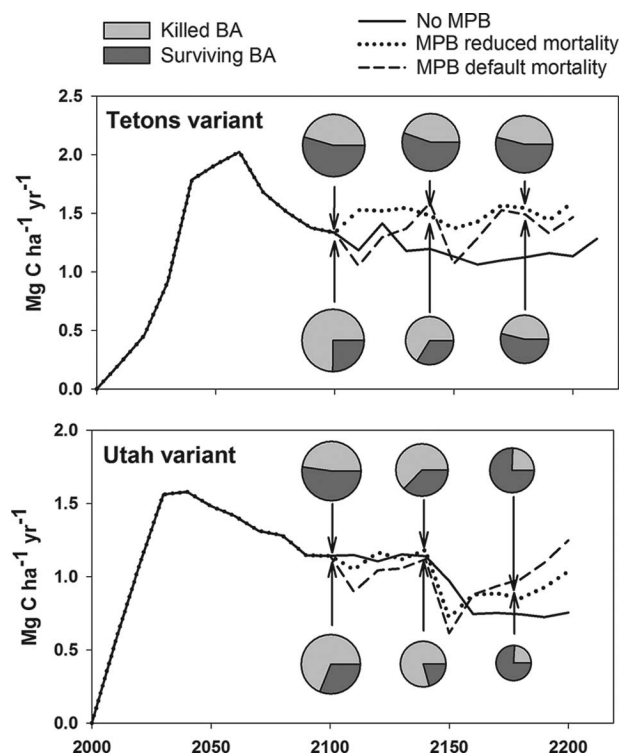

Figure 7. C productivity (trees only) under developmental trajectories of no disturbance and cycles of mountain pine beetle (MPB) disturbance every 40 years using "bare-ground" Tetons and Utah variant FVS simulations. The "MPB default mortality" simulations used the default settings for beetle-caused mortality rates and the "MPB reduced mortality" simulations used the QValues keyword to reduce the probability of beetle-caused mortality (especially among smaller diameter classes) and the MaxYears keyword to reduce the outbreak duration from 10 to 6 years. The initial lodgepole pine density was 3,100 stems ha^{-1}, and the first mountain pine beetle outbreak was scheduled at age 100 years. The circles represent surviving and beetle-killed basal area at the end of each outbreak and are proportional to the total basal area (BA) at the end of the initial outbreak in the time sequence.

Figure 5) before returning to a net C sink for the remainder of the simulation. Bare-ground simulations using the moderated rate-of-loss model (i.e., reduced outbreak severity) generally returned to positive C balance about 10 years earlier.

FVS Simulations: C Productivity

Among simulations using the empirical data, 100-year averaged tree C productivity was generally similar for trajectories with and without of mountain pine beetle disturbance (Table 5). Among Tetons variant simulations, the undisturbed trajectory had significantly greater 100-year averaged C productivity among simulations using data from undisturbed stands ($F_{1, 5} = 15.87$, $P = 0.011$), whereas the repeated mountain pine beetle disturbance trajectory had greater averaged C productivity for simulations using data from stands infested from ca. 1999 to ca. 2006 ($F_{1, 10} = 6.98$, $P = 0.025$). The two trajectories did not significantly differ among simulations using data from all other variant-class combinations (Tetons variant, infested ca. 1974: $F_{1, 2} = 0.32$, $P = 0.626$; Tetons variant, infested ca. 1930: $F_{1, 2} = 5.84$, $P = 0.138$; Utah variant, undisturbed: $F_{1, 3} = 2.57$, $P = 0.208$; Utah variant, old-growth: $F_{1, 3} = 3.09$, $P = 0.177$; Utah variant, infested ca. 1984: $F_{1, 8} = 0.09$, $P = 0.777$).

Among the bare-ground simulations, the undisturbed trajectory averaged 1.24 Mg C ha^{-1} $year^{-1}$ over 200 years for the Tetons variant compared with 1.33 Mg C ha^{-1} $year^{-1}$ for the repeated mountain pine beetle trajectory using the default rate-of-loss model and 1.41 Mg C ha^{-1} $year^{-1}$ for the moderated rate-of-loss model. Using the Utah variant, the undisturbed trajectory averaged 1.09 Mg C ha^{-1} $year^{-1}$, whereas the mountain pine beetle trajectories using the default and reduced mortality rate-of-loss models averaged 1.12 Mg C ha^{-1} $year^{-1}$ each. Simulations with infestations were slightly more productive than undisturbed simulations because long-term gains in productivity more than offset short-term losses (Figure 7).

