

Long-term precommercial thinning effects on *Larix occidentalis* (western larch) tree and stand characteristics

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Abstract: Precommercial thinning (PCT) is used to increase tree size and shorten harvest rotation time. Short-term results from PCT studies often show a trade-off between individual-tree growth and net stand yield, while longer-term effects of PCT on tree growth and stand yield are less well documented. We used a 54-year-old PCT study to test long-term effects of forest density and thinning schedules on stand yield and tree-level characteristics in even-aged western larch (*Larix occidentalis* Nutt.) stands. The study has three target densities (494, 890, and 1680 trees·ha⁻¹) crossed with three thinning schedules (target density achieved through one, two, or four entries). Analysis of variance (ANOVA) and linear contrasts were used to test the effects of density and number of entries on tree- and stand-level attributes. Thinning before stand age 10 years leads to long-term constant yield (219.0–269.5 m³·ha⁻¹; $P > 0.05$) across the tested densities. We also found constant volume growth across stand densities during the most recent measurement interval (5.42–6.41 m³·ha⁻¹·year⁻¹; $P > 0.05$). Number of entries did not affect any tree- or stand-level attribute. The primary effect of early PCT is to control whether wood volume and growth are concentrated on few large, stable trees or spread over many small, unstable trees.

Key words: density management, stand density, competition, stand dynamics, growth and yield.

Résumé : L'éclaircie précommerciale (EPC) est utilisée pour augmenter la taille des arbres et devancer l'âge de la récolte du peuplement. À court terme, les résultats de l'EPC montrent souvent un compromis entre la croissance des arbres individuels et la production nette du peuplement, alors que les effets à long terme de l'EPC sur la croissance des arbres et la production des peuplements sont moins bien documentés. Nous avons utilisé une étude sur l'EPC, vieille de 54 ans, pour évaluer les effets à long terme de la densité des peuplements et du calendrier des éclaircies sur la production des peuplements et les caractéristiques des arbres dans des peuplements équiennes de mélèze occidental (*Larix occidentalis* Nutt.). L'étude comprenait trois densités cibles du peuplement (494, 890 et 1680 arbres·ha⁻¹) et trois calendriers des éclaircies (densité cible atteinte après un, deux ou quatre interventions). Nous avons utilisé des analyses de variance et des contrastes linéaires pour tester les effets de la densité du peuplement et du nombre d'interventions sur les caractéristiques des arbres et des peuplements. Une éclaircie réalisée avant l'âge de 10 ans a mené à une production constante à long terme (de 219,0 à 269,5 m³·ha⁻¹; $P > 0,05$) pour l'ensemble des densités testées. Nous avons aussi trouvé une croissance en volume constante entre les densités de peuplement au cours du plus récent intervalle de mesures (5,42 à 6,41 m³·ha⁻¹·an⁻¹; $P > 0,05$). Le nombre d'interventions n'a influencé aucune caractéristique des arbres et des peuplements. L'effet principal d'une EPC précoce est de déterminer si le volume et la croissance du bois sont concentrés sur un nombre limité de gros arbres stables ou répartis sur de nombreux petits arbres instables. [Traduit par la Rédaction]

Mots-clés : gestion de la densité, densité du peuplement, compétition, dynamique du peuplement, croissance et production.

1. Introduction

Forest stand density affects the timing and intensity of competitive interactions between neighboring trees (Oliver and Larson 1996; Long et al. 2004; Harrington et al. 2009). In high-density stands, tree crowns rapidly occupy the site and trees begin to compete for limited resources such as light, water, and nutrients early in stand development. The result of competitive interactions is slower growth for all trees (Sjolte-Jorgensen 1967; Reukema 1979). In lower density stands, more space and resources are allocated to each individual tree, the result of which is delayed onset of intense intertree competition, leading to an increase in tree growth and a decrease in time required to reach merchantable size (Assmann 1970; Reukema 1975; Smith et al. 1997; Tappeiner

et al. 2007). However, the trade-off for rapid individual-tree growth at lower densities is a period when trees do not fully occupy the site, and therefore, stand yield may lag behind yields obtained from high-density stands.

While it is well established that individual-tree size and growth increase at lower stand densities (Sjolte-Jorgensen 1967; Smith et al. 1997; Marshall and Curtis 2002; Tappeiner et al. 2007), there is still uncertainty over how long-term yield, defined as total net cubic stem wood volume per unit ground area, responds to early density management (Oliver and Larson 1996). Stand yield is the sum of the individual trees in a stand, but does the increase in individual tree size at lower densities make up for fewer trees? Current wisdom generally suggests that yield increases with increasing density (Zeide 2001; Curtis et al. 1997; Marshall and Curtis

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2002). However, at least one long-term precommercial thinning study has found the opposite result. Forty-two years after thinning, thinned plots contained 15% more total gross volume than unthinned plots in a mixed *Abies balsamea* (L.) Mill. (balsam fir) – *Picea rubens* Sarg. (red spruce) forest in northwestern New Brunswick, Canada (Pitt and Lanteigne 2008). This may be due to the greater individual-tree growth rates caused by greater crown sizes of large trees grown at lower density (Stephenson et al. 2014) combined with the deleterious effects of tight spacing on these same attributes, as well as elevated mortality in high-density stands causing a decrease in net cubic volume (Drew and Flewelling 1979; Oliver and Larson 1996; Newton 1997).

The volume of a tree stem depends on tree height, diameter, and stem taper (Flewelling and Ernst 1996), so a reduction of height growth at higher density would be expected to reduce total cubic volume. For two trees of equal diameter, volume is roughly proportional to height (Drew and Flewelling 1979). It is a near axiomatic concept in forest density management that the height of dominant conifer trees in a stand, referred to here as top height and defined here as the height of the tallest 100 trees·ha⁻¹, is independent of stand density (Sjölte-Jørgensen 1967; Lanner 1985; Smith et al. 1997; Marshall and Curtis 2002; Tappeiner et al. 2007). However, early results from some thinning trials show top height sorting along a density gradient with low-density stands having greater top height (Schmidt and Seidel 1988; Schmidt 1997; Martin and Barber 1995). If top height increases faster in low-density stands, this will have strong effect on yields of both total cubic volume and merchantable volume.

Tree height variability, or height differentiation, is an important indicator of stand development processes. This is especially true in evenly spaced even-aged stands in which differentiation may be weak, leading to an earlier loss of height growth at higher densities (Oliver and Larson 1996; O'Hara and Oliver 1999). In single-species, even-aged stands, tree size differentiation trends through time can reveal a dominant role of size asymmetric competition (indicated by increasing size variation; Weiner 1990) or of size symmetric competition (indicated by stable or declining size variation; Weiner 1990; Stoll et al. 1994). Size asymmetric competition is most strongly associated with intense competition for light, while size symmetric competition is typical of belowground competition for nutrients (Weiner 1990; Schwinning and Weiner 1998).

The ratio of height to diameter of the largest 200 trees·ha⁻¹ ($H:D_{200}$), an indicator of tree stability and resistance to physical damage (Cremer et al. 1982; Wilson and Oliver 2000; Wonn and O'Hara 2001), may indirectly affect stand yield. Stands with high $H:D_{200}$ are more susceptible to windthrow and stem breakage, and stands grown at higher densities have higher $H:D_{200}$ (Cremer et al. 1982; Wilson and Oliver 2000; Wonn and O'Hara 2001). This predisposes a greater proportion of the standing volume to damage and mortality, which reduces net stand yield.

Finally, mortality rates affect total net yield. Measures of competition such as relative density, the proportion of the maximum stand density index for a species (sensu Drew and Flewelling 1979), identify thresholds at which the probability of mortality increases. Relative density can also be used to identify levels of competition at which volume growth is highest. Newton (1997) identified relative densities between 40% and 55% of maximum as the zone of peak forest growth. Growth rates for relative densities below 40% were lower as the trees did not fully occupy the site, and net growth rates (gross growth minus mortality) above 55%, the beginning of the zone of imminent competition mortality, were lower due to a loss of volume to mortality (Drew and Flewelling 1979; Newton 1997).

A target stand density may be achieved through many alternative thinning schedules. Is there a benefit to achieving a final target density with multiple light thinnings over single heavy thinning? From an operations and cost perspective, the most advantageous system may be a single thinning directly to a target

density, which will allow trees to grow to a merchantable size before competition reaches a level at which volume is lost to mortality. However, there are potential benefits to making multiple thinning entries in a stand. If the stand has not yet begun to differentiate when it is initially thinned, moving the stand to an intermediate density and allowing trees to begin to express dominance may result in a larger tree size than if stands were initially thinned to a low density (O'Hara and Oliver 1988). Multiple light thinnings also preserve the potential to replace damaged or killed trees. However, the benefit of the ability to select ideal trees must be weighed against the increased levels of competition that the stand experiences while it is at higher densities, as well as increased costs of multiple entries.

