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ARTICLE

Density-dependent woody detritus accumulation in an even-aged, single-species forest

Michael S. Schaedel, Andrew J. Larson, Cullen J. Weisbrod, and Robert E. Keane

Abstract: Deadwood in forests influences fire intensity, stores carbon and nutrients, and provides wildlife habitat. We used a 54-year-old density management experiment in *Larix occidentalis* Nutt. forests to evaluate density dependence of woody detritus accumulation. Based on self-thinning theory, we expected woody detritus produced by the current stand to increase with stand density. Density-dependent woody detritus accumulation was apparent for fine woody debris and snags and for all woody detritus pools combined. Clear size–density relationships were apparent for coarse woody debris (CWD) and snags; mean piece size decreased with increasing stand density. Legacy CWD that originated from the preharvest old-growth stands accounted for about 45% of total woody detritus biomass. Live trees were largest in the low-density thinning treatments. Greater woody detritus biomass in the high-density and unthinned treatments originates primarily from past self-thinning, with additional inputs from density-dependent top breakage due to snow and ice and branch self-pruning. Because our results were driven by self-thinning mortality, the general trend of increasing woody detritus accumulation with increasing stand density should hold for maturing even-aged stands in other cool temperate and boreal forests.

Key words: self-thinning, coarse woody debris, fine woody debris, surface fuels, *Larix occidentalis*.

Résumé : Le bois mort présent en forêt influence l'intensité des feux, entrepose du carbone et des nutriments et fournit un habitat faunique. Nous avons utilisé un dispositif d'aménagement de la densité établi il y a 54 ans dans des forêts de *Larix occidentalis* Nutt. pour évaluer la dépendance à la densité de l'accumulation de débris ligneux. Suivant la théorie de l'auto-éclaircie, nous avons anticipé que les débris ligneux produits par le peuplement actuel allaient augmenter avec la densité du peuplement. Une dépendance à la densité de l'accumulation des débris ligneux était apparente pour les petits débris ligneux, les chicots et l'ensemble des formes de débris ligneux. Des relations claires entre la taille des débris ligneux et la densité des peuplements étaient apparentes dans le cas des débris ligneux grossiers (DLG) et des chicots. Dans ces deux cas, la taille des débris diminuait avec la densité du peuplement. Les legs de DLG provenant des vieux peuplements antérieurs à la coupe correspondaient à environ 45 % de la biomasse totale de débris ligneux. Les plus gros arbres vivants étaient dans les traitements d'éclaircie à forte intensité. La plus grande biomasse de débris ligneux dans les traitements à intensités d'éclaircie faible et nulle provenait principalement de l'auto-éclaircie passée avec des apports additionnels provenant des bris du haut de la cime des arbres causés par la neige et la glace et l'auto-élagage des branches, tous deux dépendants de la densité des peuplements. Parce que nos résultats sont fortement liés à la mortalité causée par l'auto-éclaircie, on devrait observer cette tendance générale selon laquelle l'accumulation de débris ligneux augmente avec la densité des peuplements dans le cas des peuplements équiennes presque à maturité, établis dans d'autres forêts tempérées froides et boréales. [Traduit par la Rédaction]

Mots-clés : auto-éclaircie, débris ligneux grossiers, petits débris ligneux, biocarburant de surface, *Larix occidentalis*.

Introduction

Dead woody structures are essential attributes of forest ecosystems (Sollins 1982; Harmon and Hua 1991). Downed fine (FWD) and downed coarse (CWD) woody debris and standing dead trees (snags) provide a wide range of forest ecosystem functions (Harmon et al. 1986; Manning and Edge 2008). Downed deadwood is a key element of the surface fuel complex, contributing to fire behavior and effects (Keane 2015). Woody detritus is a major reservoir of carbon and other nutrients (Harmon et al. 1986), including charcoal in forests with active fire regimes (Ward et al. 2017), and also provides sites for nitrogen fixation (Jurgensen et al. 1987). Deadwood, including FWD (Kruys et al. 1999; Manning and Edge 2008), provides essential habitat for biological diversity (e.g., McClelland and McClelland 1999; Squires et al. 2008). Given the importance of deadwood to ecosystem function, forest managers now recognize deadwood management as a core component of sustainable forest management and conservation of forest biodiversity (Lindenmayer and Franklin 2002; Jonsson et al. 2005).

