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Carbon storage in old-growth and second growth fire-dependent western larch (*Larix occidentalis* Nutt.) forests of the Inland Northwest, USA

S.M. Bisbing [a,b,1], P.B. Alaback [a], T.H. DeLuca [b,*]

[a] *College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*
[b] *The Wilderness Society, Ecology and Economics Research Department, 503 West Mendenhall, Bozeman, MT 59715, USA*

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ABSTRACT

There is limited understanding of the carbon (C) storage capacity and overall ecological structure of old-growth forests of western Montana, leaving little ability to evaluate the role of old-growth forests in regional C cycles and ecosystem level C storage capacity. To investigate the difference in C storage between equivalent stands of contrasting age classes and management histories, we surveyed paired old-growth and second growth western larch (*Larix occidentalis* Nutt)–Douglas-fir *(Pseudostuga menziesii* var. *glauca)* stands in northwestern Montana. The specific objectives of this study were to: (1) estimate ecosystem C of old-growth and second growth western larch stands; (2) compare C storage of paired old-growth–second growth stands; and (3) assess differences in ecosystem function and structure between the two age classes, specifically measuring C associated with mineral soil, forest floor, coarse woody debris (CWD), understory, and overstory, as well as overall structure of vegetation. Stands were surveyed using a modified USFS FIA protocol, focusing on ecological components related to soil, forest floor, and overstory C. All downed wood, forest floor, and soil samples were then analyzed for total C and total nitrogen (N). Total ecosystem C in the old-growth forests was significantly greater than that in second growth forests, storing over 3 times the C. Average total mineral soil C was not significantly different in second growth stands compared to old-growth stands; however, total C of the forest floor was significantly greater in old-growth (23.8 Mg ha^{-1}) compared to second growth stands (4.9 Mg ha^{-1}). Overstory and coarse root biomass held the greatest differences in ecosystem C between the two stand types (old-growth, second growth), with nearly 7 times more C in old-growth trees than trees found on second growth stands (144.2 Mg ha^{-1} vs. 23.8 Mg ha^{-1}). Total CWD on old-growth stands accounted for almost 19 times more C than CWD found in second growth stands. Soil bulk density was also significantly higher on second growth stands some 30+ years after harvest, demonstrating long-term impacts of harvest on soil. Results suggest ecological components specific to old-growth western larch forests, such as coarse root biomass, large amounts of CWD, and a thick forest floor layer are important contributors to long-term C storage within these ecosystems. This, combined with functional implications of contrasts in C distribution and dynamics, suggest that old-growth western larch/Douglas-fir forests are both functionally and structurally distinctive from their second growth counterparts.

1. Introduction

Old-growth forests are an important element in the debate over maintenance of forest biodiversity and carbon (C) storage in the western United States. As the overall acreage of old-growth diminishes, management of the remaining areas becomes a more critical issue for conservation. The most detailed information on old-growth forests in the western U.S. is available for the temperate rainforests of the Pacific Northwest (PNW). Old-growth forests of the PNW are known to possess ecological attributes that are distinct from those found on younger stands and managed forests (Franklin and Spies, 1991a,b; Franklin et al., 2002; Smithwick et al., 2002; Franklin and Van Pelt, 2004). Old-growth forests in the PNW are also distinctive in their functional attributes, including their disturbance processes and their accumulation and distribution of biomass (Grier et al., 1981; Spies and Franklin, 1988; Halpern and Spies, 1995; Franklin et al., 2002; Franklin and Van Pelt, 2004; Spies, 2004). The complexity of this old-growth is intrinsically associated with the forest's vertical and horizontal variabilities, abundance and distribution of coarse wood, accumulation of forest floor detritus, patterns of nutrient flux between vegetation and soils, and

* Corresponding author. Current address: School of the Environment, Natural Resources and Geography, 2nd Floor ECW, Bangor University, Bangor LL57 2UW, United Kingdom. Tel.: +44 077 945 22185.
E-mail address: t.h.deluca@bangor.ac.uk (T.H. DeLuca).
[1] Current address: Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, CO 80523, USA.

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understory plant diversity—with each of these attributes contributing to a significant portion of a stand's long-term C storage (Thomas et al., 1988; Franklin et al., 2002).

As biomass accumulates through stand development, forest ecosystems can become crucial C sinks, playing significant roles in regional C budgets (Harmon et al., 1990; Suchanek et al., 2004). Coarse wood is a major C component of old-growth ecosystems and may equal or surpass other organic biomass components in the forest floor. Dead wood in these forests plays a major role in soil C cycling, nitrogen fixation, wildlife habitat, and erosion control (Harmon et al., 1986, 2004; Franklin et al., 2002). In addition, coarse woody debris (CWD) has the potential to store a large amount of C in the forest ecosystem; its role in storing C often overlooked in forest C studies (Sollins et al., 1980; Spies et al., 1988; Harmon and Hua, 1991).

Studies suggest that ecosystem C can decline up to 20% following harvest and requires an extensive recovery period to return to pre-harvest levels, which can be up to 200 years for forests of the PNW and the Northern Rockies (Harmon et al., 1990; Turner et al., 1995). Forest harvesting results in significant changes in C storage in forest ecosystems (Lussayaert et al., 2008), but its effects on soil C are less understood (Law et al., 2003; Sun et al., 2004). Disturbance can alter soil C inputs and reserves and significantly affect the amount of woody debris found on the forest floor. Timber management practices may also impact soil physical, chemical, and biological properties resulting in a reduction in the long-term productivity of a given site (Powers, 2006).