Discussion
Carbon Stocks

Results from our field measurements suggest that total ecosystem C stocks remain relatively stable despite mountain pine beetle disturbance. Only plots in stands infested twice, with the last infestation ca. 2002, had significantly smaller C stocks than old-growth plots, but all other pairwise comparisons were not significantly different despite the range in time since outbreak (3–80 years) (Table

4). Combining infested and undisturbed class plots into two categories revealed that infestations were associated with reduced total C stocks (~19% among our plots). Nevertheless, C stocks remained at robust levels despite the disturbance. These results are similar to Kashian et al.'s (2013) result wherein total C among undisturbed stands aged 134–262 years did not significantly differ from that of similarly aged stands infested 25–30 years before measurements. These collective results support Pfeifer et al.'s (2010) conclusion that C stocks in lodgepole pine systems are resilient to impact by mountain pine beetle disturbance.

FVS simulation results were somewhat different in that mountain pine beetle outbreaks often, *although not always*, resulted in long-term reductions in C stocks (Table 5; Figure 5). The total C accumulation modeled by FVS under a trajectory of no disturbance (Figure 5), however, is notably higher than that indicated by the empirical results of Kashian et al. (2013) wherein C stocks were not found to significantly increase with advancing age among stands older than 70 years. Similarly, Bradford et al. (2008) found little change in C stocks among three subalpine landscapes in Colorado and Wyoming after the first 100 years following stand-replacing disturbance. Thus, FVS may be overpredicting C stocks and productivity for older stands, possibly because of limited parameterization data from old-growth lodgepole pine stands. We also considered that FVS may overestimate decomposition rates, but FVS default values are in line with published values from lodgepole pine systems (Fahey 1983, Busse 1994). Meanwhile, it is sensible to expect reduced C stocks after outbreaks because the death of each infested tree immediately results in reduced stand productivity compared with that of undisturbed stand development (Hansen 2014) (Figure 2, bottom left panel). Whether this effect is observed in the field may depend on outbreak severity, the magnitude and timing of postoutbreak recovery (Figure 7), and the decomposition rate of infested trees. Thus, the modest discrepancy between our empirical and simulated results may be due to empirical sample sizes insufficient to detect the relatively small impact of beetle outbreaks on C stocks (1–30% reduction in C stocks compared with undisturbed trajectories, according to our FVS simulations) or overprediction of productivity among old-growth stands by FVS. Regardless, we are confident that stand-level C stocks remain high in infested stands even if lagging levels had the stand not been infested.

Although total C stocks were robust despite mountain pine beetle disturbance, infestations were associated with redistribution of ecosystem C from live (active C sinks) to dead pools (potential C sources). Not surprisingly, the primary effect of mountain pine beetle outbreaks is the transfer of C from live overstory trees to standing dead and downed woody materials (Table 4) (Kashian et al. 2013). Our empirical data suggest that the live overstory C pool may not recover to preoutbreak levels for up to 80 years. The recalcitrance of dead C pools, however, combined with live pool recovery results in resilience of total C stocks. Surprisingly, our data indicate that the forest floor C pool is unaffected by mountain pine beetle disturbance (Table 4; also see Litterfall and Forest Floor Decomposition Rates below). In analyses of combined infested and undisturbed class plots, litterfall (i.e., forest floor inputs) was significantly less among infested plots, but this was, apparently, offset by reduced decomposition rates (i.e., forest floor outputs). This observation is contrary to other investigations in which forest floor C was generally responsive to intermediate-severity disturbances (Van Miegroet and Olsson 2011). We did find, however, that mineral soil C pools were lower among plots infested a second time ca. 2002 than among undisturbed plots. This may reflect decomposition of fine roots by ~7 years postoutbreak followed by fine root recovery thereafter.

