Forest Ecology and Management 389 (2017) 187–198

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Early forest thinning changes aboveground carbon distribution among pools, but not total amount

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ARTICLE INFO

*Article history:*
Received 18 September 2016
Received in revised form 17 December 2016
Accepted 19 December 2016

*Keywords:*
*Larix occidentalis*
Western larch
Carbon storage
Density management
Precommercial thinning
Climate change
Long-term studies
Climate change mitigation
Climate change adaptation

ABSTRACT

Mounting concerns about global climate change have increased interest in the potential to use common forest management practices, such as forest density management with thinning, in climate change mitigation and adaptation efforts. Long-term effects of forest density management on total aboveground C are not well understood, especially for precommercial thinning (PCT) implemented very early in stand development. To assess the climate change mitigation potential of PCT, as well as tradeoffs with climate change adaptation, we examined total aboveground C stores in a 54-year-old western larch (*Larix occidentalis* Nutt.) precommercial thinning experiment to determine how different PCT treatments affect long-term aboveground C storage and distribution among pools. Four aboveground C pools (live overstory, live understory/mid-story, woody detritus, and forest floor) were measured and separated into C accumulated prior to initiation of the current stand (legacy C) and C accumulated by the current stand (non-legacy C). PCT had no influence on the total non-legacy aboveground C stores 54 years after treatment. Live tree C was nearly identical across densities due to much larger trees in low density treatments. Low density stands had more understory and mid-story C while unthinned plots had significantly more non-legacy woody detritus C than thinned stands. Legacy pools did not vary significantly with density, but made up a substantial proportion of aboveground C stores. We found that: (1) fifty-four years after PCT total aboveground C is similar across treatments, due primarily to the increase in mean tree C of trees grown at lower stand densities; (2) deadwood legacies from the pre-disturbance forest still play an important role in long-term C storage 62 years after current stand initiation, accounting for approximately 20–25% of aboveground C stores; and (3) given enough time since early thinning, there is no trade-off between managing stands to promote individual tree growth and development of understory vegetation, and maximizing stand level accumulation of aboveground C over the long term. We infer that early PCT can be used to simultaneously achieve climate change mitigation and adaptation objectives, provided treatments are implemented early in stand development before canopy closure and the onset of intense intertree competition.



## 1. Introduction

Mounting concerns about anthropogenic climate change have increased interest in enhancing forests' capacity to capture and store atmospheric carbon dioxide ($CO_2$). Forests in the United States store an estimated 22 Tg of carbon (C) year$^{-1}$ (Heath and Smith, 2004; Birdsey et al., 2006), and increasing attention is being directed towards understanding how to mitigate climate change effects by maintaining or increasing C storage in forest ecosystems through management actions (Pregitzer and Euskirchen, 2004; Birdsey et al., 2006; Millar et al., 2007; McKinley et al., 2011). Even global political leaders are beginning to recognize the important role of forest ecosystems in a global C management strategy, evidenced by the inclusion of forest C specific management strategies in the 2015 Paris Climate Agreement, (UNFCCC, 2015). Despite increasing policy interest and recent research, there remains uncertainty over long-term effects of common forest management practices, such as density management with thinning, on C storage.

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http://dx.doi.org/10.1016/j.foreco.2016.12.018
0378-1127/

Carbon accumulates in the form of woody biomass and foliage in trees and, at the stand level, generally increases with time as mean tree size increases (Pregitzer and Euskirchen, 2004; Peichl and Arain, 2006). Any management actions that increase tree growth also have the potential to increase forest C accumulation and storage; conversely, management actions that reduce the number of trees on a site may potentially reduce forest C accumulation and storage.

Thinning is a common management activity used to manipulate the growth rate, size, and form of individual trees, as well as the structure and yield of forest stands (Sjolte-Jorgensen, 1967; Smith et al., 1997; Tappeiner et al., 2007). Thinning involves the selective removal of some trees such that more resources and growing space are allocated to the residual trees, thereby increasing their growth rates. Thinning in second growth forests is often suggested as a climate change adaptation strategy (Bradford and D'Amato, 2012; Churchill et al., 2013), because thinning can be used to promote the development of complex stand structures resilient to disturbances and drought. However, these climate change adaptation outcomes attainable with thinning generally require a tradeoff with climate change mitigation objectives: most studies have shown decreased forest C storage in thinned stands (Bradford and D'Amato, 2012).

Different methods of thinning—i.e., different methods of tree selection for removal and retention during thinning treatments—can have strong, differential effects on long-term forest C storage (Hoover and Stout, 2007). Thinning from above (preferential removal of the largest trees) or across the tree size distribution decreases aboveground C storage both immediately and over the long-term (Hoover and Stout, 2007; Harmon et al., 2009; Chatterjee et al., 2009; D'Amato et al., 2011; Zhou et al., 2013). However, studies of thinning from below (selective removal of the smallest trees) implemented early in stand development, a practice also termed precommercial thinning (PCT) when the thinned trees have no commercial value, show inconsistent results. Some PCT studies of this type found that decreasing stand density decreased total forest C stores (Skovsgaard et al., 2006; Jiménez et al., 2011), while others noted that the increased growth rate of trees grown at lower densities can maintain or increase live tree C (Hoover and Stout, 2007; Dwyer et al., 2010), especially in the case of longer-term responses to thinning (Horner et al., 2010). Short-term studies of PCT effects on aboveground C have shown consistent decreases in aboveground C (Campbell et al., 2009; De las Heras et al., 2013; Jiménez et al., 2011; Dwyer et al., 2010), indicating that low densities of small trees do not fully occupy the site (Turner et al., 2016). Given these conflicting results, it is still unclear whether PCT is compatible with the climate change mitigation goal of forest C storage (Jiménez et al., 2011).

The age at which a forest is thinned has a strong effect on aboveground C storage. Evidence from the few PCT studies that considered timing of thinning shows that total stem volume, which is a large component of the aboveground C (Harmon et al., 2004), is greater in stands thinned early as compared to stands thinned later (Varmola and Salminen, 2004). This is consistent with stand dynamics theory, which suggests that wood volume growth rates recover more quickly from early thinnings than from late thinnings (Oliver and Larson, 1996; Long et al., 2004; Varmola and Salminen, 2004).

Understory vegetation, woody detritus, and forest floor material are also important pools of aboveground C. Understory vegetation—composed of shrubs, subcanopy trees, forbs, and grasses—can be a major C pool, especially early in stand development or at lower stand densities (Campbell et al., 2009). Woody detritus, including snags, coarse woody debris (CWD; diameter $\geqslant$7.62 cm), and fine woody debris (FWD; diameter <7.62 cm), can store large amounts of C, especially in temperate forests where trees may attain large sizes and decompose slowly (Harmon and Hua, 1991). Forest floor C is composed of litter, duff, and soil wood. Forest floor components can store significant amounts of C especially as large logs decay and become part of the forest floor in old-growth forests (Page-Dumroese and Jurgensen, 2006).

Other pools can store large amounts of C, but are not strongly affected by density management. Substantial C is stored in mineral soil (Johnson and Curtis, 2001; Page-Dumroese and Jurgensen, 2006; Bisbing et al., 2010), however evidence suggests that these soil C stocks are not as sensitive to density management as aboveground C pools, and often show little change following thinning (Johnson and Curtis, 2001; Nave et al., 2010; Zhou et al., 2013; Hoover and Heath, 2015). In second growth forests, where large woody structures from the previous stand were left onsite, both the woody debris and forest floor pools can be largely composed of biomass produced by the pre-disturbance, old-growth stand (Franklin et al., 2002). These C stores, referred to as legacy C, can make up a substantial proportion of the C stored in a second growth forest (Spies et al., 1988; Sturtevant et al., 1997; Franklin et al., 2002), however we would not expect these C stores to be strongly affected by early density management with PCT.