Although the ecological structure and C storage of old-growth forests in the coastal PNW are well-documented, few studies have focused on forests of the interior west, where fires and other disturbances are generally thought to effect ecosystem structure and C accumulation in old-growth forests (Spies et al., 2006; Suchanek et al., 2004; Zhou et al., 2007; Gough et al., 2008). Studies from the PNW region have demonstrated total ecosystem C to be much greater – up to 3 times more – in old-growth forests as compared to second growth forests (Grier et al., 1981; Spies et al., 1988; Harmon et al., 1990, 2004). There is, however, limited understanding of the C storage patterns or the ecological distinctiveness of interior old-growth forests, leaving little ability to evaluate the role of these old-growth forests in regional C cycles and ecosystem level C storage capacity.

Additionally, to our knowledge, there have been no studies documenting the structure, function, and C storage capacity of old-growth western larch (*Larix occidentalis* Nutt.) forests in North America. Old-growth larch was a key element in the pre-settlement landscape of Montana, dominating millions of hectares (Habeck, 1990; Arno et al., 1997). During the mid-1800s, loggers began harvesting larch trees over 60 cm diameter, leading to regional losses of old-growth forest structure and forest cover conversion to *Pseudotsuga* and *Abies* types (Hessberg et al., 2005). In the 20th century, harvesting of mature larch stands reached a peak in the 1960s (at about 50 million m^3/yr), resulting in noted decline in the occurrence of old-growth larch forests in the western US (Lowery, 1977). The current total area of the western larch forest type in the United States is estimated at more than 2.3 million acres, half of which resides in Montana. Western larch forests are managed primarily by the US Forest Service and account for 3% of the timberland in its range (Conner and O'Brien, 1995). Today's remnant stands are highly valued as recreational and natural areas (Arno et al., 1997).

To investigate the variability of C storage and ecological structure between equivalent stands of contrasting age classes and management histories, paired old-growth and second growth mixed western larch stands were surveyed in northwestern Montana. In this study, the term old-growth follows the United States Forest Service (USFS) Region 1 definition for old-growth western larch/Douglas-fir (*Pseudotsuga menziesii* (*Mirb.*) *Franco* var. *glauca* (Beissn.) Franco) forests (Green et al., 1992): (1) at least 20 dominant trees per hectare (ha) with a minimum age of 170 years and a minimum diameter-at-breast-height (dbh) of 53 cm and (2) a minimum total stand basal area of 18.3 m^2/ha. For the purpose of this study, second growth stands are those stands clearcut harvested within the last 50 years.

The primary objectives of this study were to: (1) estimate ecosystem C of old-growth and second growth western larch stands in western Montana, (2) compare C storage of paired old-growth–second growth western larch stands and (3) assess differences in ecological function and structure between these two age classes, specifically measuring C associated with mineral soil, forest floor, CWD, understory, and overstory, as well as overall diversity and structure of vegetation. This study helps fill a major gap in the literature on the storage and distribution of C in interior, dry, old-growth forests (Suchanek et al., 2004; Spies et al., 2006) and of the structure and function of old-growth western larch forests in this environment.

2. Methods

2.1. Study area

All study areas reside in the Swan Valley on the Swan Lake Ranger District of the Flathead National Forest of northwestern Montana, USA. The Valley's unique checkerboard landscape – a mix of public and private land – is the result of a staggered-setting harvest system in which 10–20 ha clearcuts were dispersed amongst areas of older forest. This location was chosen because of well-documented remnant old-growth stands with adjacent harvested pairs, providing a valuable opportunity for a comparison study. Study areas were selected on the east side of the Swan Valley within 10 km of Condon and about 65 km southeast of the Swan Lake weather station, extending from 47°26′ to 47°37′N and 113°36′ to 113°44′W (see Fig. 1). Both maritime and continental climates influence the Swan Valley, resulting in forests composed of Pacific Coast and intermountain species, allowing for comparisons to nearby, well-studied Pacific Northwest ecosystems. Mean annual air temperature of the area is 4.5 °C (40 F) (Swan Lake weather station, NOAA 2008). Mean annual precipitation is 70 cm (28 in.), with almost half falling as snow. Major forest tree species of the area include western larch, interior Douglas-fir, and Ponderosa pine (*Pinus ponderosa* C. Lawson). Western larch, the species of interest for this study, is a long-lived, fire-resistant tree of the Northern Rockies and is the largest species of the genus *Larix*, reaching over 2 m in diameter, 60 m in height, and over 700 years in age (Arno et al., 1997). Although often found on north slopes, western larch occupies mixed species to pure stands in dry montane to subalpine zones (approximately 700–2000 m elevations) of the northern Rockies, west to the east slope of the Cascade Mountains and north to southern British Columbia.

2.2. Site selection

Due to the close proximity of old-growth and adjacent second growth stands, the Swan Valley is an ideal location for a comparison study. In this study, 15 pairs of old-growth and second growth western larch–Douglas-fir stands were sampled. Three separate study areas were selected, with each area possessing five sets of paired stands. Each stand pair consisted of one old-growth and one adjacent second growth stand, comparable in soils, hydrology, habitat type and topographic settings.