The primary objective of this study was to evaluate long-term precommercial thinning effects on tree size and form, as well as stand growth and yield. We analyze data from a *Larix occidentalis* Nutt. (western larch) density management experiment in northwestern Montana, USA. The long-term post-treatment response period (54 years) and well-replicated design (four blocks spanning a productivity gradient) allow for a rigorous investigation of long-term precommercial thinning effects. A secondary objective is to analyze and report tree- and stand-level characteristics of this experiment at nominal full-rotation age (62 years from stand initiation). We ask two research questions which guide our statistical analyses.

1. How does stand density affect tree- and stand-level attributes 54 years after one PCT treatment?
2. Do multiple precommercial thinning entries result in tree and stand attributes that differ from those resulting from a single entry?

2. Methods

2.1. Study sites and treatments

The Western Larch Density Management Study (WLDMS) was established by USDA Forest Service research scientists in 1961 (Schmidt 1964). Four study sites (blocks) with similar initial stocking and topo-edaphic conditions (Table 1) were chosen to capture the *Larix occidentalis* productivity gradient in northwestern Montana (Fig. 1). All sites were harvested using even-aged methods between 1951 and 1953 (Table 1) and regenerated naturally in the good *Larix occidentalis* seed years of 1952 and 1954 (Schmidt 1964), resulting in even-aged populations of *Larix occidentalis* at all sites. This resulted in high densities (25 000 to 63 000 trees·ha⁻¹) of primarily *Larix occidentalis*, but included lesser amounts of *Picea engelmannii* Parry ex Engelm. (Engelmann spruce), *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco (interior Douglas-fir), *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), and *Betula papyrifera* Marshall. (paper birch) (Schmidt 1964).

Treatment plots (experimental units) were established at each site between the summer of 1961 and the winter of 1962. The stand age at initial treatment was 9 years for two of the sites and 7 years for the other two (Table 1), so a mean age of 8 years was used as the age of initial treatment. Treatment plots are square 20.12 m × 20.12 m plots surrounded by a buffer of at least 10 to 20 m that was thinned with the same treatment (Fig. 1). Thinning treatments were randomly assigned to each plot. Treatments included a core 3 × 3 factorial design, which was replicated once at all four study sites. The core treatments consisted of three different target densities (spacing): 494 trees·ha⁻¹ (4.6 m × 4.6 m), 890 trees·ha⁻¹ (3.6 m × 3.6 m), and 1680 trees·ha⁻¹ (2.4 m × 2.4 m). These three densities were chosen in 1961 to test proposed ideal densities at which to grow *Larix occidentalis* (Schmidt and Shearer 1961). These densities were achieved with three different thinning schedules (hereafter referred to as entries): one-entry, two-entry, or four-entry treatments (Fig. 2). One-entry treatment plots were thinned directly to the target density in 1961. Two-entry plots were thinned to an intermediate density in 1961 and then to the final target

Table 1. Characteristics of the four study sites of the Western Larch Density Management Study.

Study site	Harvest date	Harvest method	Site preparation	Habitat type ^a	SDI maximum ^b	SI (m) ^c	Elevation (m)	Aspect (°)	Slope (%)
Coram 1	1951	Clearcut, seed-tree	Dozer piled, broadcast burn	<i>Abies lasiocarpa</i> – <i>Clintonia uniflora</i> , <i>Aralia nudicaulis</i> phase	496	24	1200	350	21
Coram 2	1951	Shelterwood	Broadcast burn	<i>Abies lasiocarpa</i> – <i>Clintonia uniflora</i> , <i>Aralia nudicaulis</i> phase	496	23	1200	300	25
Cottonwood Lakes	1953	Clearcut	Dozer piled, scarified, piles burned	<i>Abies lasiocarpa</i> – <i>Clintonia uniflora</i> , <i>Vaccinium caespitosum</i> phase	456	19	1450	355	20
Pinkham Creek	1953	Clearcut	Dozer piled, scarified, piles burned	<i>Abies lasiocarpa</i> – <i>Clintonia uniflora</i> , <i>Clintonia uniflora</i> phase	518	24	1475	65	20

Note: Reported aspects and slopes are site averages.
^aHabitat types described in Pfister et al. (1977).
^bStand density index (SDI) maximum was calculated using a stochastic frontier model (Kimsey 2013), which incorporates species composition, topo-edaphic factors, and climate variables and is reported in English units.
^cSite index (SI) was calculated with the *Larix occidentalis* equation from Milner 1992.

Fig. 1. (A) Map showing locations of the four blocks across the northwest portion of Montana that make up the Western Larch Density Management Study. The black stars are the study sites. There are two sites located relatively close to each other in Coram Experimental Forest, which are represented by one star. (B) Map of the Pinkham Creek study site. The solid squares are the 20.12 m × 20.12 m treatment plots and the dashed lines are the buffers that were thinned with the same treatment. (Map credit: Brian Battaglia.) [Colour online.]

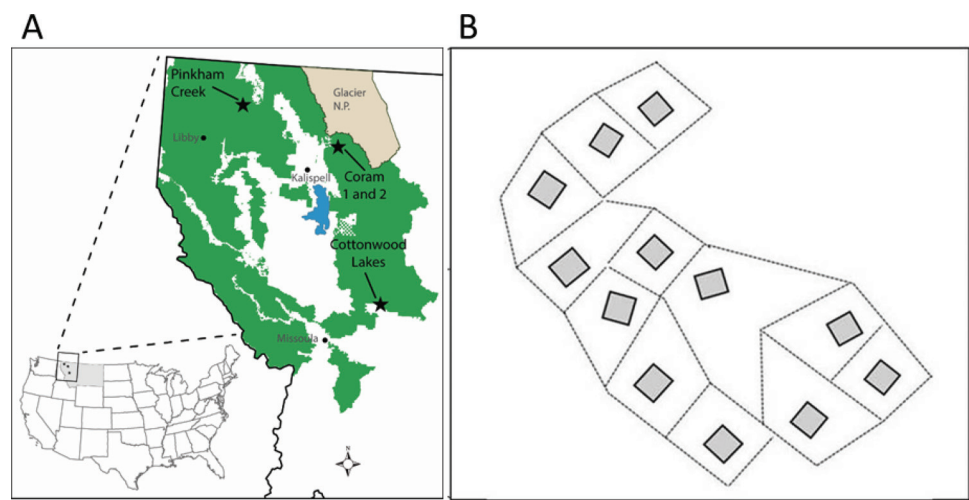


Fig. 2. The experimental design of the Western Larch Density Management Study. (A) The three number-of-entry pathways for achieving the 494 trees·ha⁻¹ target density. The x axis shows both stand age and the calendar year. Years in grey indicate years in which thinnings occurred. Note that all three pathways converge by 1991, the date of the final thinning in the four-entry pathway. While all treatments achieve the same final density, trees experienced different amounts of competition depending on the number of entries, with multiple-entry treatments developing for longer times at high stand densities. (B and C) The 890 trees·ha⁻¹ and 1680 trees·ha⁻¹ target density treatments, respectively. Note that the magnitudes of the thinnings are different depending on the final target density. This shows why the experimental factors have been nested and are being treated as nine separate treatments. [Colour online.]