The relationship of decreasing mean plant size with increasing population density in even-aged plant monocultures, including forest stands (Drew and Flewelling 1979), is a foundational principle in plant population biology (Yoda 1963). The maximum size–density relationship arises, proximately, from self-thinning in competing plant populations — density-dependent mortality due to intense size-asymmetrical competition (Weiner and Thomas 1986). Little is known, however, about how stand density influences accumulation of woody detritus in even-aged forests (Sturtevant

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Table 1. Experimental design and 2015 stand structure and stocking for the Western Larch Density Management Study.

Target density (trees·ha^{-1})	No. of entries	Year(s) thinned	2015 stand structure and stocking treatment means QMD (cm)	Tree height (m)	Basal area (m^2·ha^{-1})	Density (trees·ha^{-1})	SDI	RD (%)
494	1	1961	26.8	23.5	26.46	463	522	41.8
	2	1961, 1981	26.9	24.8	27.78	488	548	43.8
	4	1961, 1971, 1981, 1991	25.7	23.6	25.44	488	510	41.0
890	1	1961	22.4	23.0	32.98	828	698	56.0
	2	1961, 1981	21.0	22.5	28.38	815	618	49.3
	4	1961, 1971, 1981, 1991	19.7	22.0	26.77	859	592	47.3
1680	1	1961	18.1	18.1	34.27	1334	788	62.8
	2	1961, 1981	17.1	18.0	32.78	1415	767	61.3
	4	1961, 1971, 1981, 1991	16.4	17.5	28.52	1371	685	54.8
Unthinned	0	—	8.7	10.4	28.70	4474	886	70.0

Note: QMD, quadratic mean diameter; SDI, stand density index (Reineke 1933) calculated using metric units; RD, relative density (percentage of maximum SDI).

et al. 1996, 1997). This is remarkable, given the importance of size–density relationships in forest structural development (Long and Smith 1984) and forest management (Drew and Flewelling 1979; Sturtevant et al. 1996) and the foundational role of these concepts in plant ecology theory.

Density-dependent tree growth and mortality should strongly influence the structure and amount of woody detritus in maturing even-aged forests. A newly established cohort of trees will compete for space and resources as they grow following stand-initiating disturbance (Long and Smith 1984). In high-density stands, tree crowns rapidly close and trees begin to compete earlier and more intensely than in low-density stands (Drew and Flewelling 1979). These competitive interactions result in branch self-pruning (Sorrensen-Cothern et al. 1993), followed by self-thinning mortality (Larson et al. 2015), leading to the accumulation of woody detritus in developing even-aged stands (Grier et al. 1981). Density-dependent effects on tree crown development should influence FWD accumulation in even-aged stands, even in the absence of self-thinning mortality. Mean crown and branch size are smaller in high-density stands compared with low-density stands of the same age (Maguire et al. 1991), and high-density stands sustain greater total branch mortality compared with low-density stands (Maguire 1994).

The objective of this study was to determine how forest stand density, as controlled with thinning treatments of varying intensity and frequency, affects woody detritus accumulation in even-aged, single-species forests. We used a 54-year-old density management experiment in *Larix occidentalis* Nutt. (western larch) forests to evaluate density dependence of woody detritus accumulation. We asked the following two research questions.

1. Does woody detritus accumulation depend on initial stand density?
2. For a given target stand density, do frequency and timing of thinning influence woody detritus accumulation?

Based on forest structural development and self-thinning theory, we expected woody detritus to increase with stand density, with maximum accumulation in unthinned stands. As a necessary corollary, we expected mean snag size and CWD size to decrease with increasing stand density due to the maximum size–density relationship (Drew and Flewelling 1979; Sturtevant et al. 1997). To fully assess woody detritus, we also quantified legacy CWD originating from the preharvest old-growth forest.

Methods

The Western Larch Density Management Study (WLDMS) is a precommercial thinning (PCT) trial established in 1961 by U.S. Forest Service scientists in western Montana (Schaedel et al. 2017*a*, 2017*b*). The WLDMS comprises four study sites (blocks) that span a productivity gradient across northwestern Montana (Supplementary Table S1[1]). Current stands were initiated by natural regeneration from seed in 1952 (Coram 1 and Coram 2 blocks) and in 1954 (Cottonwood Lakes and Pinkham Creek blocks) following regeneration harvests in 1951 and 1953, respectively (Schaedel et al. 2017*a*, 2017*b*). The WLDMS incudes nine core treatments (Table 1) — three target post-thinning densities (494 trees·ha^{-1}, 890 trees·ha^{-1}, and 1680 trees·ha^{-1}) crossed with three thinning schedules (one-entry, two-entry, four-entry) through which the target density was attained — as well as an unthinned control treatment (Schaedel et al. 2017*a*, 2017*b*). The two- and four-entry treatments involved thinning stands to progressively lower densities until the final target density was reached (Schaedel et al. 2017*b*). Treatments were randomly assigned to square 20.12 m × 20.12 m (404.8 m^2) experimental units (hereafter referred to as "treatment plots"); a surrounding 10 m to 20 m wide buffer received the same treatment to prevent edge effects. Treatments were replicated once within each of the four blocks. Unthinned treatments were only included at the Coram 1 and Coram 2 blocks in 1961, so unthinned treatment plots were added in 2015 in the Pinkham Creek and Cottonwood Lakes blocks at locations within the original harvest units with similar topography, soils, and habitat type as the thinned plots (Schaedel et al. 2017*a*).