Carbon Productivity

Our empirical results indicate that mountain pine beetle outbreaks cause an immediate reduction in C productivity (Figure 2, bottom left panel) and that stands recover, within a few decades, to levels similar to those of undisturbed stands, which have ever-declining productivity ("Old-growth" in Figure 2). The scope of our disturbance history classes may not have been adequate to address our hypothesis that ANPP* of infested stands would exceed that of undisturbed stands over long time spans (e.g., 100 years postoutbreak). For example, we were unable to find undisturbed stands of ages similar to those infested ca. 1930. Nevertheless, our field data do not support the hypothesis.

The FVS simulations similarly indicated an immediate postoutbreak drop in C productivity followed by recovery to levels of undisturbed stands after 10–60 years. Moreover, the reduced mortality bare-ground Tetons variant simulation indicated no loss of stand productivity at the scale of the 10-year time steps. In fact, this bare-ground simulation had heightened productivity compared with that of the undisturbed reference for the entire postoutbreak interval (Figure 7). For simulations based on our empirical plot data, long-term (100 years) averaged postoutbreak C productivity was generally similar among simulations with and without mountain pine beetle outbreaks for all disturbance history classes (Table 5), because of long-term productivity recovery among infested stands compared with ever-declining productivity among undisturbed stands. Although the bare-ground simulations support our hypothesis that mountain pine beetle outbreaks can result in heightened C productivity over large time scales compared with that of undisturbed trajectories (Figure 7), our field data suggest that such an outcome will not be commonly observed. The magnitude and rate of recovery will depend on infestation severity, the numbers and sizes of surviving trees (Hicke et al. 2012), successful recruitment into canopy gaps, release rates of nutrients bound in snags (Edburg et al. 2011), and stand age in relation to the pattern of declining stand C productivity.

Overall, our C productivity results are similar to those of other investigators. In an empirical study, mountain pine beetle infestation in Wyoming lodgepole pine stands resulted in a ~25% reduction in annual bole volume increment but stands recovered to, or exceeded, preoutbreak levels after 5–15 years (Romme et al. 1986). Likewise, using a process-based ecosystem model and a hypothetical infestation, Edburg et al. (2011) found that the infestation reduced net primary productivity by ~30% with full recovery to uninfested values after ~40 years. In addition, our FVS results support Edburg et al.'s (2011) finding that outbreak severity can influence the magnitude of mountain pine beetle-caused productivity declines and the duration of recovery (Figure 7). Kashian et al. (2013) reported that lodgepole pine stands infested 25–30 years before measurements had aboveground C productivity not significantly different than that of similarly-aged undisturbed stands. On the other hand, Pfeifer et al. (2010) used infested plot data from stands near our central Idaho plots to initialize FVS simulations and had *dissimilar* results. Among surveyed and simulated stands, aboveground C production did rebound for some but did not fully recover for any of 12 stands over 200-year simulations (Pfeifer et al. 2010). Their simulations, however, used only the surviving secondary stand structure (i.e., without recruitment), which probably explains the discrepancy.

Litterfall and Forest Floor Decomposition Rates

Postdisturbance changes in forest floor C are the combined result of changes in the timing, amount, and quality of litterfall as well as potential changes in microclimate (Van Miegroet and Olsson 2011). Five years postoutbreak, Page and Jenkins (2007) found a significant increase in litter biomass, compared with that of uninfested stands, as infested trees shed their needles. After needlefall of infested trees is complete, litterfall is expected to decrease due to reduced live crown volume, resulting in reduced forest floor biomass relative to that of uninfested stands. Our results, however, are not consistent with this expectation. We did not observe increased forest floor C stocks over the short term (< 10 years postoutbreak) or decreased forest floor C stocks over the long term (25–35 years postoutbreak) (Table 4). Although litterfall was significantly reduced among plots infested ca. 1974 compared with the undisturbed history class plots (Figure 3) and among combined infested class plots compared with combined undisturbed class plots, this did not lead to observable changes to forest floor C stocks. Forest floor C pools were essentially unresponsive to mountain pine beetle disturbance. In Wyoming lodgepole pine stands, Griffin et al. (2011) similarly found that lodgepole pine litter biomass was not significantly different among undisturbed, red stage (~2 years postattack), gray stage (~4 years postattack), and 30-year postattack stands.