Prior to selection of study areas, a complete stand list was obtained from the Swan Lake Ranger District of the Flathead National Forest. A list of Swan Valley stands possessing western

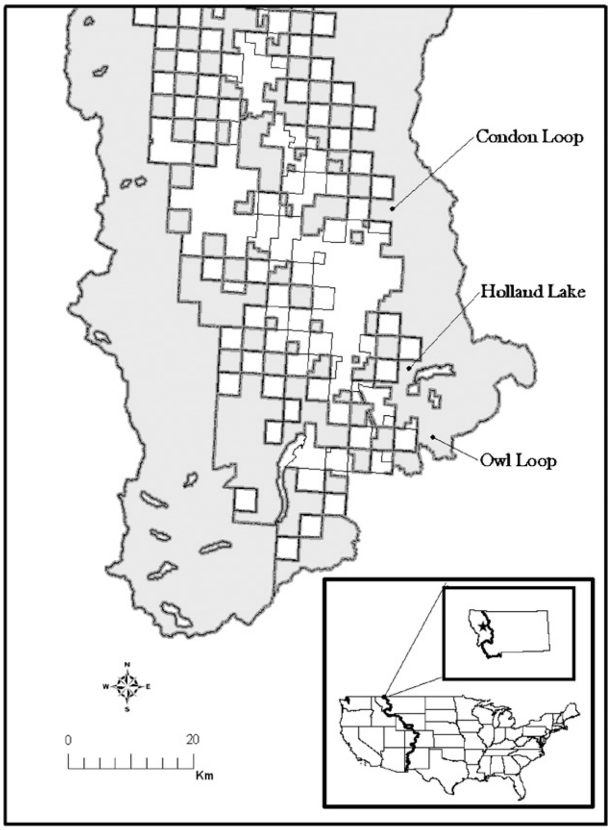

Fig. 1. Study areas for old-growth and second growth carbon storage study (Swan Lake Ranger District, Flathead National Forest, Montana, 130 km Northeast of Missoula, Montana, USA). US Forest Service land is represented in gray, and private land is represented in white. Continental Divide appears as thick, black line on reference maps.

larch and Douglas-fir that meet the Region 1 old-growth definition was determined from queries of georeferenced USFS databases of the Swan Lake Ranger District (Jane Ingebretson, Personal Communication, 2007, USDA Forest Service, Swan Lake Ranger District, Flathead National Forest). Queries of USFS stand records were then used to locate forest stands that met the USFS old-growth definition, had dominant western larch and Douglas-fir trees, common soil type, and common habitat type. The majority of stands meeting these requirements and possessing adjacent harvested stands were found in the following areas within the Swan Valley: Condon Loop, Holland Lake, and Owl Loop. Consequently, these regions were chosen as the three study areas for this research (Fig. 1).

All selected stands are mid-elevation (1000–1400 m) sites representing the three distinct habitat types found along this elevational gradient in the Swan Valley (Pfister et al., 1977). Selected stands fall within the following habitat types, representing relatively narrow segments of environmental conditions: *Pseudotsuga menziesii*/*Symphoricarpus albus* (Douglas-fir/snowberry, warm/dry), *Abies grandis*/*Clintonia uniflora* (grand fir/queencup beadlily, warm/moist), and *Abies lasiocarpa*/*Clintonia uniflora* (subalpine fir/queencup beadlily, cool/moist) (Pfister et al., 1977). Soils at Holland Lake and Owl Loop sites are Typic Haplocryalfs, and Condon Loop sites are predominantly Typic Dystrocryepts (USDA Soil Survey Staff, 1999). Both soil types are loamy in texture, well-drained, and skeletal. Thick quaternary alluvial, colluvial, and glacial till deposits are characteristic of these glaciated valley bottom stands (Montagne et al., 1982).

Old-growth stands showed little or no evidence of recent human disturbance and displayed structures associated with late-successional forests, as defined by Franklin and Spies (1991b). Second growth stands were approximately 30–50 years old at the time of sampling, originating following clearcut logging of old-growth stands between 1961 and 1979. In addition to regeneration from USFS planting, unharvested, remnant old-growth patches acted as natural seed sources for regeneration of adjacent clearcut stands.

2.3. Field methods

A modified version of the USFS FIA (Forest Inventory and Analysis) protocol (USDA Forest Service, 2007) was applied at all stands. FIA data collection focuses on tree mensurational characteristics, while understory vegetation structure and woody debris data is only collected on a subset of FIA plots. In this study, data collection deviated from the standard FIA data collection procedures by including: an extensive understory vegetation survey; thorough sampling of CWD; tree age and height information on every stand; and soil, forest floor, and CWD chemical analysis.

The following plots were established within each stand: one 0.405 ha (4050 m^2) large-diameter plot for site characteristics, four 1/10th ha (1000 m^2) sampling plots, four 1/100th ha (100 m^2) subplots for intensive sampling, and four 1/1000th ha (10 m^2) microplots for tree seedling/sapling counts. Sampling included collection of data on live trees (species, diameter-at-breast-height (dbh), height, age), dead trees/snags (species, dbh, height, decay class), understory vegetation composition (species, percent cover class, biomass), CWD (species, decay class, end diameter, middle diameter, top diameter, length), soil composition, and forest floor matter.