At the time of the first thinning, stand age was 9 years at the Coram 1 and Coram 2 blocks and 7 years at the Pinkham Creek and Cottonwood Lakes blocks (Supplementary Table S1[1]); for clarity, we use an average stand age of 8 years at initial thinning. The initial 1961 thinning occurred before canopy closure and the onset of intense competition and self-pruning (Schaedel et al. 2017*b*) and, thus, was a manipulation of initial stand density. All shrubs were cut in the initial thinning, and residual old-growth snags were felled. Thinned plots were weeded (i.e., tree species other than *L. occidentalis* were removed) in 1966 to maintain target densities and ensure single-species composition, but no weeding occurred after 1966. All cut material was left on site in every thinning entry. One strength of this study design is the lack of a confounding effect of slash from the initial 1961 thinning treatment. Residues originating from thinning small trees in 1961 were

[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2017-0129.

decomposed beyond detection (88% to 98% mass loss) by 2015 (Keane 2008).

All aboveground downed FWD (<7.6 cm diameter) was collected in four randomly located 1 m^2 quadrats per treatment plot. In the laboratory, FWD samples were sorted into three size classes corresponding to the woody surface fuel time-lag classes used in fuel and fire behavior models (Keane 2015): <0.6 cm (1 h fuels), 0.6 to 2.5 cm (10 h fuels), and 2.5 to 7.6 cm (100 h fuels). A subsample from each time-lag class in each treatment plot was weighed and oven-dried to constant mass at 105 °C, from which we calculated average moisture content and total dry biomass.

The aboveground portions of all downed deadwood pieces with diameter ≥ 7.6 cm (i.e., CWD; equivalent to the ≥1000 h fuel time-lag class) were individually measured on all treatment plots. Each CWD piece was designated as legacy (originating from the preharvest old-growth stand) or nonlegacy (produced by current stand) in the field based on assessment of size and decay; aboveground portions of old-growth stumps were included as legacy CWD. CWD measurements included large-end diameter, midpoint diameter, small-end diameter, length, and decay class (Maser et al. 1979). CWD piece volume was calculated from these measurements using Newton's formula for a frustum of a second-degree paraboloid. Diameter at breast height (dbh), total height, top diameter, diameter at root collar, and decay class were measured for the aboveground portion of every snag in each treatment plot, and snag volume was calculated as a conical frustum. Volumes were converted to biomass using decay class specific *L. occidentalis* wood densities (Bisbing et al. 2010).

We analyzed the data ($n = 40$ experimental units: 10 treatments replicated once at four blocks) as a one-way randomized block ANOVA, with site as the blocking variable and treatment as a composite variable of both target density and number of entries. We used this approach because the experimental design is not a true factorial cross of density and thinning schedule: the magnitude of each intermediate thinning treatment depended on target density (Schaedel et al. 2017*a*, 2017*b*). Several of the woody detritus pools exhibited variance heteroscedasticity, so different variance structures were modeled for each level by fitting models with generalized least square regression using the "gls" function in the "nlme" package in R (R Core Team 2016).

We used a priori linear contrasts to answer our research questions. We used three contrasts to test our predictions for initial stand density effects on woody debris biomass (Table 1): the 494 trees·ha^{-1}, one-entry treatment was compared against each higher density one-entry treatment, as well as the unthinned treatment. We focused on the one-entry treatments as they experimentally isolate the effect of initial stand density on woody debris accumulation, with no confounding effect of thinning slash. To evaluate the effect of the number of entries, we compared (at each density) the one-entry treatment against the two-entry treatment, and the one-entry treatment against the four-entry treatment (Table 1). We used the "multcomp" (Hothorn et al. 2014) package to implement the linear contrasts in R (R Core Team 2016), with Bonferroni correction for multiple tests. We set $\alpha = 0.1$ and considered P values < 0.1 indicative of significant differences.