Several factors suggest that any postoutbreak increase in forest floor biomass will be ephemeral and difficult to detect. First, based on lodgepole pine needle longevity (Schoettle 1990), annual needle fall will be 5–20% of total foliar volume *even without mountain pine beetle disturbance*, masking the increased needle fall from infested trees. Second, not all trees are killed by an outbreak and the timing of mortality among infested trees in a stand is more a distribution rather than a discrete event (Simard et al. 2012, Hansen 2014). Third, needle fall from killed trees is also a nondiscrete event, with some needles remaining on trees 5 or more years after infestation. Finally, needles decompose relatively quickly, with estimated half-lives of 2–3 years (Fahey 1983) (Figure 3). Thus, the litter biomass of infested stands might be slightly elevated for just a few years, relative to that of undisturbed stands, becoming reduced thereafter, depending on the surviving stand structure and recovery rates (Simard et al. 2012).

Although decomposition rates of the forest floor (i.e., inverse MRT) were not significantly different among the disturbance history classes (Figure 3), combined infested classes had significantly lower inverse MRT than combined undisturbed and old-growth classes. That is, decomposition was decelerated among infested plots, possibly because the reduced canopy cover may have resulted in relatively dry conditions. There were almost no significant differences, however, for decay rates of tongue depressors and litterbags, either by disturbance history class or combined infested and undisturbed classes. In summary, mountain pine beetle outbreaks likely result in the following: increased litterfall 3–5 years postoutbreak (although our observations did not detect this); decreased litterfall until the overstory recovers; and slowed decomposition of the forest floor until the overstory recovers. The net outcome of these changes is stable forest floor pool sizes regardless of beetle disturbance.

Net C Balance

Our empirical results indicate that mountain pine beetle outbreaks have little *long-term* impact on net C balance. Plots infested ca. 1984 were the only infested disturbance history class found to have reduced and negative net C balance compared with that of undisturbed plots. All other infested class plots had positive net C balances that were not significantly different from that of the undisturbed plots (Figure 4), and combined infested classes did not significantly differ from combined undisturbed classes. Our FVS results, based on both the field data and bare-ground simulations, suggest that an initial outbreak (i.e., the first in an otherwise undisturbed stand) can result in substantially reduced net C balance and switch stands from net C sinks to sources (Figures 5 and 6). The negative C balance after this initial outbreak generally lasted 10–20 years but extended up to 60 years for one of four old-growth plots. Stands with previous infestation, however, commonly remained net C sinks despite further disturbance (Figure 4), and, thus, the potential for infested stands to switch from net C sinks to net C sources (Kurz et al. 2008, Hicke et al. 2012) will depend on stand age and disturbance history as well as on factors such as infestation severity (Edburg et al. 2011) (Figure 7).

Several factors mitigate the switching from C sink to source after infestation. Decomposition is negligible in snags as well as in downed boles not in contact with the soil (Fahey 1983, Harvey 1986, Busse 1994). In addition, snagfall can be delayed for many years (Mitchell and Preisler 1998), and, even after falling, many stems may remain elevated off the forest floor in jackstraw piles. Moreover, stems in contact with the forest floor can take many decades to fully decay (Fahey 1983, Busse 1994, Brown et al. 1998). The relative importance of decomposition in net C balance was illustrated by Kashian et al. (2013) in that postfire live C accumulation (77.8 Mg C ha^{-1} over 100 years) greatly exceeded C losses via decomposition (19.6 Mg C ha^{-1} over 100 years). Autotrophic inputs are the primary drivers of net C balance in lodgepole pine systems (Brown et al. 2012, Kashian et al. 2013, Moore et al. 2013). Thus, the temporary losses of live lodgepole pine from mountain pine beetle infestation are more important to net C balance than the increases in substrates subject to heterotrophic decomposition (i.e., snags and downed woody materials). Although mountain pine beetle outbreaks reduce C productivity of affected systems, possibly switching them temporarily from net C sinks to sources, our results indicate that lodgepole pine ecosystems are typically net C sinks except in the immediate aftermath of an *initial* outbreak (Figures 4–6). Combustion during wildfires is probably the primary pathway of C losses in these systems, but, even then, postfire C stocks are substantial and recover to near prefire levels after a few decades (Kashian et al. 2013).