In this study, the term overstory refers to total aboveground tree mass, including bark, stemwood, branches, and foliage. The term mineral soil C is used to refer to the total C present in the mineral soil and fine roots, excluding that present in the forest floor. The term forest floor is used to refer to all dead organic matter in the O-horizon, including humus, litter, and fine woody debris (FWD). Coarse woody debris refers to all snags (standing dead trees) and downed logs greater than 10 cm in diameter at the large end of the piece and 1.5 m in length (Harmon and Sexton, 1996; Smithwick et al., 2002).

2.4. Overstory sampling

As in the standard FIA protocol, all trees were tallied by diameter class on our smallest plot sizes (1/1000th ha, and 1/100th ha), and trees greater than 20 cm were sampled in our largest plots (1/10th ha) (Fergusen et al., 2001). We recorded species and dbh for all sampled trees. Height and age information were also collected on the four largest, oldest trees in each 1/100th ha subplot. This information was used to determine the average age of the dominant and co-dominant trees within the stand, information linked directly to stand origin, maturity, and productivity. Tree age was estimated from ring counts derived from increment cores taken about 1 foot above the ground line, on the downhill side of the tree (no correction was made for stump height in age estimates).

2.5. Understory vegetation sampling

On each 1/100th ha subplot, information was also gathered on understory vegetation composition. A species list was developed, consisting of all species present as well as their respective percent cover class. Percent cover of each vascular plant species was estimated by assigning one of the following coverage classes (Pfister et al., 1977): + = present in stand but not in plot, T = trace (0–1%), 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, or 6 = 95–100%. Species were identified and classified as native or exotic based on descriptions from regional floras (Hitchcock and Cronquist, 1973; USDA, NRCS, 2008).

Understory biomass sampling was also conducted on each 1/100th ha subplot. A 0.25 m^2 square plot was placed within 3 m of each plot center. All vegetation falling within this plot was clipped and reserved for lab analysis.

2.6. Mineral soil and forest floor sampling

Information was collected on soil and organic matter characteristics at the 1/100th ha subplot level. A grid system and a random number table were used to select random points for collection of both soil and forest floor samples. Soil samples were taken to 1-m depth at a random point within each subplot (120 total samples). Samples were collected at the following depths: 0–10 cm, 20–30 cm, 50–60 cm, and 90–100 cm. If samples could not be collected at each depth, sample mass was corrected for depth. Samples were then mixed together to create one composite sample for each individual subplot. Total coarse fragment content was recorded as a percent of total mineral soil in each layer. To obtain a forest floor sample, a 15.24 cm (6-in.) diameter ring was dropped in a random point within each 1/100th ha subplot (120 total samples), and all material was removed down to the mineral soil layer. A slide hammer was used to take a soil bulk density sample down to 5 cm depth at each site location (30 total samples). Dense occurrence of rocks in the subsurface precluded collection of deep soil bulk density samples, however, increasing density with depth (which would increase soil C estimates) was offset by increasing coarse fragment content with depth creating a reasonable estimate of total mineral soil C to 1 m depth.

2.7. Coarse woody debris sampling

CWD was sampled along 120 m line transects (Brown, 1974; Harmon and Sexton, 1996). Along the transect, variables recorded for each inventoried log included: diameters at both ends and at the midpoint, length, species, and decay class (Keane, 2006). Diameters were measured using calipers, while the length of logs was paced out using a 1-m PVC pipe (Harmon and Sexton, 1996). Unless the shape of the log was obvious, rotten wood that was fully incorporated into the forest floor or buried, falling under decay class five, was not included in the inventory. In addition to collecting mensurational characteristics of downed woody debris, five samples of each decay class assessed (decay classes one through four) were cut from both Douglas-fir and western larch downed wood samples from within one old-growth stand within each study area, making a total of 120 samples. These samples were collected for use in determining total C and N concentration and local wood densities for each of these species at each level of decay.

2.8. Laboratory analysis

Collected downed wood samples were used to determine local wood densities of Douglas-fir and western larch for each decay class (Keane, 2006). To obtain wood density for each decay class of each species, samples were soaked and weighed, and volume was determined by displacement in water.

Following Lamlom and Savidge (2003), CWD decay samples were then prepped through a series of steps to determine C/biomass ratios. Samples were air-dried in a greenhouse at 40 °C for 1 week. Samples were drilled to 0.2 mm, and composite samples were ground, dried, and analyzed for total C and N concentration using a LECO Truspec CN 3 175 dry combustion analyzer.

Similar procedures were followed for the analysis of mineral soil, forest floor, and understory samples. Understory samples were dried to a constant weight at 60 °C, ground, and analyzed for total C, as described above. Soil samples were dried, weighed, sieved through a 2-mm mesh sieve (#10), and milled to 270 μm. Soil bulk density cores were dried at 105 °C for 24 h and weighed, and bulk density was calculated as mass divided by core volume.

2.9. Calculations

Plot-level biomass and C estimates were calculated on a per-unit-area basis, expressed in Mg ha^{-1}, and determined by summing the biomass values for the individual component on each plot and estimating values for the land area covered by the plot (Jenkins et al., 2003). Biomass/C ratios were derived from biomass studies (Harmon and Sexton, 1996; Lamlom and Savidge, 2003; Jenkins et al., 2003) and used to estimate the total overstory C for each forest stand as described below.