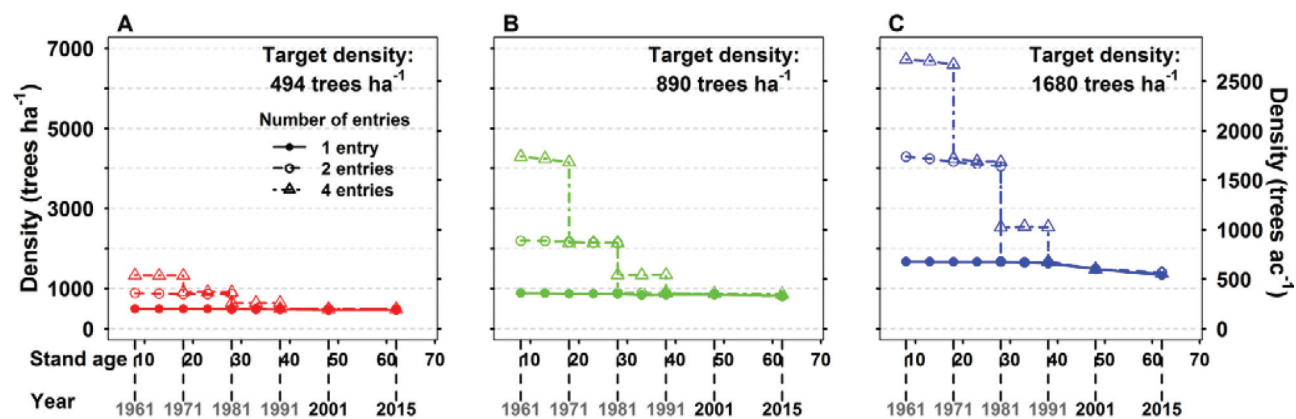
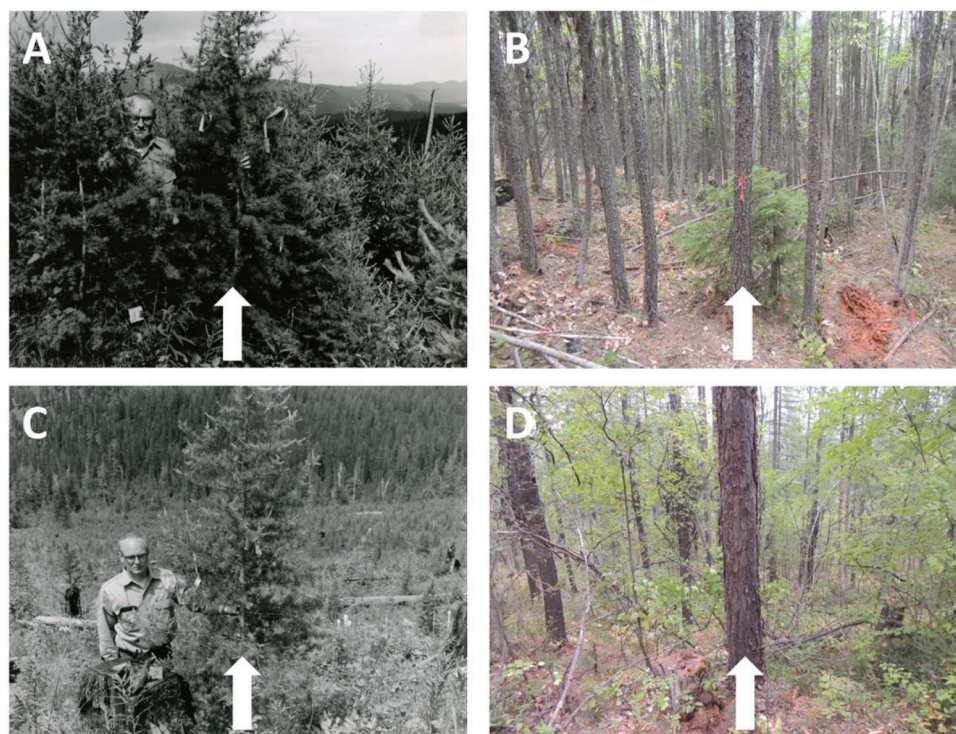


Fig. 3. (A) Photo of the unthinned stand at Coram 2 at the initiation of the study in 1961. Stand density was 47 500 trees·ha⁻¹. (B) Photo of the same stand in 2015 when stand density was 4200 trees·ha⁻¹. The white arrows point at the same tree in A and B. (C) Photo of a tree in the 494 trees·ha⁻¹, one-entry treatment at Coram 2 in 1961 and (D) the same tree in 2015. The white arrows point at the same tree in C and D. For each pairing, the photos were taken from the same permanently marked photo point at the same distance from the tree. [Colour online.]



density in 1981. Four-entry plots were thinned to progressively lower densities in 1961, 1971, and 1981 and then thinned to the final target density in 1991. The different number of entries created a gradient of competition pathways by which stands reached the final target density. Within a target final density, one-entry treatments experienced low levels of competition while four-entry treatments experienced much higher levels of competition (Fig. 2). Thinnings were from below, removing small and damaged trees. All cut material was left on site. During the initial thinning in 1961, all shrubs were cut in all thinned plots. Unthinned plots (shrubs not cut) and a very low density one-entry treatment (272 trees·ha⁻¹, 6.1 m × 6.1 m, single thinning in 1961) were installed at the Coram 1 and Coram 2 sites.

2.2. Measurements

All trees inside each treatment plot were tagged. In the unthinned plots, trees were not tagged, rather all trees within 10 systematically located 4.05 m² permanent subplots were measured. Tree growth was measured on a 5-year cycle for the original 40-year duration of the study: 1961, 1966, 1971, 1976, 1981, 1986, 1991, and 2001. All tagged trees in treated plots were measured, as were each of the trees in the 4.05 m² subplots within the unthinned plots. The 1996 measurement was missed for all plots, and the 2001 measurement was missed for just the unthinned plots. All plots were remeasured in 2015, yielding 54 years of post-treatment data. Tree measurements included dbh (stem diameter at 1.37 m), total height, crown base height (defined as the height to the lowest live whorl), height to the widest point in the crown, and crown width at two perpendicular axes.

2.3. Data reduction

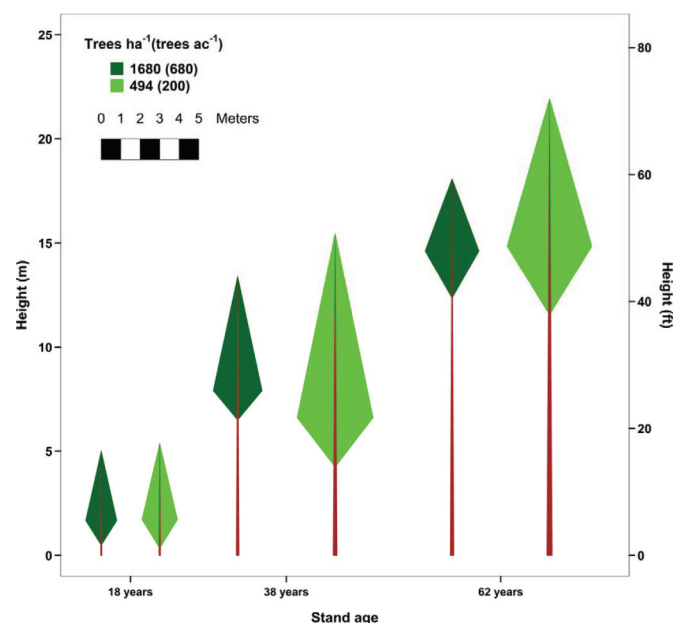
Plot-level averages were calculated for several response variables, including quadratic mean diameter (QMD), mean height, top height (defined as the mean height of the tallest 100 trees·ha⁻¹), $H:D_{200}$, and crown volume. We used the coefficient of variation

(CV) to characterize tree height variation (i.e., stand differentiation) within treatment plots, as recommended (McGown et al. 2016). Crown volume, which has been linked to tree photosynthetic capacity (Biging and Dobbertin 1992; Burkhart and Tomé 2012), was modeled as the sum of two cones, one right-side up and the other upside down, calculated from measurements of total height, crown base height, height to widest point in the crown, and crown width. Measurements of dbh and height were applied to the equations of Flewelling and Ernst (1996) to calculate per-tree total cubic volume of stem wood from the ground to the tip of the trunk, which was summed per plot and expanded to a stand-level value (expressed as m³·ha⁻¹). Net periodic annual increment (PAI) of total cubic volume (expressed as m³·ha⁻¹·year⁻¹) was calculated from 2001 to 2015 (1991 to 2015 for the unthinned plots). Merchantable cubic volumes were calculated using the taper profile equations of Flewelling and Ernst (1996) for the merchantable portion of the bole from a 0.3 m stump to two minimum merchantable top diameters common in the Northern Rockies (volume to a 11.4 cm (4.5 in.) top and to a 15.2 cm (6 in.) top).

Stand density index (SDI; Reineke 1933) was calculated for each plot using the stand density at the time of measurement and QMD. SDI was then converted to relative density (RD; sensu Drew and Flewelling 1979) by relativizing SDI to a percentage of maximum SDI. Maximum SDI (Table 1) was calculated for each site using a stochastic frontier model that incorporates species composition, topo-edaphic factors, and climate variables (Kimsey 2013). This was done because maximum SDI values for *Larix occidentalis* are poorly established in the literature and because maximum SDI may vary by site quality (Jack and Long 1996). Annual mortality rates for the period of 2001 to 2015 (1991 to 2015 for unthinned plots) were calculated as a percentage using the following annual compounding equation:

$$(1) \quad m = 1 - [1 - (M_1/N_0)]^{1/t}$$

Fig. 4. Mean crown and stem form of trees of two differing densities (494 trees·ha⁻¹ and 1680 trees·ha⁻¹) thinned in one entry to the target densities at age 8 years. Trees from the lower density plots (light green in online version) show much larger crowns, greater height, and greater diameter than trees from the higher density plots. The shapes of the crowns were drawn from the treatment mean values for total height, crown base height, height to the widest point in the crown, and crown width (mean of two perpendicular measurements). Stems were drawn using mean total height and QMD. Diameter at root collar was calculated using the principle of triangles of equal proportion. Figures are drawn to scale in both the horizontal and vertical dimensions. [Colour online.]