Questions remain about how early thinning affects long-term total aboveground C because many studies, (1) focused on controlling the "level of growing stock" with repeated thinning entries throughout the duration of the study (e.g. Skovsgaard et al., 2006, D'Amato 2011); (2) involved treatments applied relatively later in stand development ($\geqslant$30 years after stand initiation), after tree canopy closure and the onset of intense competition and crown recession, a scenario in which we would only expect a negative C impact from thinning (e.g. Finkral and Evans, 2008; North et al., 2009; D'Amato et al., 2011); (3) collapsed many different types of thinning treatments into one catch-all category (e.g., Powers et al., 2012); (4) only examined a short-term post-treatment response (e.g. Campbell et al., 2009; De las Heras et al., 2013; Jiménez et al., 2011; Dwyer et al., 2010); or (5) did not measure all aboveground pools (Skovsgaard et al., 2006; Horner et al., 2010; D'Amato et al., 2011; De las Heras et al., 2013; Zhou et al., 2013).

We overcame these constraints by measuring all aboveground C pools in a replicated, long-term (54-year-old) western larch (*Larix occidentalis* Nutt.) precommercial thinning experiment. Our objectives were to determine how different PCT treatments affect total aboveground C storage, and C distribution among different aboveground pools. We tested four predictions for the effect of tree density management with PCT on aboveground C pools.

(1) *Live overstory conifer C will increase with stand density.* Forest structural development theory suggests that overstory tree C increases with increasing density (Turner et al., 2004, 2016; Kashian et al., 2013); at high densities mean C per tree is smaller but the greater number of trees compensates for the small mean tree size.

(2) *Live non-conifer C (understory and subcanopy trees, shrubs, forbs, and grasses) will decrease with increasing stand density.* Forest structural development theory predicts that as canopies close and light becomes limited below the main canopy, understory plants and subcanopy trees will be competitively excluded (Long and Turner, 1975; Peet and Christensen, 1987; Oliver and Larson, 1996; Franklin et al., 2002). This occurs earlier and more completely at high stand densities, resulting in less mass of understory vegetation (Campbell et al., 2009).

(3) *Non-legacy deadwood C—dead woody material produced since initiation of the current stand—will increase with stand density.* Self-thinning theory predicts that as a stand nears a maximum size-density relationship, mortality will increase

(Reineke, 1933; Yoda et al., 1963; Peet and Christensen, 1987) shifting C from live pools to the deadwood pools (snags and woody detritus). Stands with higher densities will experience more tree mortality, leading to relatively more C stored in non-legacy deadwood compared to low density stands.

(4) *Total aboveground non-legacy C will increase with density.* Past studies of carbon storage in temperate forests suggest that the overstory tree pool and the deadwood pool generally drive C dynamics, even in second growth forests (Harmon et al., 2004; Bisbing et al., 2010; Powers et al., 2012).

To fully quantify aboveground C stocks, we sampled legacy deadwood and the forest floor above the surface of mineral soil, though we did not expect these pools to respond to the experimental treatments given their dominance by legacy inputs from the previous old-growth stands.

## 2. Methods

### 2.1. Study sites

Our study is superimposed on the Western Larch Density Management Study (WLDMS), a western larch precommercial thinning study located in northwestern Montana, USA and established in 1961 by the USDA Forest Service (Schmidt, 1964). The WLDMS is replicated at four sites (i.e., blocks), which were chosen for their uniform stocking and to capture the productivity gradient of western larch forests in western Montana (Fig. 1a). WLDMS replicates were located in areas of old-growth forest harvested using even-aged methods between 1951 and 1953 (Table 1), and that regenerated naturally in the good western larch seed years of 1952 and 1954. Those conditions resulted in high initial (pre-treatment) densities (25,000 to 63,000 trees per hectare) of primarily western larch as well as lesser amounts of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and paper birch (*Betula papyrifera* Marshall) (Schmidt, 1964).

The WLDMS has a nested factorial design with two factors: target density and number of thinning entries (hereafter referred to as entries). There are three levels of target density (494 trees ha$^{-1}$, 890 trees ha$^{-1}$, and 1640 trees ha$^{-1}$) which were originally chosen to determine the ideal spacing for western larch growth (Schmidt and Shearer, 1961). Nested within each level of the target density are three different thinning regimes Table 2). The one-entry treatments attained the target density in one thinning in 1961; the two-entries treatments thinned to a prescribed intermediate density in 1961 then met the target density with a second thinning in 1981; the four-entries treatments thinned to prescribed intermediate densities in 1961, 1971, and 1981 then met the target density with a final thinning in 1991 (Table 2). There are also unthinned plots at each site. Thus, the experimental design includes nine unique thinning treatments and one unthinned plot per replicate (i.e., treatments are not replicated within blocks). Unthinned plots were only established at two of the sites (Coram 1 and Coram 2) at the start of the study, so prior to the 2015 measurement unthinned plots were established at the remaining two replicates in areas within the original harvest units in which the WLDMS experimental plots are located, and of similar topography, soil, and habitat type as the thinned plots.

At each site, experimental plots and thinning treatments were established in the winter of 1961/62 before the growing season. All snags were felled and residual seed trees removed prior to plot establishment (Schmidt, 1964). Treatment plots (the experimental unit) are 0.04 ha in size and all trees that were present at study initiation were tagged. To minimize edge effects, each plot was surrounded by a 10 m to 20 m wide buffer that was thinned with the same treatment (Fig. 1b). Plots were installed in uniformly stocked areas of similar aspect, slope, habitat type, and soil conditions then treatments were randomly assigned to each plot.

Initial thinning in 1961 established a relatively uniform spacing of leave trees, but since the primary variable of interest was stand density, not spacing, the individual tree quality took precedence over uniform spacing in all thinnings (Schmidt, 1964). All shrubs were cut in all treated plots at the time of initial thinning because of the difficulty of not cutting some shrubs while thinning, though no shrubs were cut after the initial thinning. Subsequent entries were thinned from below, removing trees with damage or from

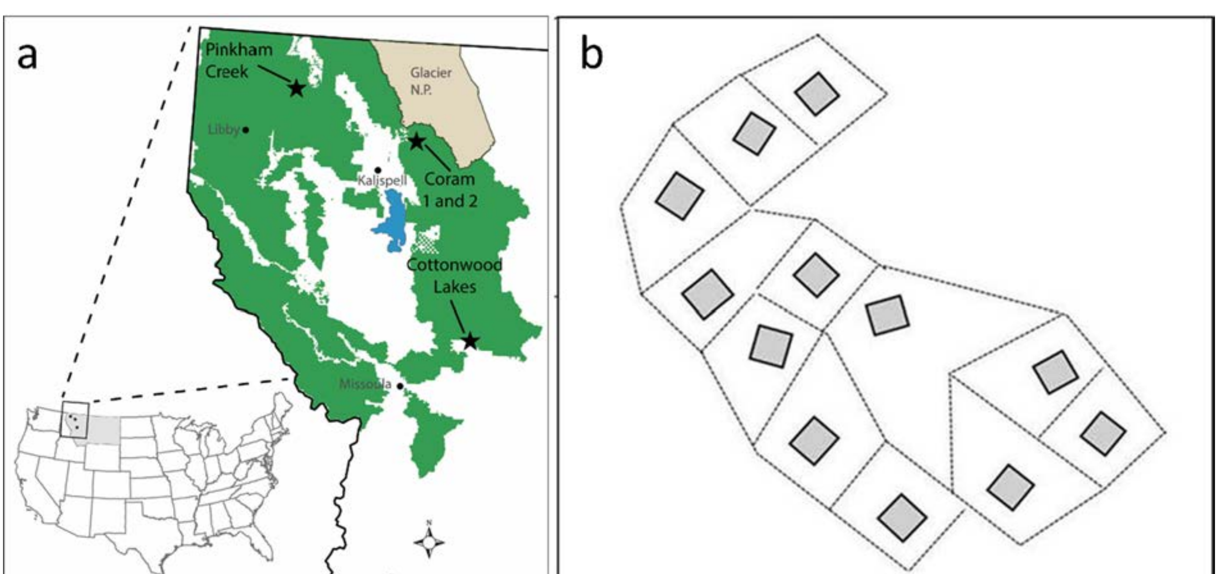


**Fig. 1.** (a). Locations of the four study sites (i.e. blocks) of the Western Larch Density Management Study in the northwest Montana, USA. (b). An example layout of the plots within a site. Gray squares are the 0.04 ha treatment plots (i.e., experimental units) and the white polygons demarcated by the dashed lines are buffer zones thinned with the same treatment.