Tree diameters for each species group were used in the regression equation to estimate overstory biomass. The equation used is as follows (Jenkins et al., 2003):

$$\mathrm{bm} = \mathrm{Exp}(\beta_0 + \beta_1 \ln \mathrm{dbh})$$

where bm is total overstory biomass (kg dry weight) and dbh is the diameter-at-breast-height (cm).

Although 50% is widely used as a generic value for wood C content, C content in conifers ranges from 47.21% to 55.2% (Lamlom and Savidge, 2003). In addition to this range of variability, C content of early wood is often found to be higher than that in corresponding late wood. Because C content varies substantially among species and within varying age classes of species, C content by species and age class was derived from Lamlom and Savidge (2003) for use in determining overstory C content.

Volume was then determined for all CWD (snags and logs). Transect length and log top and end diameters were used to determine the volume of each downed log sampled (Harmon and Sexton, 1996). Volume per-unit-area ($m^3\,m^{-2}$) was calculated using (Harmon and Sexton, 1996):

$$V = 9.869 \times \sum \frac{d^2}{8L}$$

where V is the volume, L is the transect length, and d is the round equivalent diameter (derived from log top and end diameters), respectively.

To determine biomass of CWD, volumes were multiplied by average decay class-specific wood densities (Table 1) and totalled on a per-unit-area basis (Mg ha^{-1}). Coarse woody debris C was then calculated using biomass/C ratios obtained from laboratory analysis (Table 2). For estimation of soil C, stand bulk densities and soil pit depths were used to calculate C pools (Mg C ha^{-1}). Understory C estimates were obtained by averaging subplot biomass values and using C concentrations from laboratory analysis.

2.10. Coarse root biomass estimations

Coarse root biomass can contribute significantly to total ecosystem C, but was not directly measured on our stands. To account for this proportion of stand C, biomass of the coarse root system was calculated using an allometric equation based on aboveground conifer biomass. After thorough review of the literature and applicable equations, the following equation for the world's upland forests was selected for coarse root biomass estimation (Cairns et al., 1997):

$$\mathrm{RB_S} = 0.26\mathrm{AB_S}$$

where RB_S is softwood root biomass (Mg ha^{-1}) and AB_S is softwood aboveground biomass (Mg ha^{-1}). We chose to use the wood C

Table 1
Estimates of mean wood densities for coarse woody debris decay classes for conifer species found in Swan Valley, Montana.

Species	Decay	Wood density ($g\,cm^{-3}$)			
		This studv	Harmon and Sexton (1996)	Means et al. (1992)	Liu et al. (2006)
Pseudotsuga menziesii	1	0.462	0.45	0.416	0.44 (Conifer)
	2	0.356	0.341	0.317	0.36 (Conifer)
	3	0.288	0.277	0.274	0.29 (Conifer)
	4	0.220	0.137	0.224	0.28 (Conifer)
Larix occidentalis	1	0.463	–	–	0.44 (Conifer)
	2	0.353	–	–	0.36 (Conifer)
	3	0.269	–	–	0.29 (Conifer)
	4	0.215	–	–	0.28 (Conifer)
Abies lasiocarpa	1	–	0.414	–	0.44 (Conifer)
	2	–	0.238	–	0.36 (Conifer)
	3	–	0.25	–	0.29 (conifer)
	4	–	0.177	–	0.28 (Conifer)
Pinus contorta	1	–	0.405	–	0.44 (Conifer)
	2	–	0.405	–	0.36 (Conifer)
	3	–	0.37	–	0.29 (Conifer)
	4		0.176	–	0.28 (Conifer)

Table 2
Average C content (standard error) for CWD by species and decay class for dominant tree species in Swan Valley, Montana ($n = 15$, per species per class).

Species	Decay class			
	1	2	3	4
Larix occidentalis	50.57 (0.08)	50.16 (0.07)	51.50 (0.09)	57.18 (0.09)
Pseudotsuga meziesii	50.61 (0.17)	50.34 (0.11)	53.95 (0.59)	57.21 (0.08)

estimate of 50%, as it extremely close to values we obtained in analysis and is a standard value used in estimating forest C stocks (Lamlom and Savidge, 2003).

2.11. Statistical analysis

For analytical purposes, the data from the four subplots was averaged into one plot value. Effects of landscape context by study area (Condon Loop, Holland Lake, Owl Loop) were tested by stand type (old-growth, second growth) and their correlations with each C component.

An unpaired wilcoxon test of untransformed data was conducted for each ecological component of old-growth versus second growth. To determine whether or not C storage was greater in old-growth, mean (± se) C estimates were compared for old-growth and second growth pairs within each study site for each forest component. All statistical analyses were conducted using R 2.10.0.