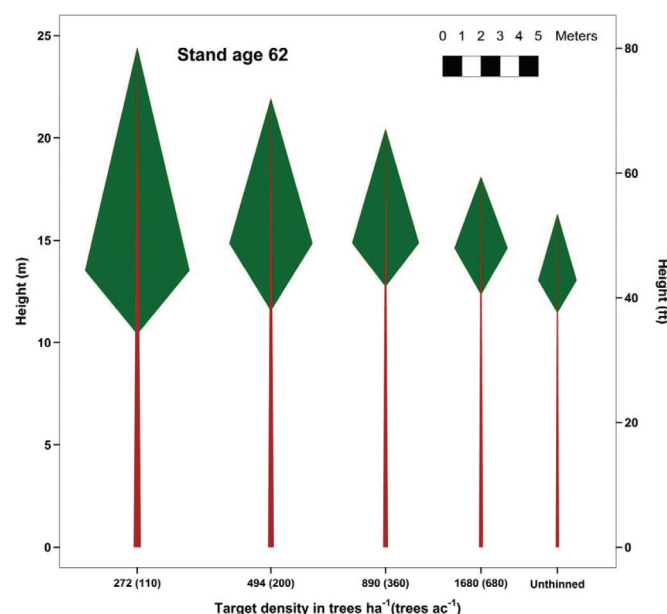
where N_0 is the number of trees alive at the time of previous measurement, M_1 is the number of trees that died between the previous measurement and the current measurement, and t is the number of years between measurements (Larson and Franklin 2010).

2.4. Statistical analysis

Statistical analysis was completed using the 2015 (stand age 62 years) measurements. Data were analyzed for the fully replicated nine experimental treatments: three densities (494, 890, and 1680 trees·ha⁻¹) crossed with the three different thinning schedules. The low-density treatment (272 trees·ha⁻¹ via one thinning) and the unthinned plots are graphically presented but were not statistically analyzed due to their low replication ($n = 2$).

For this experimental design, the number of thinnings factor is nested within the target density factor. In other words, the intensity of intermediate thinnings (the number of trees removed) depended on the final target density (Fig. 2). Because of this nested design, 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 (Schaedel et al. 2017). The resulting explanatory variable was a factor with nine levels (three entries $\times$ three target densities). Once a significant result was discovered in the omnibus ANOVA test, we used linear contrasts to test our specific research questions. To examine how density in once-thinned stands affected tree- and stand-level variables, we used two linear contrasts: the first contrast compared the 1680 trees·ha⁻¹ density with the 890 trees·ha⁻¹ and the 494 trees·ha⁻¹ densities, the second compared the 890 trees·ha⁻¹

Fig. 5. Mean crown and stem form at stand age 62 years for *Larix occidentalis* stands thinned at stand age 8 years with one entry to different target densities. Crowns and stems were drawn using the same methods as in Fig. 4 and are drawn to scale in both the horizontal and vertical dimensions. [Colour online.]



density with the 494 trees·ha⁻¹ density. The last two densities most closely represent the current management zone for *Larix occidentalis* in the Northern Rockies and Inland Northwest and so were of high interest. To evaluate the effect of the number of entries within each of the three target densities, we tested two contrasts: (i) the one-entry treatment against the two- and four-entry treatments and (ii) the two-entry treatment against the four-entry treatment. All statistical analyses were conducted using R 3.2.4 (R Core Team 2016). The multcomp (Hothorn et al. 2014) package was used to implement the linear contrasts, and Bonferroni corrections were applied to ensure family-wide type I error rates of 0.05.

3. Results

3.1. Long-term trends of tree size and stand yield

Most trends in tree-level attributes diverged by density early in the experiment, and the effect of density on tree size was obvious by stand age 62 years (Figs. 3, 4, and 5). QMD differentiated rapidly by density, where lower density stands had much larger tree diameters (Supplementary Fig. S1¹). The QMD of unthinned plots increased much more slowly than that of any of the thinned plots (Supplementary Fig. S1¹). By stand 62 years, the 272 trees·ha⁻¹ treatment had a QMD nearly four times greater than that of unthinned stands (Table 2; Fig. 4). Differences in diameter between the tested densities were significant at stand age 62 years ($P < 0.001$; Table 3).

Mean tree height showed similar trends to QMD, with low-density plots having greater mean heights than high-density plots (Table 2; Fig. 4; $P = 0.003$). Top height followed a different pattern (Fig. 6). Top height decreased along the gradient of increasing competition created by the treatments early in the experiment, but differences were relatively small until stand age 38 years, after which differences in top height became significant ($P = 0.0159$; Fig. 6D; Table 3). $H:D_{200}$ separated by density early in the experiment (Fig. 7), with denser stands having higher $H:D_{200}$ as early as

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2017-0074>.

Table 2. Tree-level variables 54 years after treatment for *Larix occidentalis* thinned to different target densities with different numbers of entries to achieve those densities.

Target density (trees·ha ⁻¹)	Thinning entries	QMD (cm)	Mean height (m)	Top height ^a (m)	Mean tree volume ^b (m ³)	Height: diameter ratio ^c	Live crown ratio (%)	Mean tree crown volume (m ³)
272	1	34.0 (1.4)	24.4 (0.6)	24.3 (1.0)	0.78 (0.03)	70 (2.3)	57 (5.3)	119.52 (41.78)
494	1	26.8 (1.3)	21.9 (1.5)	23.5 (1.6)	0.47 (0.08)	77 (2.6)	47 (4.7)	54.81 (8.29)
	2	26.9 (1.6)	22.5 (1.9)	24.8 (1.6)	0.49 (0.08)	78 (4.5)	43 (3.4)	50.19 (8.53)
	4	25.7 (1.4)	22.6 (1.9)	23.6 (1.6)	0.45 (0.08)	81 (2.7)	43 (3.9)	53.50 (4.72)
	Mean	26.4 (0.8)	22.3 (0.9)	24.0 (0.9)	0.47 (0.04)	79 (1.9)	44 (2.2)	52.83 (3.91)
890	1	22.4 (1.3)	20.4 (2.1)	23.0 (2.0)	0.33 (0.06)	83 (3.9)	38 (2.9)	27.93 (3.85)
	2	21.0 (1.0)	19.9 (1.6)	22.5 (1.2)	0.27 (0.04)	86 (3.7)	35 (2.8)	22.64 (4.61)
	4	19.7 (1.7)	19.5 (2.2)	22.0 (2.2)	0.25 (0.06)	89 (2.2)	39 (2.5)	27.24 (8.02)
	Mean	21.0 (0.8)	20.0 (1.1)	22.5 (1.0)	0.28 (0.03)	86 (1.9)	37 (1.5)	25.94 (3.10)
1680	1	18.1 (1.2)	18.1 (2.0)	21.6 (1.8)	0.20 (0.05)	90 (3.8)	32 (1.6)	15.54 (4.75)
	2	17.1 (1.8)	18.0 (2.5)	20.5 (2.7)	0.18 (0.05)	88 (5.7)	32 (2.3)	14.59 (3.59)
	4	16.4 (1.4)	17.5 (1.7)	21.6 (1.6)	0.16 (0.04)	92 (5.8)	33 (2.0)	14.65 (2.80)
	Mean	17.2 (0.8)	17.9 (1.1)	20.8 (1.2)	0.18 (0.03)	90 (2.8)	32 (1.0)	14.92 (1.99)
Unthinned	0	8.7 (0.4)	10.4 (0.6)	19.1 (1.2)	0.11 (0.02)	107 (3.3)	29 (0.1)	6.45 (1.12)

Note: The reported values are means (standard errors). QMD, quadratic mean diameter.

^aMean height of the tallest 100 trees·ha⁻¹.

^bTotal cubic stem volume from ground level to tip of the tree.

^cHeight-to-diameter ratio of the 200 largest trees·ha⁻¹.

Table 3. The analysis of variance (ANOVA) results for tree- and stand-level variables for *Larix occidentalis* thinned to different target densities with different numbers of thinning entries.