**Table 1**
Characteristics of the four study sites where the Western Larch Density Management Study was installed. The aspect and slope are the average of all treatment plots within each block.

| Study site | Harvest date | Harvest method | Site preparation | Habitat type[a] | SI[b] (m) | Elevation (m) | Aspect | Slope | Soil texture[c] |
|---|---|---|---|---|---|---|---|---|---|
| Coram 1 | 1951 | Clearcut/ Seed-tree | Dozer piled, Broadcast burn | *Abies lasiocarpa/Clintonia uniflora, Aralia nudicaulis* phase | 24 | 1200 | 350° | 21% | Ashy silt loam |
| Coram 2 | 1951 | Shelterwood | Broadcast burn | *Abies lasiocarpa/Clintonia uniflora, Aralia nudicaulis* phase | 23 | 1200 | 300° | 25% | Ashy silt loam |
| Cottonwood Lakes | 1953 | Clearcut | Dozer piled, scarified, piles burned | *Abies lasiocarpa/Clintonia uniflora, Vaccinium caespitosum* phase | 19 | 1450 | 355° | 20% | Gravelly ashy silt loam |
| Pinkham Creek | 1953 | Clearcut | Dozer piled, scarified, piles burned | *Abies lasiocarpa/Clintonia uniflora, Clintonia uniflora* phase | 24 | 1475 | 65° | 20% | Ashy silt loam |

[a] Pfister et al. (1977).
[b] Site index (base age 50 years at breast height) was calculated with the equations of Milner (1992).
[c] Soil texture information from Web Soil Survey.

**Table 2**
The experimental design of the Western Larch Density Management Study. The target densities indicate the desired density of a treatment after its final thinning.

| Target density (Trees ha$^{-1}$) *Spacing* (m) | Number of entries | Year(s) thinned: | Intermediate thinned densities |
|---|---|---|---|
| Unthinned | 0 | – | – |
| **494** | 1 | 1961 | 494 |
| *4.56 × 4.56* | 2 | 1961 | 890 |
| | | 1981 | 494 |
| | 4 | 1961 | 1329 |
| | | 1971 | 890 |
| | | 1981 | 638 |
| | | 1991 | 494 |
| **890** | 1 | 1961 | 890 |
| *3.35 × 3.35* | 2 | 1961 | 2199 |
| | | 1981 | 890 |
| | 4 | 1961 | 4305 |
| | | 1971 | 2199 |
| | | 1981 | 1329 |
| | | 1991 | 890 |
| **1680** | 1 | 1961 | 1680 |
| *2.44 × 2.44* | 2 | 1961 | 4260 |
| | | 1981 | 1680 |
| | 4 | 1961 | 6726 |
| | | 1971 | 4260 |
| | | 1981 | 2562 |
| | | 1991 | 1680 |

subordinate crown classes. All plots were initially weeded of conifer ingrowth to maintain the target densities as well as a composition of pure larch, but no weeding occurred after 1966. Experimental treatments created a range of stand structures, stocking levels, and tree sizes by 2015 when aboveground C pools were measured for this study (Table 3).

### *2.2. Field methods*

We aggregated C in different plant life forms and organic detritus types into four pools to test our hypotheses. We separated overstory conifers from other non-conifer trees and refer to this pool as live conifer C. This separation is due to the goal of the original study to examine western larch growth. The live conifer pool was composed entirely of the western larch in the thinned experimental treatments but included a few individual trees of other conifer species in unthinned plots. Live conifer C includes all aboveground tissues, including stem wood, bark, branches, and foliage. The live non-conifer pool includes mid-story paper birch (*Betula papyrifera*), shrubs, herbs, and graminoids. We divided the woody debris pool into legacy woody debris (defined as woody debris produced by the previously harvested old-growth stand) and non-legacy woody debris (defined as woody debris produced by the current second-growth stand). The non-legacy deadwood pool includes snags, coarse woody debris (CWD; >7.62 cm), and fine woody debris (FWD; <7.62 cm), but excludes woody structures that were not produced by the current stand (legacy C). The forest floor refers to all dead organic material that is above the mineral soil and includes litter, duff, humus, and soil wood (defined as decay class 5+ logs whose central axis has sunk beneath the forest floor surface; Page-Dumroese and Jurgensen, 2006). Total non-legacy C is the sum of live conifer C, live non-conifer C, and non-legacy woody debris C. Total C with legacy includes the legacy deadwood C as well as the forest floor C. The forest floor was considered a legacy pool because it was dominated by large amounts of soil wood originating from highly decomposed old-growth logs, although the forest floor obviously includes some C fixed by the current stand.

**Table 3**
Stocking information from the 2015 remeasurement of the Western Larch Density Management Study. Relative density is calculated using the method of Drew and Flewelling (1979). The SDI maximum is calculated using the stochastic frontier model of Kimsey (2013).

| Target density (trees ha$^{-1}$) *Spacing* (m) | Number of entries | Actual density (trees ha$^{-1}$): | QMD (cm) | BA ha$^{-1}$ (m$^2$ ha$^{-1}$) | Relative density |
|---|---|---|---|---|---|
| Unthinned | 0 | 4474 | 8.7 | 28.70 | 70.0 |
| **494** | 1 | 463 | 26.8 | 26.46 | 41.8 |
| *4.56 × 4.56* | 2 | 488 | 26.9 | 27.78 | 43.8 |
| | 4 | 488 | 25.7 | 25.44 | 41.0 |
| **890** | 1 | 828 | 22.4 | 32.98 | 56.0 |
| *3.35 × 3.35* | 2 | 815 | 21.0 | 28.38 | 49.3 |
| | 4 | 859 | 19.7 | 26.77 | 47.3 |
| **1680** | 1 | 1334 | 18.1 | 34.27 | 62.8 |
| *2.44 × 2.44* | 2 | 1415 | 17.1 | 32.78 | 61.3 |
| | 4 | 1371 | 16.4 | 28.52 | 54.8 |

*2.2.1. Live conifer sampling*

Overstory sampling included measurements of diameter at breast height (DBH), total height, height to the base of the live crown, height to the widest point in the live crown, and crown width were measured and recorded for each tagged tree.

*2.2.2. Large hardwood, shrub and herbaceous vegetation sampling*

Inside the 0.04 ha treatment plots, the species, DBH, status (live or dead), and total height of every hardwood tree was measured and recorded. Diameter at root collar (DRC) and species were recorded for all shrub stems >2.54 cm DRC. Shrubs smaller than 2.54 cm DRC were clipped in three randomly located 1 $m^2$ quadrats per treatment plot. Herbaceous vegetation (herbs, graminoids, sedges, etc.) was clipped in three 0.25 $m^2$ quadrats per treatment plot. Clipped vegetation was bagged, taken to the lab, and dried and weighed.