Results

Density-dependent woody detritus accumulation was apparent for the 1 h and 100 h time-lag classes of FWD and snags and for all nonlegacy woody detritus pools combined ($P < 0.1$; Fig. 1). Treatment means and standard errors for all woody detritus pools are presented in tabular format in the supplementary materials (Supplementary Table S4[1]) to facilitate future use in models and meta-analyses. Linear contrasts revealed significant differences between the 494 trees·ha^{-1} and 1680 trees·ha^{-1} treatments and between the 494 trees·ha^{-1} and the unthinned treatments (Table 2). The 494 trees·ha^{-1} and 890 trees·ha^{-1} treatments did not differ for any woody detritus pool individually or for all pools combined (Table 2). Snag biomass was 20 Mg·ha^{-1} greater in the unthinned treatment than in the 494 trees·ha^{-1} treatment (Fig. 1*e*), but the high variability among the unthinned plots rendered this difference statistically insignificant (Table 2).

Thinning schedule strongly affected CWD biomass at all three target densities. CWD biomass was 3.8 to 4.8 times greater in the four-entry treatment than in the corresponding one-entry treatment at all three target densities (Fig. 1), all three of which were significant differences (Table 2). With the exception of snag biomass in the 890 trees·ha^{-1} treatments, other woody detritus pools were not affected by the thinning schedule (Table 2).

Clear size–abundance (Figs. 2*a* and 2*b*) and size – stand density (Figs. 2*c* and 2*d*) relationships were apparent for CWD and snags. CWD size–abundance patterns depended on thinning frequency (Fig. 2*a*), whereas snag size–abundance patterns depended on target stand density (Fig. 2*b*). Mean CWD piece diameter ranged from 8.9 cm to 13.0 cm (Supplementary Table S2[1]), and mean snag dbh ranged from 4.9 cm to 15.7 cm (Supplementary Table S3[1]). Both CWD and snag diameter increased with decreasing target stand density.

Legacy CWD biomass (Supplementary Fig. S1[1] and Supplementary Table S4[1]) from the preharvest old-growth stand was unrelated to treatment ($P = 0.802$). Legacy CWD averaged 10.83 Mg·ha^{-1} across all treatment plots (range: 0.34 to 47.99 Mg·ha^{-1}). Experiment-wide, legacy CWD accounted for 46.5% of all total woody detritus stocks (treatment plot-level range: 6.4% to 78.9%). Average large-end diameter across all legacy CWD pieces was 48.0 cm.

Discussion

Woody detritus accumulation during the 54 years after early thinning was related to tree density in these even-aged *L. occidentalis* forests (Fig. 1). The 1 h, 100 h, and snag detritus pools were all sensitive to stand density, with the largest magnitude differences in the 100 h and snag pools (Table 2). Greater biomass of 100 h FWD in the unthinned treatments likely originates primarily from past self-thinning (Fig. 3; Schaedel et al. 2017*b*): trees that died standing before attaining stem diameters > 7.6 cm and have subsequently fallen to the ground. Density-dependent stem breakage due to snow and ice (Wonn and O'Hara 2001) is another likely contributor to increased 100 h biomass in the unthinned treatment. Tree stability (as measured by height to diameter ratio) was highest in the low-density thinned stands, and long-term measurements documented less top breakage in the low-density treatments (Schaedel et al. 2017*b*). High snag biomass in the unthinned and 1680 trees·ha^{-1} treatments was largely due to self-thinning mortality, which was clearly apparent in the long-term mortality rates for those treatments (Schaedel et al. 2017*b*), as well as in their size–density trajectories (Fig. 3). Because our results were driven largely by self-thinning mortality, we expect that the general trend of increasing woody detritus accumulation with increasing stand density will hold for maturing even-aged stands in other cool temperate and boreal forests, notwithstanding density-independent and noncompetitive mortality agents, which sometimes cause substantial inputs to woody detritus pools in young forests (Lutz and Halpern 2006). This interpretation and our core results are consistent with past work that documented greater CWD and snag biomass (or volume) in unmanaged second-growth forests compared with thinned second-growth forests (Duvall and Grigal 1999; Graves et al. 2000; Hura and Crow 2004; Silver et al. 2013). Nevertheless, our study provides an important advance. The WLDMS design allowed experimental isolation of initial stand density effects on woody detritus accumulation — our results are not confounded by timber harvest, fuel removal treatment, or thinning slash.