Variable	Treatment df	Error df	Model MS	Error MS	F	Prob > F
QMD	8	24	67.66	2.18	31.05	<0.001
Mean height	8	24	15.53	2.04	7.61	<0.001
Top height	8	24	8.71	2.84	3.06	0.0159
H:D ₂₀₀	8	24	119.12	10.27	11.60	<0.001
Crown volume	8	24	1154.99	75.06	15.39	<0.001
Total cubic volume	8	24	1947.00	1912.00	1.02	0.449
Cubic volume PAI ^a	8	24	0.10	1.86	0.54	0.818
Merchantable volume (11.4 cm (4.5 in.) top)	8	24	3196.00	1875.00	1.70	0.149
Merchantable volume (15.2 cm (6 in.) top)	8	24	8218	1902	4.32	0.002

Note: The results for the blocking variable are not shown, but block effects were large for every variable. QMD, quadratic mean diameter.

^aCubic volume periodic annual increment (PAI) is for the period of stand age 48–62 years.

age 18 years (10 years after treatment). These differences stayed relatively constant throughout the experiment, but H:D₂₀₀ continued to increase with time across all plots (Fig. 7) and differences were significant at stand age 62 years ($P < 0.001$; Table 3).

Relative variability of tree height as measured by coefficient of variation (CV_{ht}) decreased through time in all thinned treatments (Fig. 8). CV_{ht} reached minima in most stands at the 1991 measurement (35 years after initial treatment), then either was stable after 1991 or increased slightly between 1991 and 2001, and then stabilized between 2001 and 2015. CV_{ht} was markedly higher and followed a different trajectory in the unthinned stands (Fig. 8). In the unthinned stands, CV_{ht} increased during the first measurement interval and then subsequently declined. In the 2015 measurement, CV_{ht} increased with increasing relative density across all thinned and unthinned treatments (Fig. 8D). Results were nearly identical for CV_{dbh} (Supplementary Fig. S2¹).

Stand-level attributes exhibited different temporal trajectories compared with tree-level attributes. Early in stand development, plots with higher density had higher basal area and total cubic volume (Fig. 9), with unthinned stands having the highest value for both variables. However, with time, basal area and total cubic volume of the 890 and 1680 trees·ha⁻¹ plots surpassed those of the unthinned plots, while lower density plots continued to have lower total cubic volume. However, at stand age 62 years, differences in cubic volume were not significant ($P = 0.449$; Table 3). PAI of total cubic volume peaked early in the higher density stands, and both the unthinned and 1680 trees·ha⁻¹ stands declined below peak levels. Stands with 890 and 494 trees·ha⁻¹ initially had lower

PAI values but continued to increase through stand age 62 years such that at age 62 years differences in volume PAI were not significant ($P = 0.818$; Table 3). The low-density 272 trees·ha⁻¹ plots had much lower PAI values than the other thinned stands.

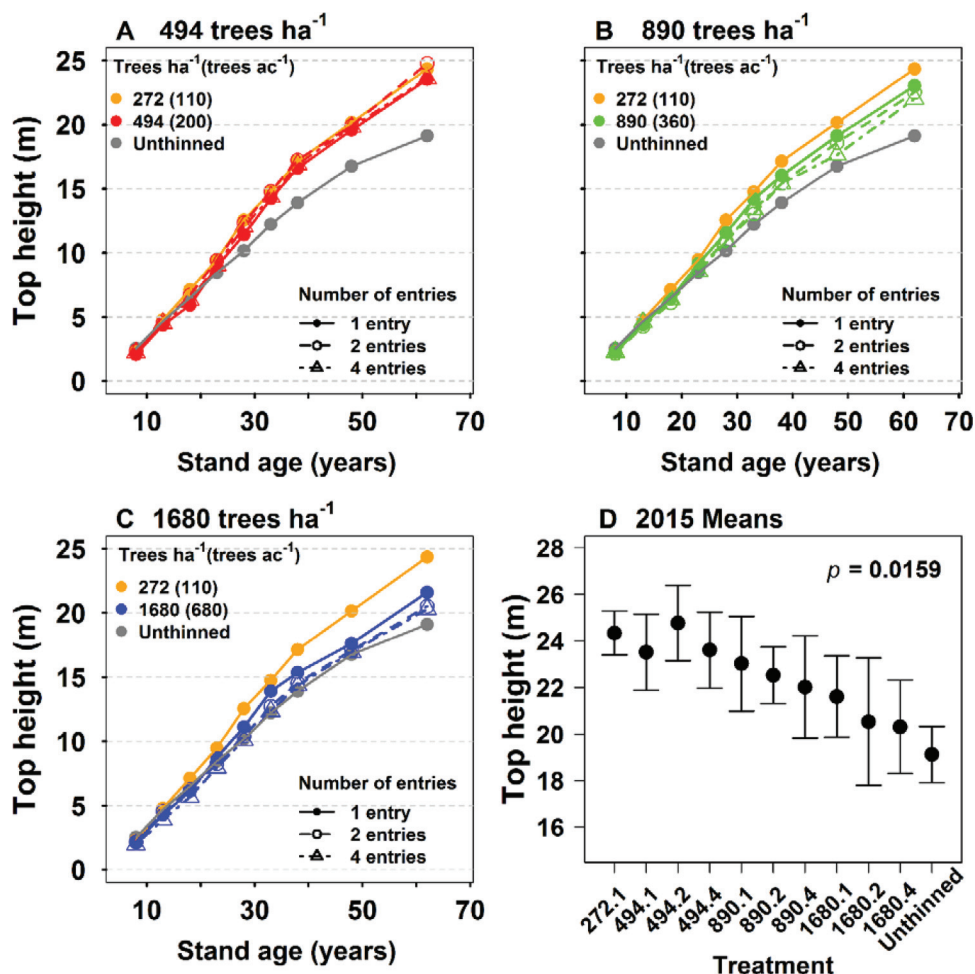
Trends in merchantable volume were highly dependent on the utilization standard (minimum top diameters inside bark) that was used (11.4 cm top versus 15.2 cm top; Fig. 10). When a 11.4 cm top was used, the 272 trees·ha⁻¹ treatment initially had the highest volume but was rapidly surpassed by the 890, 494, and 1680 trees·ha⁻¹ densities (Fig. 10A). The 890 trees·ha⁻¹ treatment had the greatest merchantable volume throughout the majority of the experiment, while the 1680 and 494 trees·ha⁻¹ treatments were lower but quite similar to each other. The differences in merchantable volume to an 11.4 cm top were not significant ($P = 0.149$; Table 3). The 272 trees·ha⁻¹ density had lower merchantable volume than the core densities, and the unthinned treatments had the lowest merchantable volumes in 2015 (Fig. 10A). Merchantable volume to a 15.2 cm top was substantially less than merchantable volume to an 11.4 cm top in the 1680 trees·ha⁻¹ treatment. Differences in merchantable volume to a 15.2 cm top between the tested densities were significant ($P = 0.002$; Table 3). The unthinned plot had no merchantable volume that meets the 15.2 cm top utilization standard (Fig. 10B).

3.2. Effects of stand density in once-thinned treatments

3.2.1. Tree-level attributes

Quadratic mean diameter (QMD) differed significantly among the one-entry core target densities ($P < 0.001$). QMD was inversely

Fig. 6. Top height (defined as the mean height of the tallest 100 trees·ha⁻¹) through time by target density for all treatments. All panels include the unthinned treatment (grey) and 272 trees·ha⁻¹ density treatment (orange in online version) to serve as reference. (A) Top height for all three thinning schedules (target density achieved through one, two, or four entries) for the 494 trees·ha⁻¹ target density. (B and C) Top height for all three thinning schedules of the 890 trees·ha⁻¹ and 1680 trees·ha⁻¹ target densities, respectively. (D) Top height means for all treatments in 2015. Error bars are equal to one standard error of the mean. The x axis describes the treatment: the target density is before the period and the number of thinnings is after the period. The *P* value of 0.0159 is the result of the omnibus ANOVA test, indicating that there is a significant treatment effect. [Colour online.]



related to stand density (Table 2). Among the tested densities at stand age 62 years, QMD was 26.8 cm, 22.4 cm, and 18.1 cm for the 494 trees·ha⁻¹, 890 trees·ha⁻¹, and 1680 trees·ha⁻¹, respectively, and the differences in QMD between all levels were significant. The effect of density on mean tree height was also significant ($P < 0.003$; Table 4). Mean tree height increased as density decreased, with the 1680 tree·ha⁻¹ treatment having significantly lower heights than the 890 and 494 trees·ha⁻¹ treatments ($P < 0.003$; Table 4); the difference between the 890 and 494 trees·ha⁻¹ treatments was not significant ($P = 0.30$; Table 4). Mean tree height included all trees in a plot; therefore, higher density stands, which had a greater number of trees in subordinate crown classes, were expected to have lower mean heights than low-density stands. Top height within the one-entry treatments decreased with increasing density, but differences were not significant ($P = 0.269$; Table 4).