Conclusion

Mountain pine beetle outbreaks significantly modify lodgepole pine C dynamics, but the changes are ephemeral and should be considered in the context of lodgepole pine system development from stand initiation through old-growth. From this ecological perspective, it can be seen that mountain pine beetle outbreaks are an intermediate-level disturbance that may decrease long-term C stocks by ~1–30% depending on outbreak severity, among other factors (the degree of this impact appears similar regardless of single or repeated outbreaks). Postoutbreak C productivity and net C balance are reduced, relative to that of undisturbed stands, for up to 60 years although the period is usually much shorter, depending on factors such as stand age, previous disturbance, and infestation severity. Our hypothesis that long-term averaged, postoutbreak C productivity is heightened by outbreaks compared with undisturbed development was not supported by our field data (Figure 2) and had limited support from our FVS simulations (Table 5; Figure 7).

Instead, it appears that long-term gains in postoutbreak C productivity are typically offset by short-term reductions.

Mountain pine beetle is an agent of reorganization in the inevitable cycle of ecosystem creation and destruction (Holling 1992, Kay 2000). Lodgepole pine systems are not only resilient to but are also reliant on disturbance (Lotan et al. 1985). From a management perspective, mountain pine beetle outbreaks present many challenges to human values of lodgepole pine systems, but recognition of the role of mountain pine beetle disturbance in ecosystem function can shape our expectations and inform vegetation management decisions regarding C sequestration and stocks among postoutbreak stands.

Endnote

1. For more information, see www.fs.usda.gov/detail/r1/forest-grasslandhealth/?cid=stelprdb5410518.

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Appendix A: Soils and Climate

Soils at central Idaho plots are Inceptisols, classified as Typic Cryumbrepts or Typic Cryochrepts, generally with a silt loam to sandy loam texture (Terry Hardy, Soil Scientist, Sawtooth and Boise National Forests, pers. comm., Aug. 26, 2011). Dataloggers installed at a subset of plots from 2010 to 2012 showed average air temperatures of $-8.9°$ C in January and 13.7° C in July. Mean annual precipitation at the nearest SNOTEL stations (Banner Summit, elevation 2,146 m; Galena Summit, 2,676 m; www.wcc.nrcs.usda.gov/snow/) ranges from 77 to 105 cm. This precipitation falls mostly as snow during long winters with summers being relatively arid.

Soils at a subsample of Henry's Lake Mountains plots were classified as Inceptisols and Andisols: Vitrandic Dystrocryepts, Vitrixerandic Humicryepts, and Humic Vitricryands (John Lott, Soil Scientist, Targhee National Forest, pers. comm., Aug. 15, 2011). Dataloggers installed at a subset of plots from 2010 to 2012 showed average air temperatures of $-9.0°$ C in January and 14.4° C in July. Mean annual precipitation at nearby SNOTEL stations (Madison

Plateau, 2,362 m; Whiskey Creek, 2,072 m^2) ranges from 88 to 105 cm, falling mostly as snow with summers being relatively dry.

Soils at a subset of Uinta Mountains plots were classified as Lithic Cryorthents, Lithic Haplocryepts, and Ustic Haplocryalfs (Sarah Leahy, Soil Scientist, Ashley National Forest, pers. comm. Oct. 2, 2011). Dataloggers installed at a subset of plots from 2009 to 2012 showed average air temperatures of −7.6° C in January and 12.8° C in July. Mean annual precipitation at nearby SNOTEL stations (Chepeta Lakes, 3,228 m; King's Cabin, 2,660 m; Mosby Mountain, 2,899 m; Trout Creek, 2,901 m) ranges from 66 to 80 cm, with a relatively uniform seasonal distribution albeit falling mostly as snow due to the short summer season.