*2.2.3. Woody detritus*

Attributes of all snags (standing dead trees) in the treatment plots were measured and recorded, including species, DBH, DRC, top diameter, total height, and decay class (Keane et al., 2006). We measured every piece of CWD inside the treatment plots. Variables recorded for each CWD piece included species (if identifiable), decay class, total length as well as the major and minor axis diameters at the middle and both ends of the log. Each snag and CWD piece was classified in the field as legacy or non-legacy based on assessment of size, decay class, and type (e.g., large diameter old-growth stumps were always classified as legacy CWD). Fine wood debris (diameter < 7.62 cm) were collected in four randomly located 1 $m^2$ quadrats inside each treatment plot and taken back to a lab to be dried and weighed. All FWD was assumed to have been produced by the current stand and classified as non-legacy.

*2.2.4. Forest floor*

Forest floor subsamples were collected at the center of three of the FWD quadrats per treatment plot. All organic material (litter, duff, humus, and soil wood) was collected inside a 30 cm diameter ring down to the mineral soil surface. Forest floor depth was measured at five locations per subsample (the center of the ring and the four corners of the 1 $m^2$ FWD sampling quadrat).

## 2.3. Laboratory analysis

FWD was sorted by size class: <0.64 cm (1-h), 0.64–2.54 cm (10-h), and 2.54–7.62 cm (100-h), then a subsample of each size class from each site was oven dried to a constant mass at 105 °C, as were clipped shrub biomass samples. All forest floor and herbaceous samples where oven-dried to a constant mass at 60 °C. Forest floor and herbaceous vegetation where then ground and analyzed for carbon content on a Leco TruSpec CN dry combustion analyzer (St. Joseph, MI, USA).

## 2.4. Carbon calculations

Live conifer aboveground dry biomass was estimated by calculating the sum of three aboveground components: stem wood, stem bark, and crown (branches and foliage). Total stem cubic volume and bark volume were calculated from ground level to the tip of the tree with species specific stem taper profile equations using diameter and height (Flewelling and Raynes, 1993; Flewelling and Ernst, 1996). Stem wood volume was converted to dry biomass using species-specific wood density values (Harmon et al., 2008; Jenkins et al., 2003). Bark volume was multiplied by a species-specific bark density (Miles and Smith, 2009) to calculate dry bark biomass. Tree crown volume was calculated by modeling tree crowns as two cones, one upright and one upside-down cone, using measurements of total tree height, crown base height, height to the widest point of the crown, and crown width (Burkhart and Tomé, 2012). Crown volume was then multiplied by a species-specific crown bulk density for the upper portion of the crown as well as the lower portion of the crown (Brown, 1978) to derive a mass for the crown (foliage plus live and dead branches) of each tree. Total tree biomass was calculated as the sum of these three components. Biomass was then converted to C by multiplying biomass by generic ratio of 0.5 (Sollins et al., 1987; Harmon et al., 1990, 2004).

Hardwoods and large shrubs ($\geqslant$2.54 cm DRC) consisted of *Betula papyrifera*, *Acer glabrum*, *Alnus viridis* (Chaix) DC. subsp. *sinuata* (Regel) Á. Löve & D. Löve, *Sorbus scopulina* Greene, *Salix scouleriana* Barratt ex Hook., and *Amelanchier alnifolia* (Nutt.) Nutt. Ex M. Roem. Allometric equations were used to estimate dry biomass from DBH and height for *Betula papyrifera* (Ker, 1984) and DCR for the other five species (Brown, 1976). The mass of large shrubs estimated from allometric equations and the oven dry mass of small shrubs (<2.54 cm DRC) from the three clipped 1 $m^2$ quadrats were converted to C using the generic ratio of 0.5 (Sollins et al., 1987; Harmon et al., 1990, 2004). Herbaceous samples were analyzed for proportion C content, averaged over the three subsamples per plot then expanded to Mg $ha^{-1}$.

Volume of each CWD piece was calculated using Newton's formula:

$$V = \frac{L(A_b + 4A_m + A_t)}{6}$$

where $V$ is the volume, $L$ is the length, and $A_b$, $A_m$ and $A_t$ are the areas of the base (large end), middle and top (small end), respectively (Harmon and Sexton, 1996). The volume was then converted to biomass using species and decay class specific wood densities and biomass to C ratios (Harmon et al., 2008; Bisbing et al., 2010). FWD biomass was calculated by averaging the four 1 $m^2$ subsamples per treatment. The generic wood C to biomass ratio of 0.5 was then applied to calculate FWD C (Sollins et al., 1987; Harmon et al., 1990, 2004).

To calculate forest floor C we first calculated the sample volume using the diameter of the sample ring (30 cm) and the measured sample depth at the center of the ring. Forest floor bulk density was calculated by dividing the oven-dried mass by the subsample volume, then averaging subsamples within each treatment plot. To expand to mean forest floor biomass per treatment plot we calculated the mean forest floor volume per treatment plot using the five sample depths per subplot (15 total depth measurements per treatment plot) and multiplied mean volume by the mean bulk density. To calculate mean C per treatment plot we multiplied the mean forest floor biomass per plot by the corresponding mean C content.

## 2.5. Statistical analysis

Due to the nested design of the two factors (entries nested within target density) we analyzed the data as a one-way randomized block ANOVA, with site as the blocking variable and treatment as a composite variable of both target density and entries. The resulting explanatory variable was a factor with 10 levels (3 entries $\times$ 3 target densities plus the control). Several of the carbon pools exhibited variance heteroscedasticity, so different variance structures were modeled for each level of target density by fitting the model with generalized least square regression using *gls* function in the *nlme* package in R (R Development Core Team, 2016) then specifying the *weights* argument. Residual plots were checked to confirm that modeling different variances improved the model fit over a linear model.

We used *a priori* mutually orthogonal contrasts to test our predictions. We first used three contrasts to test our predictions for stand density effects on C storage: (1) the unthinned treatment against the thinned treatments, (2) the 1680 trees $ha^{-1}$ treatment against the 890 trees $ha^{-1}$ and 494 trees $ha^{-1}$ treatments combined; and (3) the 890 trees $ha^{-1}$ against the 494 trees $ha^{-1}$ treatment (Table 4). To evaluate the effect of the number of entries within each of the three thinned target densities we compared (at each density) the one-entry treatment against the two- and four-entry treatments combined, and the two-entry treatment against the four-entry treatment (Table 4). All statistical analyses were conducted using R 3.2.4 (R Development Core Team, 2016).

The reported results are for C in 2015, 54 years after precommercial thinning treatments began (mean stand age of 62 years). Unless otherwise noted, the means reported are the main effect of the density treatment, which is the mean of the three thinning frequencies within a given density level.

## 3. Results

### 3.1. Prediction 1: live conifer carbon

Live conifer C was not significantly affected by thinning treatment or stand density ($P > 0.10$; Table 4), contrary to our expectation. The unthinned plots had the highest average C (80.52 Mg $ha^{-1}$) but only by 3.49 Mg $ha^{-1}$ more than the average of the thinned plots, a non-significant difference (Fig. 2a). There were no significant differences between the three thinned densities (Table 4). As an experiment-wide average, live tree C made up 90% of the non-legacy aboveground C but that value ranged from a low of 80% in the unthinned treatment to 90–91% in the thinned treatments. Variability generally increased with density (Appendix A: Table A1). The effect of the number of entries was not significant for the live conifer C pool at any of the target densities ($P > 0.10$; Table 4).

The average C per tree was inversely related to stand density (Fig. 3). Average C per tree was more than twice as much in the 494 trees $ha^{-1}$ treatment than the 1680 trees $ha^{-1}$ treatments and more than eight times greater than the unthinned treatments. Within each level of target density, per tree C was higher in treatments with fewer entries (Fig. 3).