$H:D_{200}$ was significantly affected by density in the one-entry treatments ($P < 0.001$; Table 4). The lower density plots had lower average $H:D_{200}$, with 494 tree·ha⁻¹ ratios 6.8 units smaller than the 890 tree·ha⁻¹ ratios and 13.4 units less than the ratios of 1680 tree·ha⁻¹ density; all contrasts were significant.

Average crown volume per tree increased significantly with decreasing target density (Fig. 5; $P < 0.001$). Crowns were approximately twice as large in the 494 trees·ha⁻¹ treatment as they were

in the 890 trees·ha⁻¹ treatment and more than three times larger than the 1680 trees·ha⁻¹ treatment (Fig. 5; Table 4).

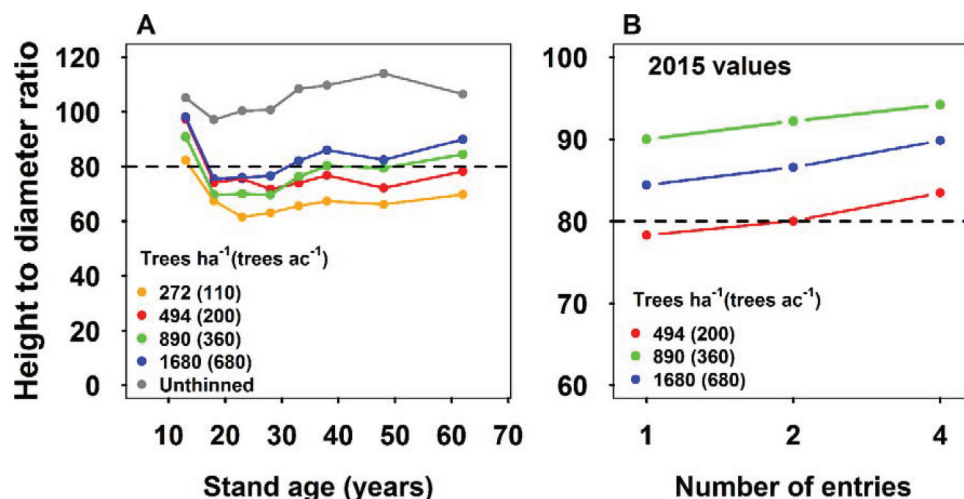
3.2.2. Stand-level attributes

Total cubic volume of stem wood from the ground to the tip of the tree was not significantly affected by density ($P = 0.244$) in the one-entry treatments. It is clear from graphical representation (Figs. 9A–9C) that by stand age 62 years, cubic volume was greater for the three core densities than it was for the 272 trees·ha⁻¹ density and the unthinned plots.

Merchantable volume (in m³·ha⁻¹) to an 11.4 cm top of the one-entry treatments followed the same trend as the total cubic volume: 890 tree·ha⁻¹ plots had the highest merchantable volume (Table 5), but differences due to density were not significant ($P = 0.421$; Table 4). Merchantable volume to a 15.2 cm top showed the same trend as the merchantable volume to a 11.4 cm top, and the differences due to density were significant ($P = 0.002$; Table 3). Merchantable volumes of both the 890 trees·ha⁻¹ and 494 trees·ha⁻¹ densities were significantly greater than the 1680 trees·ha⁻¹ density ($P < 0.05$; Table 4), but the 890 trees·ha⁻¹ and 494 trees·ha⁻¹ densities were not significantly different from each other (Table 4).

Relative density in 2015 increased with density and ranged from 23.5% in the 272 trees·ha⁻¹ to 70.0% in the unthinned treatments

Fig. 7. (A) Height-to-diameter ratio of the largest diameter 200 trees·ha⁻¹ ($H:D_{200}$) for all densities thinned once. The dashed line represents the 80:1 ratio suggested as a threshold of stability for *Larix occidentalis* by Wonn and O'Hara (2001). Values above the 80:1 threshold indicate that stands are at an elevated risk for stem breakage due to wind and snow loading, both of which have been reported to cause high levels of damage to *Larix occidentalis* stands (Schmidt et al. 1976; Wonn and O'Hara 2001). (B) An interaction plot showing 2015 $H:D_{200}$ for the tested densities at all three numbers of entries. The figure shows that stands left at higher densities for longer do not recover low height-to-diameter ratios for many years after thinning, if at all. [Colour online.]



(Table 5). Between 1991 and 2001, the 1680 trees·ha⁻¹ treatment crossed the threshold of 55% relative density (Fig. 11), which was proposed by Drew and Flewelling (1979) as the onset of competitive mortality for *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coast Douglas-fir), also known as the zone of imminent competition mortality (ZICM). By 2015, the 890 trees·ha⁻¹ density had also crossed into the ZICM. Crossing into the ZICM coincided with an increase in mortality in the 1680 trees·ha⁻¹ density to 0.86%·year⁻¹ (Fig. 11; Table 5), which was higher than the 890 (0.16%·year⁻¹) or 494 (0.00%·year⁻¹) tree·ha⁻¹ treatments during the 2001–2015 measurement interval.

Current PAI (2001 to 2015) in the one-entry treatment was highest in the 890 trees·ha⁻¹ density at 6.41 m³·ha⁻¹·year⁻¹, but differences between the core densities were small and not significant (Table 5; Fig. 12; $P = 0.7917$).

3.3. Effect of number of entries within density

3.3.1. Tree-level attributes

The effect of the number of entries within a given target density was not significant for any of the response variables tested. For QMD, within the 494 and 1680 trees·ha⁻¹ densities, there was no significant effect of the number of thinning entries ($P < 0.43$ and $P < 0.29$, respectively; Table 4); however, there was suggestive evidence of a difference between the one-entry and two- or four-entry treatments in the 890 trees·ha⁻¹ target density ($P = 0.06$; Table 4). In the 890 trees·ha⁻¹ and 1680 trees·ha⁻¹ densities, QMD decreased as the number of thinning entries increased (Table 2). It was notable that the pattern was different for the different number of entries within the 494 trees·ha⁻¹ density. While differences were nonsignificant, QMD was nearly constant for the one- and two-entry treatments and then declined in the four-entry treatment. The number of entries did not significantly affect mean height ($p = 0.8229$; Table 4). The effect of the numbers of entries factor on top height was not significant and showed a similar pattern to that of mean tree height.

3.3.2. Stand-level attributes

The effect of number of entries was not significant for any of the stand-level attributes (total cubic volume, PAI of total cubic volume, merchantable volume to an 11.4 or 15.2 cm top, and relative density; Table 4). The effect of each the number of entries on each

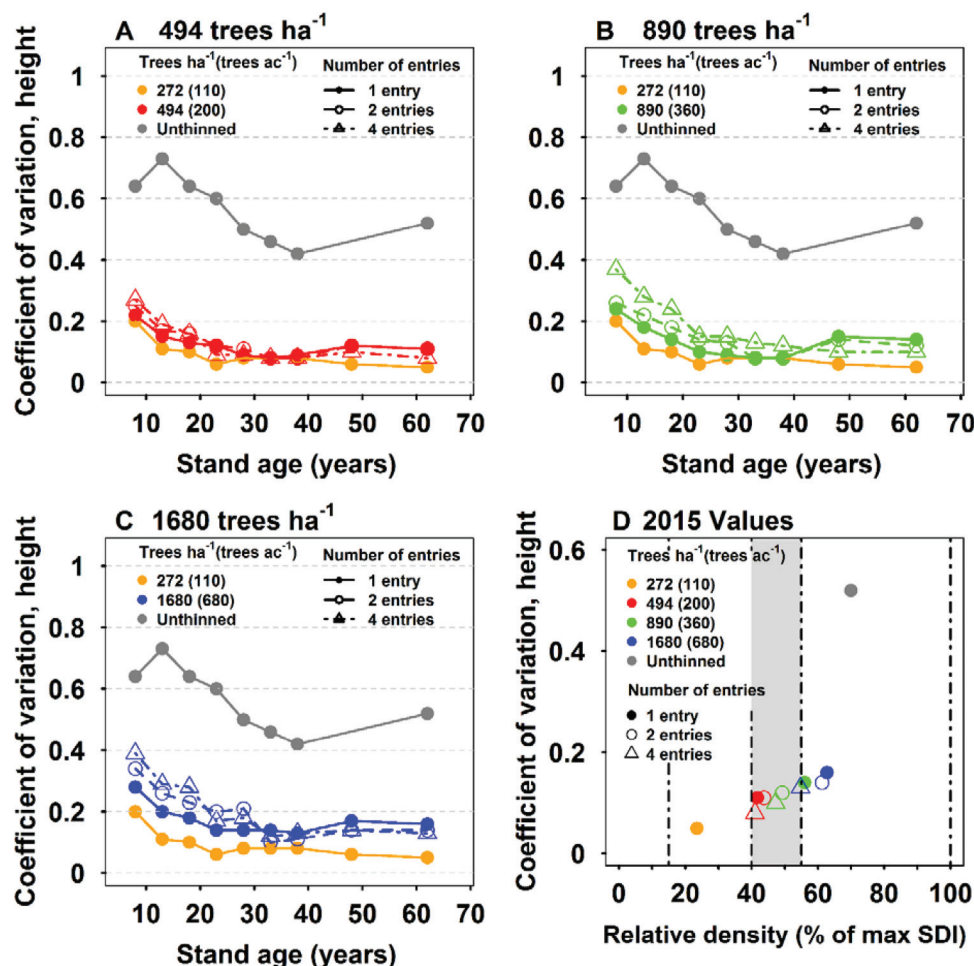
variable generally parallels that of QMD and top height; in the 890 and 1680 trees·ha⁻¹ densities, the volume (total cubic or merchantable) decreased as the number of entries increased, whereas in the 494 trees·ha⁻¹, cubic volume peaked in the two-entry treatment, but these trends were not significant.