Why was density-dependence of woody detritus accumulation not stronger? The 1680 tree·ha^{-1} treatment only entered the zone

Fig. 1. Woody detritus accumulation in even-aged *Larix occidentalis* forest 54 years after initial density management with precommercial thinning, northwestern Montana, USA. Woody detritus pools: (*a*) FWD < 0.6 cm (1 h fuels); (*b*) FWD 0.6 to 2.5 cm (10 h fuels); (*c*) FWD 2.5 cm to 7.6 cm (100 h fuels); (*d*) CWD ≥ 7.6 cm (1000 h fuels); (*e*) snags; and (*f*) total nonlegacy woody detritus (sum of panels *a* to *e*). Target density is the final desired stand density (in trees·ha⁻¹) after the last thinning entry. Error bars show one standard error. Treatment means and standard errors for all woody detritus pools are presented in tabular format in the supplementary materials (Supplementary Table S4[1]).

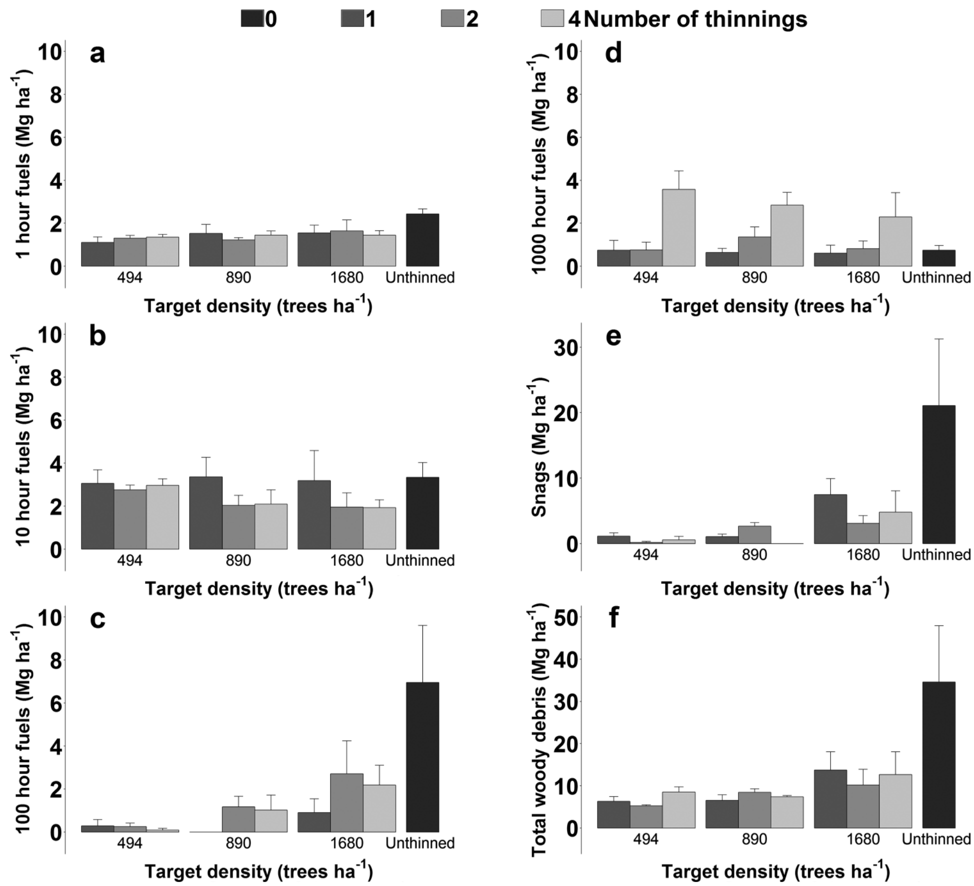


Table 2. Linear contrasts for nonlegacy woody detritus in even-aged *Larix occidentalis* forests 54 years after early thinning to three target thinning densities (494, 890, and 1680 trees·ha⁻¹).