### 3.2. Prediction 2: Live non-conifer carbon

Live non-conifer C stores differed among treatments due to density ($P = 0.006$, global test) and increased as density decreased (Fig. 2b), in agreement with our prediction for this pool. The greatest differences were between the 494 trees $ha^{-1}$ treatment (5.52 Mg $ha^{-1}$) and the unthinned treatments (3.14 Mg $ha^{-1}$). Live non-conifer C made up a small proportion of the total non-legacy C ranging from a low of 3.1% for the unthinned treatment and increasing inversely with density to 3.7%, 5.0% and 6.6% for the 1680, 890 and 494 trees $ha^{-1}$ treatments, respectively. Variability of the understory C tended to decrease as density increased (Appendix A: Table A1). Number of entries did not significantly affect the live non-conifer C pool within any target density ($P > 0.10$; Table 4).

### 3.3. Prediction 3: non-legacy deadwood

Non-legacy deadwood C pools varied among treatment densities (global test; $P = 0.031$), consistent with our prediction. However, the individual contrasts showed no significant effect of density ($P > 0.10$), likely due to the high level of variability in the non-legacy deadwood pool. The unthinned treatment had the greatest amount of C in this pool (13.43 Mg $ha^{-1}$) and was more than twice as large as the 1680 trees $ha^{-1}$, 890 trees $ha^{-1}$, or 494 trees $ha^{-1}$ treatments (Fig. 2c). The proportion of total non-legacy C was the highest in the unthinned treatment at 17.3% and decreased with density to 7.4%, 4.7% and 4.0% for the 1680, 890 and 494 trees $ha^{-1}$ treatments, respectively. Variability in deadwood C stocks increased with density (Fig. 2c; Appendix A: Table A1) and variability was very high in the unthinned treatments with standard errors more than twice as large as the other treatments. The effect of the number of entries was not significant for the non-legacy deadwood C pool for any of the target density levels ($P > 0.10$).

### 3.4. Prediction 4: total aboveground non-legacy carbon

Contrary to our expectation, total aboveground non-legacy C was not significantly affected by density ($P > 0.10$; Fig. 2d). Aboveground non-legacy C storages, which excluded both legacy woody debris C and forest floor C, ranged from 76.15 Mg $ha^{-1}$ to 100.49 Mg $ha^{-1}$ (Appendix A: Table A1). Carbon stocks generally increased with density and unthinned plots had the largest C stores (100.49 Mg $ha^{-1}$), but were not statistically different from thinned stands ($P > 0.10$; Table 4). Total aboveground non-legacy C values differed by less than 3 Mg $ha^{-1}$ between the 494 trees $ha^{-1}$ (84.20 Mg $ha^{-1}$), 890 trees $ha^{-1}$ (84.78 Mg $ha^{-1}$), and 1680 trees $ha^{-1}$ (86.31 Mg $ha^{-1}$) treatments (Fig. 2d). There was high variability in most treatments and variability in stores generally increased with density. The effect of the number of entries was not significant for the total aboveground C pool ($P > 0.10$; Table 4).

**Table 4**
Results of linear contrasts (standard error of the mean shown in parentheses) for aboveground C pools predicted to be sensitive to density management with thinning. Global density test p-values represent the significance of all three contrasts simultaneously.

| Contrast | Carbon pool | | | |
|---|---|---|---|---|
| | Live conifer (Mg $ha^{-1}$) | Other live (Mg $ha^{-1}$) | Non-legacy deadwood (Mg $ha^{-1}$) | Total non-legacy (Mg $ha^{-1}$) |
| Density | | | | |
| Global density test p-value | 0.993 | 0.0062** | 0.0314* | 0.622 |
| Unthinned vs Thinned | 3.49 (18.22) | −1.21 (0.37)** | 12.82 (6.72) | 15.39 (11.93) |
| 1680 vs 890 and 494 | 0.55 (5.00) | −1.64 (0.77) | 2.68 (1.22) | 1.82 (4.821) |
| 890 vs 494 | 1.21 (5.88) | −1.26 (0.92) | 0.59 (0.47) | 0.58 (5.83) |
| Number of entries | | | | |
| 1680: 1 entry vs 2 and 4 entries | 8.93 (8.59) | 1.37 (1.31) | 1.20 (2.54) | 11.07 (8.11) |
| 1680: 2 entries vs 4 entries | 12.72 (9.92) | 1.24 (1.52) | −0.95 (2.94) | 12.95 (9.37) |
| 890: 1 entry vs 2 and 4 entries | 15.85 (8.30) | 1.20 (1.29) | −0.74 (0.63) | 16.67 (7.71) |
| 890: 2 entries vs 4 entries | 0.55 (9.59) | −0.22 (1.49) | 0.17 (0.73) | 0.73 (8.90) |
| 494: 1 entry vs 2 and 4 entries | −2.96 (9.32) | 0.73 (1.46) | −0.24 (0.78) | −2.56 (9.78) |
| 494: 2 entries vs 4 entries | 4.05 (10.76) | 2.11 (1.69) | −1.48 (0.90) | 0.53 (11.29) |

*Significance codes (p-value): 0.001 < **<0.01 < *<0.05.*

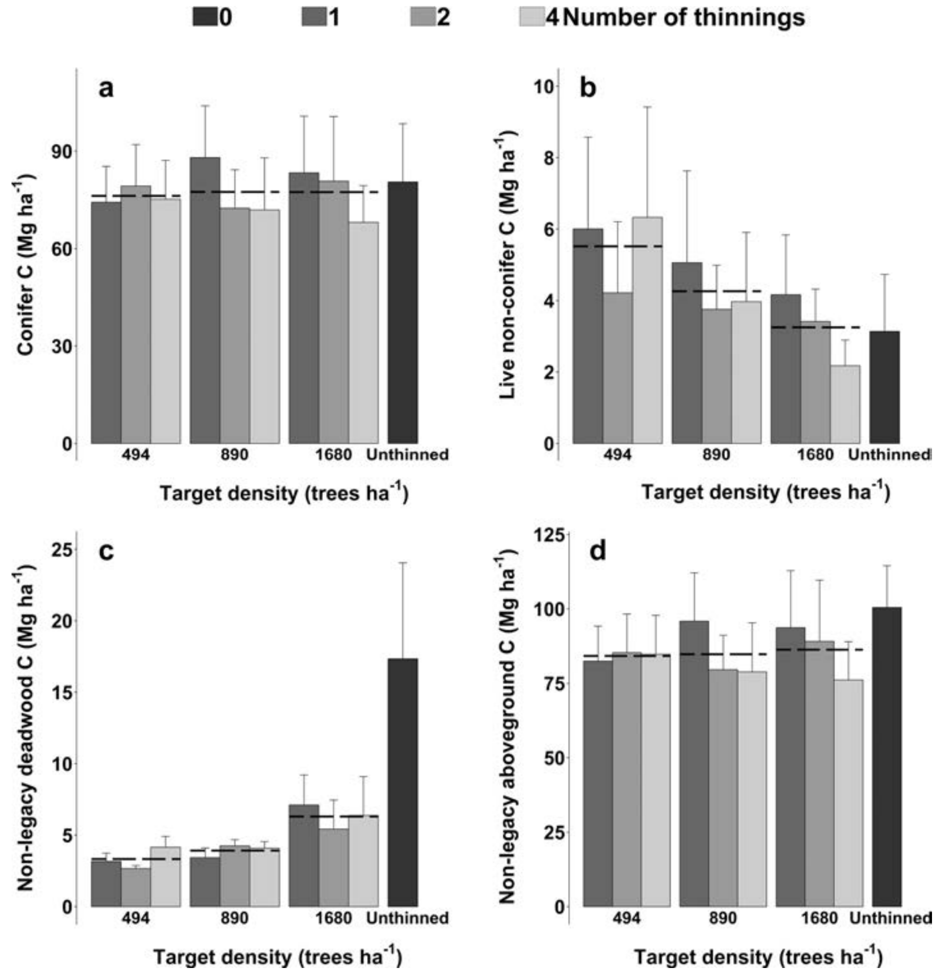


**Fig. 2.** Effects of thinning treatment on the three C pools predicted to be affected by treatment. (a) live conifers, (b) live non-conifers, (c) non-legacy deadwood. The final panel (d) is the sum of the three previous three pools. The bars are grouped by target density, shown on the x-axis. Within each density level three different thinning regimes (1, 2 or 4 entries) were used to achieve the target density (Table 2). The dashed lines across the three grouped bars are the average of all number-of-entry treatments within a density and represent the main effect of density on C stores. Error bars represent one standard error of the mean.