4. Discussion

Our analysis of this long-term experiment indicates that net stand yield (total live cubic wood volume at the final measurement) converges to similar values across a wide range of target stand densities when thinning is applied early in stand development (<10 years after stand initiation). At stand age 62 years, the primary effect of early PCT was to control whether volume is concentrated on few large trees or distributed across many small trees (see also Schaedel et al. 2017). After 54 years of post-thinning growth, the three tested densities (494, 890, and 1680 trees·ha⁻¹) did not have significant differences in total cubic volume. This indicates that while early in stand development volumes may be driven largely by stand density, by 54 years after thinning, those differences disappear (Fig. 9). In fact, very high density plots may contain less volume than lower density plots (Fig. 9), as suggested by graphical analysis of the unthinned plots, and similar results were found in another long-term PCT study (Pitt and Lanteigne 2008). Many effects of density management cannot be extrapolated from short-duration studies, highlighting the value of long-term studies such as this 54-year-old experiment for demonstrating outcomes obtainable with early PCT (Schaedel et al. 2017).

A second important finding is that top height was sensitive to the competition gradient created by the experimental treatments (Table 2; Fig. 7). While the magnitude of the effect of density on QMD is much larger than the effect on top height, as expected, a decrease in top height has strong implications for yield. A decrease in top height has similar effects on volume accumulation as a decrease in site productivity, which is often estimated with top height, e.g., site index (King 1966). Increases in factors related to tree instability such as $H:D_{200}$ may also act to increase noncompetitive mortality and decrease yield at higher densities (Wonn and O'Hara 2001). In other words, 54 years after thinning, significantly larger tree size and greater tree stability at lower densities

Fig. 8. Coefficient of variation of height (CV_{ht}) through time by target density for all treatments. All panels include the unthinned treatment (grey) and 272 trees·ha⁻¹ density treatment (orange in online version) to serve as reference. (A) CV_{ht} for all three thinning schedules (target density achieved through one, two, or four entries) for the 494 trees·ha⁻¹ target density. (B and C) CV_{ht} for all three thinning schedules of the 890 trees·ha⁻¹ and 1680 trees·ha⁻¹ target densities, respectively. (D) The relationship of 2015 relative density to the 2015 CV_{ht} means for all treatments. Relative density for stands thinned once calculated as percentage of maximum stand density index (SDI) (Drew and Flewelling 1979). The canopy closure line, at 15% relative density, indicates the beginning of intertree competition. The gray band, between relative densities of 40% and 55%, identifies the zone of maximum stand volume growth. The zone of imminent competition mortality (ZICM; sensu Drew and Flewelling 1979), where mortality due to self-thinning begins, is defined by the line at 55% relative density. [Colour online.]



compensated for fewer trees, resulting in no significant difference in total cubic volume across a gradient of stand density.

4.1. Stand growth and yield

A constant yield of total cubic volume has been seen in other long-term studies of shade-intolerant *Pseudotsuga menziesii* (Reukema 1979), *Pinus taeda* (Peet and Christensen 1987), and *Pinus ponderosa* (Cochran and Barrett 1993), as well as more shade-tolerant *Abies balsamea* and *Picea rubens* (Pitt and Lanteigne 2008). Short-term results of most PCT and spacing studies generally show that yield is proportional to density (Seidel 1987; Schmidt and Seidel 1988; Harrington et al. 2009), indicating reduced stand-level volume increment while trees initially do not fully occupy the site in the first years after treatment. Early in stand development, it is common to see PAI of cubic volume highest at high densities (Harrington et al. 2009) and then converge across a wide range of stand densities (Pitt and Lanteigne 2008; McLeod 2012), as was found in this study. Intermediate-density stands may have greater yields than high-density stands as the higher density stands enter the ZICM and some volume growth is lost to mortality (Harrington et al. 2009). Other studies showed that age at which a stand is thinned plays an important role in long-term growth and yield;

early thinning can lead to smaller reductions in yield than later thinnings (Varmola and Salminen 2004).

Our results suggest that the size-density and growth relationships proposed by Drew and Flewelling (1979) hold for *Larix occidentalis* (Fig. 12). As trees at a given density grow in diameter, their relative density (SDI/maximum SDI) increases. Drew and Flewelling (1979) suggested that the zone of maximum volume increment for *Pseudotsuga menziesii* var. *menziesii* occurs across the range of 40% to 55% relative density (RD), and that within that range, stand-level growth is unaffected by density. Subsequent studies show that this proposed zone of maximum volume increment of 40% to 55% RD holds true for other tree species (Newton 1997). Our results suggest that the zone of maximum growth for *Larix occidentalis* may extend beyond RD 55% to approximately RD 65% (Fig. 12; Cochran and Seidel 1999). As high-density stands grow, they near the maximum size density relationship (Reineke 1933; Yoda et al. 1963; Drew and Flewelling 1979), the point at which some of the accumulated gross volume is lost due to mortality (Newton 1997). This may contribute to the long-term convergence of stand yield across different initial stocking levels

Fig. 9. Total cubic volume through time by target density for all treatments. All panels include the unthinned treatment (grey) and 272 trees·ha⁻¹ density treatment (orange in online version) to serve as reference. (A) Total cubic volume for all three thinning schedules (target density achieved through one, two, or four entries) for the 494 trees·ha⁻¹ target density. (B and C) Total cubic volume for all three thinning schedules of the 890 trees·ha⁻¹ and 1680 trees·ha⁻¹ target densities, respectively. (D) The cubic volume means for all treatments in 2015. Error bars are equal to one standard error of the mean. The x axis describes the treatment: the target density is before the period and the number of thinnings is after the period. The *P* value of 0.449 is the result of the omnibus ANOVA test, indicating that there are no significant differences in any of the tested treatments. [Colour online.]