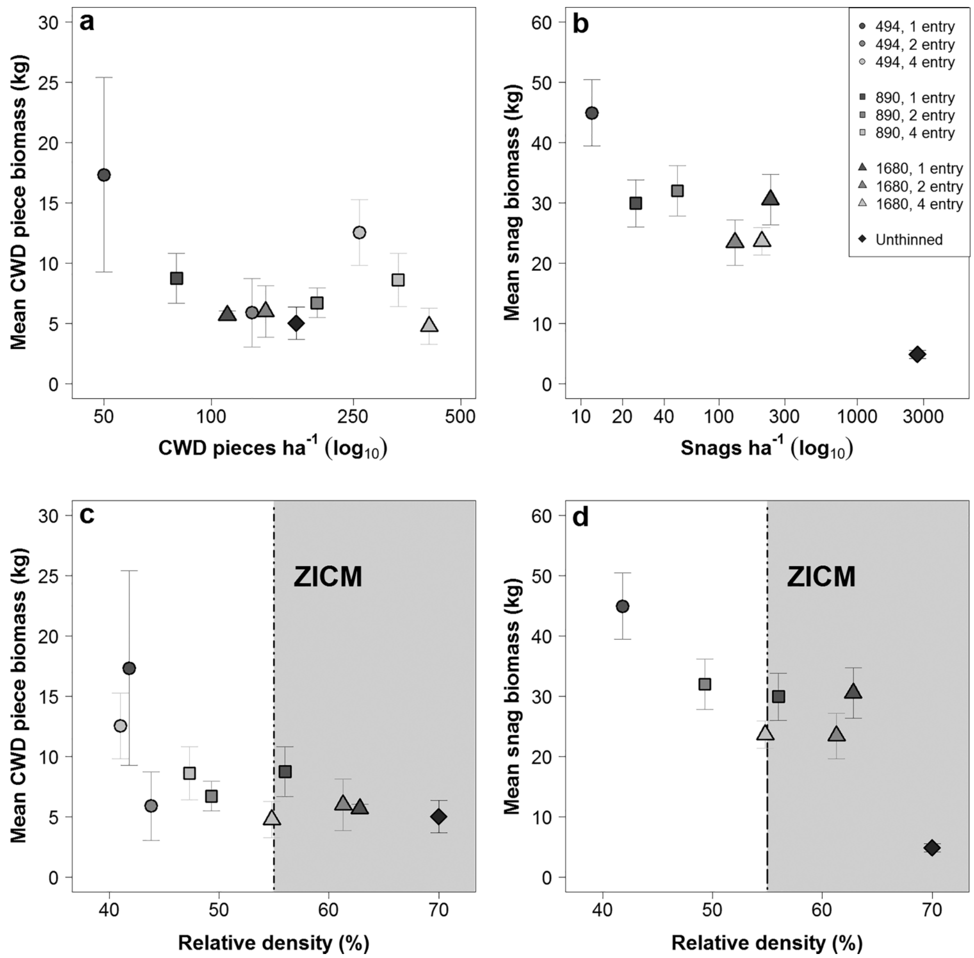
Contrast	Woody detritus pool (Mg·ha⁻¹) 1 h	10 h	100 h	CWD	Snags	Total
Density (trees·ha⁻¹)						
Global density test *P* value[a]	**0.003**	0.978	**0.096**	0.990	**0.035**	**0.085**
494 vs. unthinned	−1.33***	−0.28	−6.67*	−0.01	−19.97	−28.25
494 vs. 1680	−0.42	−0.13	−0.62	0.14	−6.36*	−1.75
494 vs. 890	−0.44	−0.30	0.29	0.10	0.07	−0.27
No. of entries within density (trees·ha⁻¹)						
1680: one entry vs. four entries	0.11	1.26	−1.28	−1.69*	2.65	1.05
1680: one entry vs. two entries	−0.10	1.24	−1.78	−0.21	4.40	3.53
890: one entry vs. four entries	0.09	1.27	−1.02	−2.20***	1.05#	−0.81
890: one entry vs. two entries	0.30	1.32	−1.17	−0.72	−1.62*	−1.87
494: one entry vs. four entries	−0.24	0.10	0.20	−2.82***	0.57	−2.19
494: one entry vs. two entries	−0.20	0.31	0.03	−0.02	0.93	1.05

Note: Bonferroni-corrected significance codes (*P* value): *** < 0.001 < ** < 0.01 < * < 0.05 < # < 0.1.

[a]Global density *P* values report the significance of the effect of treatment on the biomass of a given woody detritus pool.

of imminent competition mortality (ZICM; Drew and Flewelling 1979) in about 2001 (Fig. 3). Consequently, significant self-thinning mortality has only been occurring for about 15 years in the 1680 trees·ha⁻¹ treatment (Fig. 3). The 890 trees·ha⁻¹ treatment just crossed into the ZICM as of the 2015 measurement (Table 1; Fig. 3). Thus, across the thinned treatments, self-thinning mortality has been limited primarily to the 1680 trees·ha⁻¹ treatment for only about the most recent 15 years (Fig. 3; Schaedel et al. 2017*b*). During most of the 54-year-long experiment, density-dependent effects in the thinned treatments were largely limited to branch litter inputs from self-pruning and stochastic noncompetitive mortality and damage (e.g., snow-caused top breakage; Wonn and O'Hara 2001). Given current stand structure (Table 1), we predict woody detritus inputs to accelerate and density dependence of

Fig. 2. (*a*, *b*) Size–abundance and (*c*, *d*) size–stand density relationships for CWD ≥ 7.6 cm (1000 h fuels) and snags in an even-aged *Larix occidentalis* forest 54 years after initial density management with precommercial thinning, northwestern Montana, USA. Error bars show one standard error. ZCIM is the zone of imminent competition mortality, relative density ≥ 55% (Drew and Flewelling 1979), the stand density at which self-thinning mortality commences.