### 3.5. Legacy C pools

There was no significant effect of either target density or number of entries on legacy CWD or forest floor C (P > 0.10). These

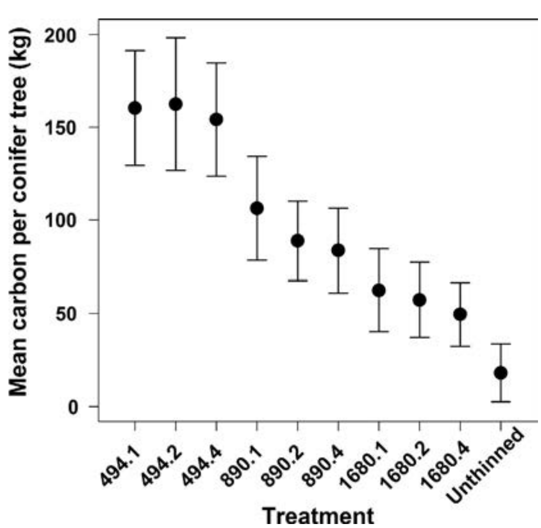


**Fig. 3.** The relationship between treatment and mean C per tree. Error bars represent one standard error. On the x-axis the target density (trees $ha^{-1}$) is listed first and the number of thinning entries is listed after the period.

pools contained C residues originating primarily from the harvested old-growth stands and were unlikely to be strongly affected by the treatments. However, they did contain substantial amounts of C (Appendix A: Table A1). The experiment-wide mean legacy CWD C load was 4.7 Mg $ha^{-1}$, and it ranged from 2.29 Mg $ha^{-1}$ to 8.09 Mg $ha^{-1}$ (Fig. 4a). Legacy CWD made up an average of 4.1% of the total aboveground C with legacy pools included. The experiment-wide mean of the forest floor pool was 22.74 Mg $ha^{-1}$ and ranged from 14.64 Mg $ha^{-1}$ to 34.46 Mg $ha^{-1}$ (Fig. 4b). Forest floor C made up an average of 20.0% of the total aboveground C with legacy pools included and together with the legacy CWD made up 24.1% of total C. The relatively high forest floor C values are due to substantial amounts of partially decomposed soil wood, especially in the sites where harvest residues were broadcast burned and not dozer piled and burned (Table 1).

### 3.6. C distribution among live and dead pools

Stands with higher target densities had a larger proportion of total C in non-legacy dead pools (Fig. 5a), consistent with our expectation. The unthinned treatment had largest proportion of C in dead pools (17.3%); the proportion of C in dead pools declined with target thinning density, with 7.4%, 4.7% and 4.0% of C in dead pools for the 1680, 890 and 494 trees $ha^{-1}$ treatments, respectively. As expected, when legacy pools are included the clear effect of treatment on the proportion of C in live and dead pools was

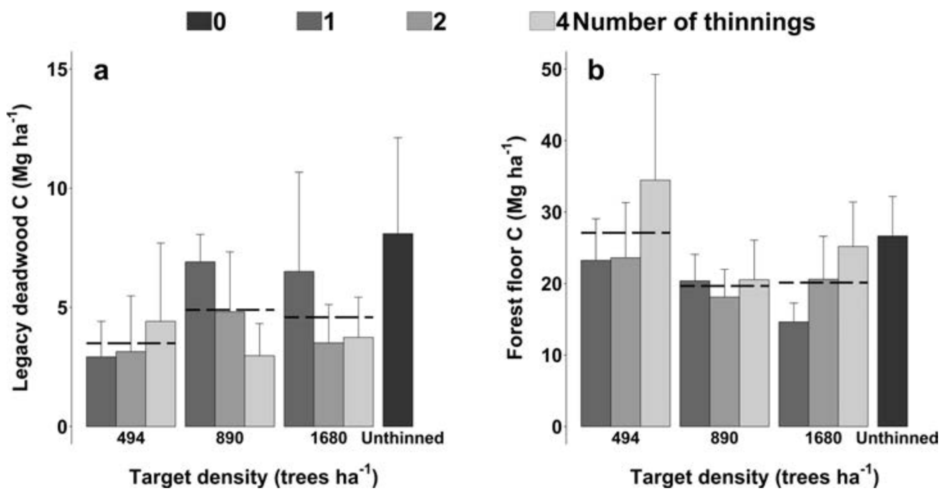


**Fig. 4.** The mean C content by treatment for legacy pools. Error bars represent one standard error. The dashed lines across the three grouped bars are the average of all number-of-entry treatments within a density and represent the main effect of density on C stores. Forest floor was considered a legacy pool due to a dominance of highly decayed soil wood.

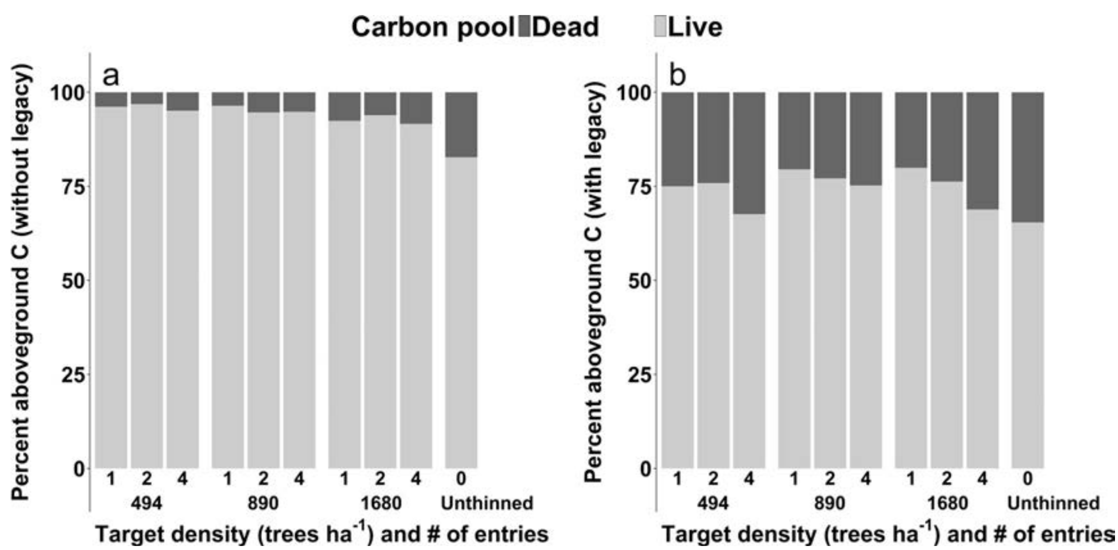


**Fig. 5.** The effect of treatment on the partitioning of C between dead and live pools. When only non-legacy pools are compared (A) there is a clear increase in C in dead pools as density increases. When legacy C pools (legacy deadwood and forest floor) are included (B), the proportion on carbon in dead pools increases by an average of 20% and the treatment effect is masked.

masked. The unthinned plots still had the largest C proportion in dead pools at 34.6% (Fig. 5b), due in part to the non-legacy deadwood pools: by chance, there were multiple very large legacy logs in two of the unthinned plots.