Appendix B: C Content Results
Tree Components

Component	Mean (SD) % carbon	No. of samples
LPP foliage[1]	55.7 (3.6)	36 CI trees, 26 HL trees, 26 UM trees
LPP bark[1]	57.0 (4.7)	36 CI trees, 26 HL trees, 26 UM trees
LPP stemwood[1]	52.0 (3.7)	36 CI trees, 26 HL trees, 26 UM trees
Subalpine fir foliage	57.4 (0.4)	1 CI tree, 1 HL tree
Engelmann spruce foliage	49.4 (NA)	Composite of two UM trees
Douglas-fir foliage	46.2 (NA)	Composite of two CI trees
Dead LPP stemwood (CI)[2]	44.5 (3.9)	26 pieces
Dead LPP stemwood (HL)[2]	53.9 (2.1)	28 pieces
Dead LPP stemwood (UM)[2]	54.9 (3.1)	20 pieces
Litterfall[3]	53.4 (6.7)	115 samples

LPP, lodgepole pine; CI, central Idaho; HL, Henry's Lake Mountains; UM, Uinta Mountains; NA, not applicable.

[1] The percentage biomass in C for LPP varied by tissue type ($F_{2, 185.4} = 74.74$, $P < 0.0001$) but not by region ($F_{2, 55.04} = 1.14$, $P = 0.3269$) or layer (overstory or understory; $F_{2, 124.7} = 0.31$, $P = 0.7335$).

[2] Carbon concentrations of dead LPP (stemwood only) were not significantly different by orientation (standing or downed: $F_{1, 71.43} = 0.05$, $P = 0.8184$), decay class ($F_{4, 68.37} = 0.42$, $P = 0.7967$), or piece size class (<3-in. diameter or ≥3-in. diameter: $F_{1, 69.75} = 0.00$, $P = 0.9538$). Carbon concentrations of dead LPP materials, however, were significantly different among the regions ($F_{2, 68.45} = 65.74$, $P < 0.0001$).

[3] Litterfall C concentrations did not significantly differ by region ($F_{2, 112} = 1.02$, $P = 0.3640$).

Seedlings

Aboveground C mass, in grams, of seedlings (includes foliage, bark, and stemwood) is given by

$$\text{Mass}_C = (0.513 + 2.096 \times \text{RCD} - 0.392 \times \text{DF} - 0.030$$
$$\times \text{ES} - 0.073 \times \text{LPP} + 0.163 \times \text{SAF})^3 \quad (A1)$$

where RCD is the root collar diameter (cm); DF = 1 if species is Douglas-fir, 0 otherwise; ES = 1 if species is Engelmann spruce, 0 otherwise; LPP = 1 if species is lodgepole pine, 0 otherwise; and SAF = 1 if species is subalpine fir, 0 otherwise. For whitebark pines, the parameters for the other species simply equal zero in the equation. Note that the observed values were cube root transformed to meet normality assumptions before analysis; this is why the equation includes cubing the product of the terms. GLIMMIX output is not interpretable for determining a coefficient of determination (R^2_{adj}), however, a regression of predicted against observed values indicated the model explains almost 95% of the variation (60 lodgepole pine seedlings sampled, 16 subalpine fir, 2 Douglas-fir, 2 whitebark pine, and 3 Engelmann spruce; DRC range: 0.25–3.00 cm).

Nontrees

Genus	Equation for C mass (g) in a 0.66 m^2 plot[1]	No. of samples	R^2_{adj}
Arnica	$(12.9 \times P) - (0.1 \times \text{HL}) + (8.2 \times P \times \text{HL})$	10	0.96
Epilobium	$(107.8 \times P)$	8	0.69
Fraxinus	$(12.0 \times P) - (0.2 \times \text{HL}) + (6.8 \times P \times \text{HL})$	10	0.96
Geranium	$(10.7 \times P)$	5	0.96
"Grass"[2]	$(19.7 \times P) - (1.7 \times \text{CI}) - (2.8 \times \text{HL}) + (29.7 \times P \times \text{CI}) + (32.7 \times P \times \text{HL})$	35	0.92
Lupinus	$(39.0 \times P)$	7	0.75
Taraxacum	$(46.5 \times P)$	2	0.99
Vaccinium	$(47.8 \times P) + (6.1 \times \text{HL})$	27	0.91

[1] P is percent cover for 0.66 m^2 subplots, ocularly estimated with a template of known comparative dimension; HL = 1 if the landscape is Henry's Lake Mountains, 0 otherwise; CI = 1 if the landscape is central Idaho, 0 otherwise.

[2] "Grass" includes *Carex* and *Calamagrostis* spp.