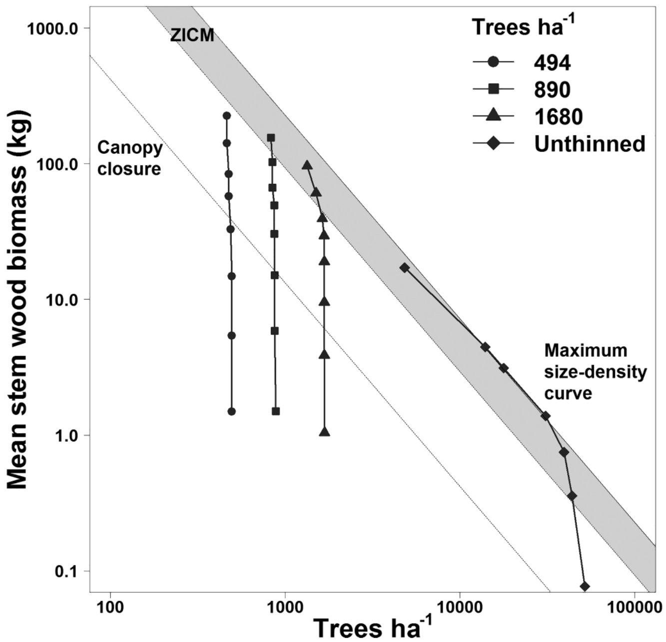


woody detritus accumulation to become stronger during the next decade as the 1680 trees·ha^{-1} and 890 trees·ha^{-1} treatments grow further into the ZICM and experience more self-thinning (Fig. 3), while the 494 trees·ha^{-1} treatment remains outside the ZICM (Fig. 3).

Our results directly inform efforts to conserve forest biodiversity through deadwood management (Sturtevant et al. 1996; Lindenmayer and Franklin 2002; Jonsson et al. 2005), including assessment of potential trade-offs with fire behavior and effects (Brown et al. 2003). Unthinned treatment plots had significantly more FWD than the once-thinned low-density treatment plots after 54 years (~8 Mg·ha^{-1} more; Table 2; Fig. 1; Supplementary Table S4[1]), resulting in approximately 410 kW·m^{-2} greater fire intensity (FOFEM calculation; Reinhardt et al. 1997). This increase in fire intensity is more than enough to kill the pole-sized overstory *L. occidentalis* (Ryan and Reinhardt 1988; Reinhardt et al. 1997). As a result, low-density thinned stands may be more resistant to fire, while also being less hazardous to people in the wildland–urban interface if a wildfire occurs. Also, while there was not much difference between FWD in the 494 trees·ha^{-1} target density stands and the other thinning density targets, the end result is that the lowest fuel accumulations 54 years after treatment are in the thinned stands (Fig. 1; Supplementary Table S4[1]), which indicates that the one-entry thinning treatments also acted as fuel reduction treatments.

Essentially all nonlegacy CWD and snags were too small to function as high-quality vertebrate wildlife habitat, regardless of treatment, despite clear size–density relationships (Fig. 2). For example, in northwestern Montana, 62% of Canada lynx (*Lynx canadensis*) dens were located beneath individual downed logs > 50 cm in diameter or aggregations of downed logs between 15 and 25 cm in diameter (Squires et al. 2008), larger than the largest mean nonlegacy CWD piece diameter in this study (Supplementary Table S2[1]). However, live trees, especially in the 494 trees·ha^{-1} treatments, were large enough in 2015 (Table 1; Schaedel et al. 2017*b*) to produce CWD suitable for lynx den sites (Squires et al. 2008). American marten (*Martes americana*) used large-diameter *L. occidentalis* snags and logs for both resting and denning in northeastern Oregon, with average diameters > 50 cm for all structures and uses (Bull and Heater 1994), much larger than the largest nonlegacy snags and CWD in this study. Additionally, 42% of subnivian access sites used by marten in southern Wyoming were created by CWD (Corn and Raphael 1992), and logs that created subnivean access points averaged 28 to 37 cm in diameter, larger than nonlegacy CWD pieces accumulated in any of the treatments (Supplementary Table S2[1]) but about the same diameter as live trees in the 494 trees·ha^{-1} treatments (Table 1). Mean snag diameters in the WLDMS (Supplementary Table S3[1]) were much smaller than the *L. occidentalis* snags used for nesting by pileated woodpeckers (*Dryocopus pileatus*) in western Montana (mean dbh of 77 cm), although live trees in the 494 trees·ha^{-1} treatments were nearly large enough to produce snags of the minimum diameter used by pileated woodpeckers (McClelland and McClelland 1999). These examples illustrate