## 4. Discussion

Our results indicate that regulation of stand density with early precommercial thinning does not decrease total aboveground C stores 54 years after treatment. These findings have numerous implications for managing second growth forests to meet both C storage (i.e., climate change mitigation) and other management objectives, such as development of complex stand structures and provision of wildlife habitat, which are elements of climate change adaptation strategies (Bradford and D'Amato, 2012). A key implication of our results is that regulating stand density to increase individual tree growth does not necessarily result in lower total aboveground C (Horner et al., 2010; Dwyer et al., 2010). This is an important finding because current understanding (D'Amato et al., 2011; Bradford and D'Amato, 2012) emphasizes that there is a tradeoff between management for climate mitigation (i.e., maximizing C storage) and management for climate adaptation (development of structurally and compositionally complex forest stands). Thinning older stands to low densities to promote structural complexity and climate change adaptation potential typically reduces aboveground C storage (Bradford and D'Amato, 2012). Our results indicate that no such tradeoff exists a half-century after precommercial thinning in young western larch forests. Low density stands had much larger trees (Table 3, Fig. 3) and more understory and midstory vegetation (Fig. 2b)—hallmarks of structural and compositional complexity—yet low density stands stored as much aboveground C as unthinned stands and stands thinned to high densities (Fig. 2).

These contrasting results arise from the very different thinning regimes studied here compared to those investigated by D'Amato et al. (2011). Here, precommercial thinning treatments were implemented at an average stand age of eight years, prior to the onset of canopy closure and intense intertree competition leading to crown recession (*c.f.* Horner et al., 2010). In contrast, thinning treatments were implemented at stand age 85 years in the red pine (*Pinus resinosa*) forests studied by D'Amato et al. (2011), with thinnings then repeated every 5–10 years in a levels-of-growing-stock (LOGS) style experiment. The results of both studies are consistent with foundational stand dynamics theory (Oliver and Larson, 1996) and should not be interpreted as contradictory. The key implication for management and policy is that not all forest thinning treatments are equal in their design or effects. This nuance needs to be communicated to policy makers and managers involved in efforts to devise forest management strategies for climate change adaptation and mitigation.

### 4.1. Mechanisms causing C storage convergence across stand densities

The fact that total non-legacy aboveground C does not vary by treatment (Fig. 2d) is largely driven by strong effects of stand density on mean overstory tree size (Figs. 3 and 2a). In a companion analysis, target density strongly affected mean tree diameter, height, and crown volume (Schaedel et al., 2016), the three variables that have the greatest effect on individual tree biomass, and therefore tree C. These results agree with density management theory (Drew and Flewelling, 1979; Harrington et al., 2009) and are consistent with the relatively small range of relative density the treatments spanned by 2015 (Table 3).

Estimating mean total tree C as the sum of the stem wood, bark, and crown components allowed us to account for the known effects of stand density on mean height and crown volume (Schmidt and Seidel, 1988; Harrington et al., 2009), which is not possible with commonly used allometric equations based on diameter alone (e.g. Jenkins et al., 2003). Mean crown volume per conifer tree follows similar trends seen in the mean tree C (Fig. 3); tree crown volumes are inversely related to both density and number of entries. However, this effect on crown C in western larch is likely less than for other species because western larch has a comparatively low crown bulk density (Brown, 1978).

Live non-conifer C was affected by target density as we anticipated: higher stand densities had lower amounts of C in this pool. This is consistent with the findings of other studies on the effect of thinning on understory C (Campbell et al., 2009; Powers et al., 2012; Zhou et al., 2013) as well as stand dynamics theory (Oliver and Larson, 1996). As stand density decreases more growing space and resources are available for understory vegetation. The result is a greater amount of shrub and mid-story hardwood C in low density stands. The non-conifer live C pool made a greater contribution to total C than was found in other studies (Campbell et al., 2009; Bisbing et al., 2010; Powers et al., 2012; Jang et al., 2015), in part because we grouped mid-story hardwood trees (*Betula papyrifera*) with shrubs and herbs. Even including these mid-story hardwoods, this pool makes a relatively small contribution to total aboveground C at this point in stand development, with an experiment wide average of 5.0% of the total aboveground C and ranging from 6.6% in the 494 trees $ha^{-1}$ to 3.1% in the unthinned treatment. This low proportion of total aboveground C is likely due to all treatment densities being closed canopy stands, which reduces understory vegetation until non-competitive mortality events create canopy gaps leading to understory re-initiation (Oliver and Larson, 1996).

Non-legacy deadwood showed strong increases with increased stand density, with unthinned plot having more than twice the C than the 1680 trees $ha^{-1}$ treatment and >5 times the C as the 494 trees $ha^{-1}$ treatment. This substantial increase in deadwood C is important from a carbon storage perspective but the patterns of variability in this pool are also noteworthy (Table 4 and Appendix A: Table A1). Early precommercial thinning increases average tree size and decreases the variability between stands; in contrast, the unthinned stands tend to be more variable (Fig. 2c and Appendix A Table A1). Our results show that for the non-legacy deadwood C pool variability generally decreases with decreasing stand density. This is likely due to self-thinning mortality in unthinned stands being spatially aggregated, with mortality concentrated in locally crowded areas (Larson et al., 2015). Since low density stands are experiencing less competition and, subsequently less density-dependent mortality, this suggests lower inputs to the woody debris pool, as well as lower variability of deadwood inputs.

We emphasize that our finding of constant yield of total aboveground C across a wide range of densities was achieved with the application of the early low thinning common to PCT; thinning treatments were implemented at an average stand age of eight years. We expect that similar results may eventually be found from long-term studies of stands planted at different initial spacing (e.g., Harrington et al., 2009). This is because early PCT is functionally similar to initial spacing—the manipulation of stand density occurs before the trees have experienced major effects of competition, such as canopy closure and crown recession. We would not expect to see similar results from studies of other thinning methods, such as thinning across the diameter range or crop tree thinning, especially when treatments are implemented at later stand ages and after canopy closure and crown recession (Hoover and Stout, 2007; D'Amato et al., 2011). In fact, there is a substantial amount of evidence from LOGS and other commercial thinning studies, which employ thinning across the diameter range and crop tree thinning, showing a consistent decrease in total aboveground C with decreases in growing stock or density (Skovsgaard et al., 2006; Chatterjee et al., 2009; D'Amato et al., 2011; Zhou et al., 2013).

The multiple thinning entries in this study (Table 2) are distinctly different from the multiple thinning entries of LOGS studies. In this study the multiple thinning entries removed the smallest trees to achieve a target density over multiple thinnings, while LOGS thinnings seek to maintain a constant level of growing stock through time, defined by basal area, bole surface area, or total cubic volume (Marshall and Curtis, 2002). The removal of larger trees in LOGS experiments results in significant loss of live tree C and reduces future inputs to woody detritus pools by reducing competition and resultant self-thinning mortality. The removal of large trees in LOGS studies also leaves gaps in the canopy which residual trees are slow to fill, especially in older stands, reducing rates of stand-level biomass accumulation (Long et al., 2004). In contrast, low thinning removes the least productive trees, which results in little loss in stand-level growth (Smith et al., 1997). If thinning is done early, before individual tree growth is reduced by inter-tree competition, the residual trees reoccupy the site more quickly than stands thinned after competition has caused self-pruning and crown recession (Long et al., 2004).