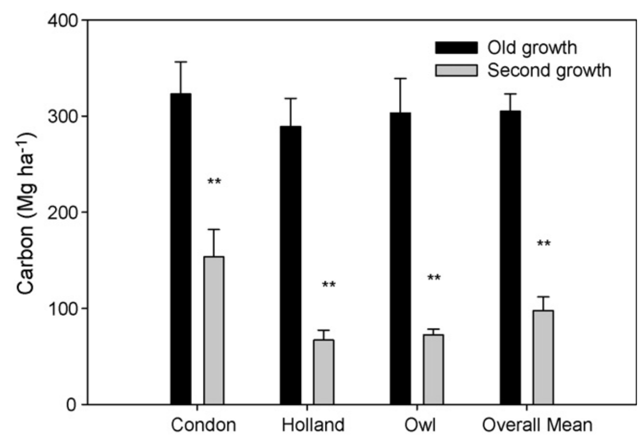

Fig. 2. Total average ecosystem C (sum of overstory, coarse roots, understory, forest floor, CWD, and mineral soil total C) for old-growth and second growth forests of Swan Valley, Montana, $^{**}p < 0.01$.

3. Results

3.1. Total ecosystem carbon

Estimates from all three study areas show clear and consistent differences in total ecosystem C as well as the C of many key forest components, suggesting there are important ecological differences

Table 3
Mean ecosystem C content (standard error) by stand ecosystem compartment for old-growth and second growth stands of Swan Valley, Montana.

Study area	Stand type[a]	Average age of dominant trees (years)	Mineral soil ($Mg\,ha^{-1}$)	Forest floor ($Mg\,ha^{-1}$)**	CWD ($Mg\,ha^{-1}$)*	Overstory ($Mg\,ha^{-1}$)**	Understory ($Mg\,ha^{-1}$)	Coarse roots ($Mg\,ha^{-1}$)**	Ecosystem C ($Mg\,ha^{-1}$)**
Condon Loop	OG	185	86.38 (28.31)	22.48 (1.41)	16.20 (4.19)	155.98 (13.76)	0.24 (0.05)	41.73 (3.55)	323.02 (33.49)
	SG	45	81.88 (9.74)	6.23 (0.69)	2.82 (0.77)	49.32 (16.5)	0.38 (0.07)	13.08 (4.41)	152.70 (28.29)
Holland Lake	OG	185	53.86 (9.70)	24.74 (1.54)	24.53 (8.54)	142.84 (11.18)	0.18 (0.04)	42.94 (4.07)	289.09 (29.43)
	SG	30	51.34 (11.07)	4.53 (0.22)	0.38 (0.26)	8.17 (1.96)	0.34 (0.04)	2.09 (0.48)	66.86 (10.39)
Owl Loop	OG	200	86.30 (23.97)	24.06 (1.82)	19.44 (5.22)	133.86 (11.49)	0.27 (0.08)	39.36 (3.67)	303.29 (35.82)
	SG	45	50.02 (4.10)	4.01 (1.30)	0.00 (0.00)	14.01 (1.15)	0.61 (0.07)	3.68 (0.29)	72.35 (6.11)
All study areas	OG		75.52 (12.52)	23.76 (0.89)	20.06 (3.47)**	144.23 (6.96)	0.23 (0.03)	41.34 (2.06)	305.14 (18.04)
	SG		61.08 (6.15)	4.92 (0.52)	1.07 (0.42)**	23.83 (7.07)	0.44 (0.05)	6.29 (1.89)	97.64 (14.24)

[a] OG: old-growth, and SG: second growth.
* $p < 0.05$.
** $p < 0.01$.

Table 4
Means (standard error) of soil physical and chemical characteristics of old-growth and second growth stands of Swan Valley, Montana.

Study area	Age class[a]	Mineral soil C		Mineral soil N		O horizon C			Soil C:N	Bulk density ($g\,cm^{-3}$)
		Mineral soil C ($Mg\,ha^{-1}$)	Concentration ($g\,kg^{-1}$)	Mineral soil N ($Mg\,ha^{-1}$)	Concentration ($g\,kg^{-1}$)	O horizon C ($Mg\,ha^{-1}$)	Concentration ($g\,kg^{-1}$)	Depth of O horizon		
Condon Loop	OG	86 (28)	29.7	3.6 (1.2)	1.3	22.5 (1.4)	4.70	4.24	24:1	0.57 (0.06)
	SG	82 (9)	27.6	3.3 (0.3)	1.1	6.2 (0.7)	4.40	1.88	25:1	0.76 (0.10)
Holland Lake	OG	54 (9)	22.1	2.0 (0.3)	0.9	24.7 (1.5)	4.90	4.34	24:1	0.48 (0.07)
	SG	51 (11)	23.5	2.1 (0.6)	0.9	4.5 (0.2)	4.30	0.96	25:1	0.78 (0.16)
Owl Loop	OG	86 (24)	21.1	2.9 (0.6)	0.8	24.1 (1.8)	4.70	4.96	24:1[**]	0.66 (0.06)[**]
	SG	50 (4)	23	1.8 (0.1)	0.8	4.0 (1.3)	4.10	0.98	28:1[**]	0.98 (0.07)[**]
All study areas ($n = 15$)	OG	76 (12)	24.3	2.8 (0.4)	1	23.8 (0.9)	4.80	4.51	24:1	0.57 (0.04)[**]
	SG	61 (6)	24.8	2.4 (0.3)	0.9	4.9 (0.5)	4.30	1.27	26:1	0.84 (0.07)[**]

[a] OG: old-growth, and SG: second growth.
[**] $p < 0.01$.