Fig. 3. Stem wood size–density trajectories of even-aged *Larix occidentalis* forests from 1966 to 2015 following initial density management with precommercial thinning at stand age 8 years in northwestern Montana, USA. Only one-entry treatments thinned initially in 1961 are shown. Temporal progression is from lower right to upper left; each symbol represents a repeated measurement (1966, 1971, 1976, 1981, 1986, 1991, 2001, and 2015). Tree size was too small in 1961 for accurate mean dry biomass estimates. The lines representing the zone of imminent competition mortality (ZICM) and canopy closure are placed at relative densities of 55% and 15%, respectively (Drew and Flewelling 1979).



the challenges of providing large deadwood structures used by many wildlife species in second-growth, even-aged stands and the potential to use early thinning to accelerate tree growth rates (Table 1) and reduce time required to produce large-diameter snags and logs (Sturtevant et al. 1996, 1997; Schaedel et al. 2017*b*).

The multiple-entry treatments are valuable because they illustrate the long-lasting increase of CWD caused by late PCT treatments compared with early PCT treatments. CWD was strongly influenced by treatment frequency, with greater CWD biomass in the four-entry treatments at all three target densities (Fig. 1; Table 2). Trees thinned in 1991 (at stand age 38 years) had attained stem diameters > 7.6 cm but had not fully decomposed by 2015. Assuming a decay constant of 0.03 (exponential decay) for *L. occidentalis* CWD deposited in the 1991 thinning (Harmon et al. 1986), about 50% of the mass should have remained in 2015. Based on FWD decay rates in northwestern Montana (Keane 2008), estimated FWD mass remaining from 1991 thinning slash ranged from 17% to 38% in the four-entry thinning treatments — apparently not enough to cause significantly different FWD accumulations from one-entry treatments in 2015 (Table 2). Trees thinned in the 1981 thinning (at stand age 28 years) in the two-entry treatments were just barely large enough to produce thinning slash in the CWD size class (Schaedel et al. 2017*b*). By 2015, only about 35% of that material would have remained, an insufficient amount to increase CWD or FWD accumulation relative to the one-entry treatments (Table 2). These results have direct implications for potential fire behavior, as well as wildlife habitat. Cutting and leaving CWD-sized trees in late PCT treatments unambiguously increases fuel loads and potential fire intensity for at least 25 years (Fig. 2), but they may also improve habitat for small mammals (e.g., mice, voles) through structural enrichment of the forest floor (Manning and Edge 2008; Dracup et al. 2015). New research that investigates use of late PCT thinning slash by wildlife species would provide forest managers with the evidence needed to inform decisions that must balance trade-offs between potential fire behavior and wildlife habitat in maturing even-aged stands.

Conclusions

Three key points emerge based on our analysis of woody detritus accumulation in this 54-year-old density management experiment.

- High-density and unthinned stands contain more deadwood biomass than do low-density stands. However, deadwood biomass in high-density and unthinned stands is concentrated in small individual pieces that primarily function as surface fuels, increasing potential fire intensity and fire-caused tree mortality relative to low-density stands.
- Low initial stand density reduces accumulation of surface fuels in the FWD size class while growing larger live trees over shorter time periods. Thus, in maturing even-aged stands, density reduction with early thinning reduces the time required to produce snags and CWD large enough to function as habitat for species of concern such as Canada lynx, American marten, and pileated woodpecker.
- Forty-five percent of total woody detritus biomass and all large-diameter CWD pieces were legacy old-growth structures. Consequently, we see a clear role for legacy wood retention in an overall forest biodiversity conservation strategy.

Our results indicate the benefits of using early thinning in even-aged stands to reduce subsequent fuel accumulation and potential fire intensity, while simultaneously decreasing the time required to replace large-diameter snags and logs used by wildlife. On lands managed primarily for commercial timber production, these simultaneous outcomes will only be realized if some large-diameter green trees are retained at harvest and allowed to become source populations of future large diameter snags and logs. Our analyses (Fig. 2) demonstrate that large-diameter deadwood stocks will not recover if some large-diameter green trees are not retained through multiple 60-year harvest rotations.

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