Even 62 years after harvest, legacy pools, primarily large CWD and soil wood in the forest floor, stored a substantial amount of C, making up an experiment-wide average of 24% of total aboveground C. Large CWD pieces have a long residence time (Harmon et al., 1986) especially in the relatively cold and dry forests of the Northern Rockies (Bisbing et al., 2010; Mobley et al., 2013). There is little evidence that the experimental thinning treatments would have significantly affected these pools—changes in decay rate due to the stand density caused changes in light and temperature are likely to be small, especially since the stands are all in closed canopy conditions (Harmon et al., 1986). The relatively slow growth rates of many western larch sites indicate that producing trees of large enough diameter to produce large snags and CWD may take 200 years or more (Bisbing et al., 2010). This underscores the importance of retaining large woody debris on site following harvest to promote long-term C storage and maintain the other important ecological functions of large CWD (Duvall and Grigal, 1999; Franklin et al., 2002). In second growth stands this also suggests that, despite an initial reduction of the amount of C in the dead wood pools due to thinning (Fig. 2c), promoting the rapid growth of large trees may be the fastest way to ultimately recover large deadwood structures (Sturtevant et al., 1997).

For timber production objectives, it is rarely economically viable to enter a stand more than once before removing a merchantable product. Similarly, for C storage and climate change mitigation objectives there is also no benefit of multiple light thinnings. Number of entries did not significantly affect any aboveground C pool, although it did subtly influence mean conifer tree C at the individual tree scale (Fig. 3). The only potential benefit to multiple light thinnings is to allow for the replacement of damaged trees, or trees lost mortality. Our results suggest that such potential benefits are marginal at best.

## 5. Conclusions and management implications

Three main conclusions follow from our examination of the effects on early thinning on total aboveground C.

- Total aboveground C storage is similar across thinned and unthinned stands fifty-four years after treatment, due primarily to the increase in mean tree C (i.e., mean size) of trees grown at lower densities.
- Deadwood legacies from the pre-disturbance old-growth forest still play an important role in long-term C storage sixty-two years after stand-initiating disturbance, accounting for approximately 20–25% of aboveground C stores.
- Given enough time since early thinning, there is no trade-off between managing to promote rapid individual tree growth and development of understory vegetation, and maximizing stand level accumulation of aboveground C.

*We infer that there is potential to use early thinning to simultaneously achieve climate change mitigation and climate change adaptation objectives, provided treatments are implemented early in stand development, before canopy closure and the onset of intense intertree competition.* We expect that there is a lower limit of stand density that will achieve these simultaneous outcomes, due to natural limitations of maximum tree size and the importance of full site occupancy to achieving high rates of C accumulation (Newton, 1997; Kashian et al., 2013).

There is great potential to use long-term silvicultural experiments to test novel ecological hypotheses and answer contemporary management questions that were not envisioned at study initiation (D'Amato et al., 2011; Bradford and D'Amato, 2012). Continuing to monitor C stocks and other attributes of stands experimentally manipulated to different target densities can provide insight into the future effects of management actions, as well as the mechanisms that govern dynamics of natural forests. For example, because large diameter, full crowned trees continuously increase C accumulation rates with increasing tree size (Stephenson et al., 2014), are more resistant to perturbations such as fire (Belote et al., 2015) and uprooting and stem breakage (Wonn and O'Hara, 2001), stands thinned to initial low density may ultimately have greater long-term C storage potential than unthinned stands or stands thinned to higher densities (Oliver and Larson, 1996). Continued measurement of the WLDMS and other long-term silvicultural experiments will permit testing of this prediction.

## Acknowledgements

We thank Wyman Schmidt and Jack Schmidt for years of diligent work on the Western Larch Density Management Study from 1961 to 2001. We thank E.K. Sutherland and D.K Wright for their assistance with access to historical data and understanding study design, as well as R.E. Keane, J. Reardon, C.C. Cleveland, M.K. Nasto and J. Tirocke for help with sample processing. We thank field crew members C.J. Weisbrod, E.E. Schneider, L. Glasgow, and W. George for help with data collection. S. Bisbing and an anonymous reviewer provided constructive suggestions that improved an earlier version of this paper.

## Appendix A

See Table A1.

**Table A1**
Mean aboveground C stores (standard error) by component pool for each thinning treatment.

| Target density | Thinning entries | Live conifer[a] ($Mg\ ha^{-1}$) | Other live[b] ($Mg\ ha^{-1}$) | Non-legacy deadwood[c] ($Mg\ ha^{-1}$) | Total non-legacy[d] ($Mg\ ha^{-1}$) | Legacy deadwood[e] ($Mg\ ha^{-1}$) | Forest Floor[f] ($Mg\ ha^{-1}$) | Total aboveground[g] ($Mg\ ha^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 494 | 1 | 74.29 (11.01) | 6.01 (2.57) | 3.17 (0.58) | 82.49 (11.71) | 2.92 (1.49) | 23.24 (5.28) | 108.66 (16.94) |
| | 2 | 79.27 (12.77) | 4.22 (1.99) | 2.67 (0.20) | 85.32 (12.96) | 3.15 (2.34) | 23.61 (7.72) | 112.08 (19.52) |
| | 4 | 75.22 (11.95) | 6.33 (3.09) | 4.15 (0.76) | 84.79 (13.07) | 4.42 (3.28) | 34.46 (14.79) | 123.67 (24.38) |
| | Mean | 76.26 (6.26) | 5.52 (1.38) | 3.33 (0.35) | 84.20 (6.59) | 3.50 (1.13) | 27.11 (5.55) | 114.80 (10.89) |
| 890 | 1 | 88.03 (15.91) | 5.06 (2.57) | 3.43 (0.68) | 95.90 (16.23) | 6.91 (1.15) | 20.38 (3.71) | 123.18 (18.58) |
| | 2 | 72.45 (11.85) | 3.75 (1.24) | 4.25 (0.43) | 79.59 (11.54) | 4.81 (2.51) | 18.11 (3.87) | 102.51 (14.84) |
| | 4 | 71.90 (16.03) | 3.97 (1.94) | 4.09 (0.46) | 78.86 (16.43) | 2.97 (1.35) | 20.53 (5.54) | 102.36 (20.15) |
| | Mean | 77.46 (8.01) | 4.26 (1.05) | 3.92 (0.30) | 84.78 (8.14) | 4.90 (1.05) | 19.67 (2.35) | 109.35 (9.85) |
| 1680 | 1 | 83.36 (17.42) | 4.17 (1.67) | 7.11 (2.11) | 93.69 (19.17) | 6.50 (4.17) | 14.64 (2.64) | 114.83 (20.91) |
| | 2 | 80.79 (19.87) | 3.41 (0.91) | 5.43 (2.03) | 89.10 (20.58) | 3.51 (1.61) | 20.60 (6.00) | 113.21 (27.95) |
| | 4 | 68.07 (11.32) | 2.18 (0.72) | 6.38 (2.71) | 76.15 (12.82) | 3.75 (1.68) | 25.17 (6.22) | 105.06 (20.00) |
| | Mean | 77.41 (8.90) | 3.25 (0.66) | 6.31 (1.22) | 86.31 (9.58) | 4.59 (1.50) | 20.14 (3.02) | 111.03 (12.20) |
| Unthinned | 0 | 80.53 (17.95) | 3.14 (1.59) | 17.34 (6.71) | 100.49 (14.00) | 8.09 (4.03) | 26.65 (5.54) | 135.23 (18.11) |

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$
[a] Live conifer includes all C in conifers but is composed only of larch in all thinned stands.
[b] Other live includes C in overstory hardwoods, shrubs, and herbaceous vegetation.
[c] Non-legacy deadwood includes all C in snags and woody debris produced by the current second-growth stands.
[d] Total non-legacy is the sum of all of the aboveground C pools most affected by treatment; the previous three columns.
[e] Legacy deadwood includes all C in woody debris that was produced by the logged old-growth stands.
[f] Forest floor includes all C in the O horizons (litter, duff, and humus) as well as soil wood (woody debris > decay class 5).
[g] Total Aboveground C is the sum of all other pools and represents both legacy and non-legacy pools.

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