between old-growth and second growth stands in our study areas (Fig. 2). Average total ecosystem C for old-growth stands was significantly different from second growth stands at 305 Mg C ha^{-1} as compared to 98 Mg C ha^{-1} (Table 3). In Swan Valley old-growth stands, C was allocated as follows: 47% in the overstory, 25% in mineral soil, 13% in coarse roots, 8% in forest floor, 7% in CWD, and <0.1% in the understory. On the other hand, C in the second growth stands was allocated in the following manner: 25% in the overstory, 6% in coarse roots, 63% in the mineral soil, 5% in forest floor, 1% in CWD, and <0.1% in the understory. Among individual attributes, comparing the C content of the CWD, forest floor, coarse roots, and overstory were found to best differentiate Swan Valley old-growth from the 30–50 year old second growth stands. There was no significant difference in mineral soil C between the age classes. Most of the difference between age classes could be explained by the vast difference between old-growth and second growth overstory and coarse root C.

3.2. Aboveground overstory and understory vegetation

As would be expected, overstory biomass increased with age, and mean tree diameter was highest in old-growth stands. Average dbh for old-growth stands was 77 cm, while average dbh for second growth stands was just over 20 cm. Due to patchy regeneration on the sites and use of a standard protocol for sampling, stand biomass of the second growth was highly variable, with values ranging from 16 to 100 Mg ha^{-1}. These values, however, were not significantly correlated with stand age or habitat type. Old-growth values were much more consistent, with biomass ranging from 266 to 310 Mg ha^{-1}. Accordingly, mean old-growth overstory C (144 Mg ha^{-1}) was significantly greater than second growth overstory C (23.8 Mg ha^{-1}). In this study, the contribution of the understory to C storage was negligible on both old-growth and second growth stands, providing less than 0.75 Mg C ha^{-1} to each stand with no difference in understory C between old-growth and second growth, even though there were obvious differences in understory structure between age classes.

3.3. Mineral soil

Mineral soil C (to a depth of 1 m) in old-growth stands averaged 75.5 Mg C ha^{-1} and was not significantly different ($p > 0.10$) from mineral soil C of second growth stands (61.1 Mg ha^{-1}). Mineral soil C concentrations were also not significantly different between old-growth and second growth stands (Table 4). Soil bulk density was significantly greater in second growth stands (0.84 g cm^{-3}) compared to old-growth stands (0.57 g cm^{-3}) (Table 4).

3.4. Forest floor and CWD

Forest floor C was significantly greater in old-growth stands (23.8 Mg ha^{-1}) compared to second growth stands (4.9 Mg ha^{-1}), however, the C concentration of forest floor was comparable between old-growth and second growth. As a result of having only 22 logs per ha in the second growth stands and over 104 logs per hectare in the old-growth stands, the CWD C was also significantly greater in old-growth stands with an average of 20.1 Mg C ha^{-1} compared to 1.1 Mg C ha^{-1} in second growth stands (Table 3).

3.5. Coarse root biomass

Coarse root biomass accounted for nearly a quarter of total ecosystem C in old-growth stands and was significantly greater in old-growth stands versus second growth stands. Coarse roots harbored an average of just over 40 Mg C ha^{-1} in old-growth stands and around 6 Mg C ha^{-1} in second growth stands (Table 3). Our confidence in these estimates is hindered by our lack of empirical data. Onsite data collection of coarse root biomass would allow for a more robust estimation.

4. Discussion

Total ecosystem C storage and its distribution within a forest may vary as a result of a number of factors, particularly climate, disturbance, and management history. This study demonstrates major differences in the sizes and distributions of C pools between old-growth and clearcut second growth stands. Overall, total ecosystem C was much higher, over 3 times greater, in old-growth compared to second growth forest stands, particularly in the overstory, coarse roots, CWD, and forest floor, despite a frequent history of fire disturbance and low forest productivity (Habeck and Mutch, 1973; Habeck, 1988). The clearcutting of mixed western larch–Douglas-fir old-growth in the study area between the 1960s and 1970s resulted in a dramatic reduction in overall ecosystem C with little recovery after three to five decades. To date, dominant trees on second growth stands averaged only 20 cm in diameter as compared to 77 cm in corresponding old-growth stands. The apparently slow regeneration and poor forest growth in our study areas over the past five decades has yielded poor recovery of aboveground C in second growth stands. Although coarse root C accounted for a significant portion of total ecosystem C, it must be emphasized that this contribution, which is based on allometric equations, is a direct reflection of the overstory C and does not account for factors such as stress induced increases in root proliferation. Conversely, the difficulties associated with field

Table 5
Total ecosystem C distribution of Swan Valley, Montana, and coastal Pacific Northwest stands.

Compartment	Average ($Mg\,C\,ha^{-1}$)								
	This study		Grier et al. (1981)[a]		Spies et al. (1988)[a]		Harmon et al. (1990)		Harmon et al. (2004)
Forest type	LAOC/PSME[b]		ABAM		PSME		PSME/TSHE		PSME
Stand type	SG	OG	SG	OG	SG	OG	SG	OG	OG
Overstory	23.83	144.23	24.52	222.77	–	–	157.50	355.50	310.03
% of total	25	47	11	35	–	–	61	58	53
CWD	1.07	20.06	40.20	116.00	21.50	33.00	3.80	97.00	70.80
	1	7	19	19	–	–	1	16	12
Forest floor	4.92	23.76	23.90	74.75	–	–	7.10	26.00	22.30
	5	8	11	12	–	–	3	4	4
Coarse roots	6.29	41.34	12.37	68.86	–	–	29.00	71.00	81.22
	6	13	6	11	–	–	11	12	14
Mineral soil[c]	61.08	75.52	114.57	142.89	–	–	61.60	61.60	96.62
	63	25	53	23	–	–	24	10	17
Total	97.19	304.91	215.56	625.27	–	–	259.00	611.10	580.97

[a] Carbon value calculated assuming 50% C content (Sollins et al., 1987; Harmon et al., 2004).
[b] LAOC = *Larix occidentalis*, PSME = *Pseudotsuga menziesii*, ABAM = *Abies amabilis*, and TSHE = *Tsuga heterophylla*.
[c] Mineral soil values include fine roots, as defined in this study.

sampling of total coarse root C across a large area often leads to poor estimates of this C pool and lends to preference for regionally developed allometric equations (Laclau, 2003).

Despite large differences in total ecosystem C between stand types (old-growth, second growth), allocation of C for a number of ecosystem components in Swan Valley old-growth stands was similar to values reported for old-growth Douglas-fir stands of the PNW region (Grier et al., 1981; Harmon et al., 1990; Homann et al., 2005) (Table 5). For example, Homann et al. (2005) reported total ecosystem C allocations for old-growth Douglas-fir forests of the PNW as 60% in overstory, 12.5% in CWD, 3.4% in forest floor matter, and 20% in mineral soil. Our findings in the Swan Valley of western Montana demonstrate an allocation of total ecosystem C as 60% in overstory and coarse roots, 7% in CWD, 8% in the forest floor, and 25% in the mineral soil. Values contrasting old-growth to second growth total ecosystem C within western larch/Douglas-fir in the Swan Valley were comparable to those of old-growth and second growth Douglas-fir forests of the PNW, with old-growth possessing 3.1 and 2.4 times more C than second growth, respectively (Harmon et al., 1990).

In this study, surface mineral soil was not significantly changed by harvest some 30–50 years prior to sampling. This stands in contrast to those studies that show a decrease in soil C following disturbance related to timber harvest (Schlesinger, 1985; Post and Kwon, 2000; Law et al., 2003), but supports the notion that forest harvesting and regeneration practices may have little short-term impact on mineral soil C (Harmon et al., 1990; Johnson, 1992; Johnson and Curtis, 2001; Czimczik et al., 2005; Qinglin et al., 2007; Hedde et al., 2008). This study may support the notion that mineral soil C does not greatly change or increase with increasing stand age in secondary succession (Czimczik et al., 2005). Multiple rotations with reduced ecosystem C, however, would likely eventually reduce mineral soil C.

Coarse woody debris is an important ecosystem component of coniferous forest structure and function, providing C, water, and nutrient storage and critical habitat for a variety of organisms (Elliott et al., 2007; Harmon et al., 1986). In this study, the relatively limited quantities of CWD reflects the unique environment of these forests, including low productivity from cool temperatures, moisture limitation, and, to a lesser degree, the role of fire in these dry forests of the interior West as contrasted with more mesic coastal ecosystems (Harmon et al., 1986; Spies et al., 1988; Tinker and Knight, 2000). Reductions of CWD associated with clearcut logging may be costly, since they result in both a long-term reduction in ecosystem C and an impact on the many beneficial ecological functions associated with CWD (Elliot et al., 2007). Although this study occurred only 50 years post-harvest, it supports evidence of extremely long recovery times for re-establishment of C in this ecosystem.

High rates of tree mortality and slow decomposition of large logs within old-growth forests favor accumulation of woody debris, leading to coarse wood C flux being strongly dependent on age class distribution among forest stands (Harmon et al., 1990). Because most CWD in young stands is carryover from the previous stands, time since last disturbance and amount of input at the time of the disturbance are most closely related to total CWD biomass. With the removal of the overstory canopy, clearcutting further reduces inputs to the system by removing any potential sources of coarse wood from future disturbances, such as input from windthrow and mortality (Harmon et al., 1990). In addition to reducing ecosystem C, the removal of the timber and CWD also reduces shade, available moisture, rooting sites for some species, and spatial heterogeneity (Harmon et al., 1986; Halpern and Spies, 1995). Franklin et al. (2002), for example, found complete stand recovery and re-establishment of such ecological components can take over 200 years. Based on our data, even longer periods of time for recovery would be expected for forests of the interior West.

Forest management strategies that maintain old-growth components in young, managed stands have the potential to improve the conservation of C, nutrient pools, ecosystem diversity, and their associated functions (Lindenmayer and Franklin, 2002). For the Northern Rockies and other comparable moisture-limited forests, however, our data suggests a particularly long period of ecosystem C recovery following harvest. As documented in this study, logging of old-growth in dry, fire-prone ecosystems can lead to long periods of recovery for ecosystem C, suggesting that the most efficient way to maintain or enhance forest C stocks is to increase retention of large structural elements, such as large live trees, snags, and logs. More research is, however, needed to evaluate if retention of these stand components is effective in minimizing long-term losses of forest C in this region. Through natural stand development, these legacies may be responsible for long-term ecosystem C storage and the persistence of the compositional, structural, and functional properties of these unique ecosystems.

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