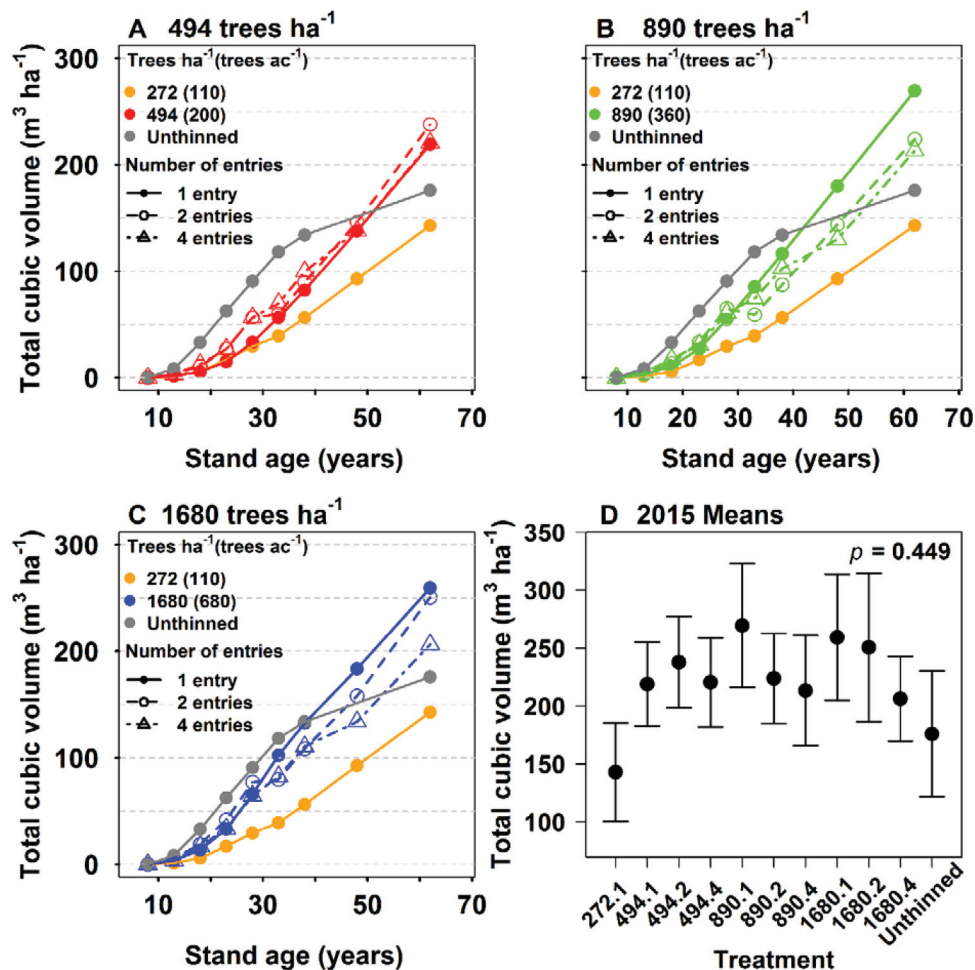


Fig. 10. Merchantable cubic volume for all densities thinned once for two utilization standards common in the Northern Rockies. (A) Merchantable volume up to an 11.4 cm (4.5 inches) top. (B) Merchantable volume up to a 15.2 cm (6 inches) top. [Colour online.]

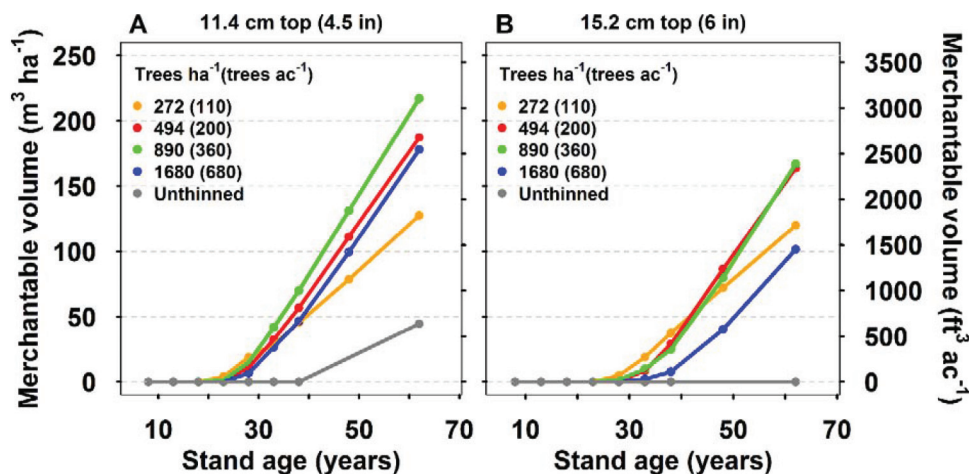


Table 4. Test results of the linear contrasts for tree- and stand-level attributes.

Contrast	Stand attribute									
	QMD ^a (cm)	Mean height (m)	Top height ^b (m)	MCRV ^c (m ³)	TCSV ^d (m ³)	PAI ^e (m ³ .ha ⁻¹ .year ⁻¹)	MV 11.4 cm top ^f (m ³ .ha ⁻¹)	MV 15.2 cm top ^g (m ³ .ha ⁻¹)	TCRV ^h (m ³ .ha ⁻¹)	H:D ₂₀₀ ⁱ
Density										
Once thinned stands										
1680 vs 890 and 494 trees·ha ⁻¹	-6.5***	-3.08**	-1.67	-25.83***	15.08	-0.69	-24.25	-63.88*	-4648	8.7***
890 vs 494 trees·ha ⁻¹	-4.4***	-1.51	-0.49	-26.88***	50.55	0.61	30.00	3.25	-2468	6.1*
Number of entries										
1680 trees·ha ⁻¹ : 1 vs 2 and 4 entries	1.3	0.36	1.18	0.92	30.82	-0.47	36.00	35.37	119	-3.2
1680 trees·ha ⁻¹ : 2 vs 4 entries	0.6	0.48	0.22	0.06	44.39	1.45	47.50	36.75	865	-2.0
890 trees·ha ⁻¹ : 1 vs 2 and 4 entries	2.1	0.71	0.75	2.99	50.86	0.57	49.50	61.37	2240	-3.8
890 trees·ha ⁻¹ : 2 vs 4 entries	1.3	0.40	0.51	-4.60	10.55	-0.25	12.00	14.25	-5122	-3.3
494 trees·ha ⁻¹ : 1 vs 2 and 4 entries	0.6	-0.61	-0.68	2.97	-10.27	-0.42	-9.125	-6.13	279	-3.4
494 trees·ha ⁻¹ : 2 vs 4 entries	1.2	-0.12	1.17	3.31	17.39	0.65	13.75	16.75	-1775	-3.4

Note: Values are the differences between the compared treatments. Significance codes (*P* values): *, *P* ≤ 0.05; **, *P* ≤ 0.01; ***, *P* ≤ 0.001.

^aQuadratic mean diameter at breast height.

^bMean height of the tallest 100 trees·ha⁻¹.

^cCrown volume of the average tree.

^dTotal cubic stem volume of live trees.

^ePeriodic annual increment of cubic stem volume from 2001 to 2015.

^fMerchantable cubic volume to a 11.4 cm (4.5 in.) top.

^gMerchantable cubic volume to a 15.2 cm (6 in.) top.

^hTotal crown volume·ha⁻¹.

ⁱHeight-to-diameter ratio of the 200 largest trees·ha⁻¹.

Table 5. Stand-level variables 54 years after treatment for *Larix occidentalis* stands thinned to different target densities with different numbers of entries to achieve those densities.

Target density (trees·ha ⁻¹)	Thinning entries	Basal area (m ² .ha ⁻¹)	Total cubic volume ^a (m ³ .ha ⁻¹)	Total cubic volume PAI ^b (m ³ .ha ⁻¹ .year ⁻¹)	MV 11.4 cm top ^c (m ³ .ha ⁻¹)	MV 15.2 cm top ^d (m ³ .ha ⁻¹)	Stand level crown volume (m ³ .ha ⁻¹)	Relative density ^e	Annual mortality ^f (%)
272	1	16.46 (4.26)	142.95 (42.55)	3.59 (0.56)	127.50 (35.50)	120 0.00 (34.00)	19 569 (361)	23.5 (6.5)	0 0.00 (0)
494	1	26.46 (2.84)	219.00 (36.22)	5.80 (1.05)	187.25 (34.55)	163.75 (35.07)	25 535 (4094)	41.8 (3.1)	0 0.00 (0)
	2	27.78 (2.92)	237.96 (39.34)	6.55 (0.87)	203.25 (37.35)	178.25 (38.13)	24 368 (3877)	43.8 (2.8)	0.09 (0.10)
	4	25.44 (2.84)	220.57 (38.56)	5.90 (1.00)	189.50 (35.62)	161.50 (37.23)	26 144 (2475)	41.0 (2.7)	0.00 (0)
	Mean	26.56 (1.52)	225.84 (20.05)	6.08 (0.52)	193.33 (18.85)	167.83 (19.36)	25 349 (1870)	42.1 (1.5)	0.03 (0.03)
890	1	32.98 (3.75)	269.55 (53.34)	6.41 (1.50)	217.25 (50.45)	167.00 (49.31)	23 067 (3043)	56.0 (4.0)	0.16 (0.16)
	2	28.38 (2.98)	223.96 (38.83)	5.71 (1.00)	173.75 (35.85)	112.75 (34.65)	18 266 (3451)	49.3 (3.4)	0.43 (0.16)
	4	26.77 (4.24)	213.42 (47.70)	5.96 (1.28)	161.75 (46.09)	98.50 (35.04)	23 388 (6941)	47.3 (5.3)	0.10 (0.10)
	Mean	29.38 (2.09)	235.64 (25.62)	6.03 (0.67)	184.25 (24.35)	126.08 (22.83)	21 574 (2608)	50.8 (2.5)	0.23 (0.09)
1680	1	34.27 (4.31)	259.35 (54.45)	5.42 (1.51)	178.00 (54.38)	101.50 (47.53)	19 653 (5142)	62.8 (5.0)	0.86 (0.32)
	2	32.78 (5.66)	250.73 (63.97)	6.61 (1.60)	165.75 (59.70)	84.50 (38.80)	19 967 (4514)	61.3 (7.5)	0.40 (0.16)
	4	28.52 (2.73)	206.33 (36.48)	5.16 (0.80)	118.25 (37.16)	47.75 (24.58)	19 102 (2159)	54.8 (3.73)	0.63 (0.30)
	Mean	31.86 (2.41)	238.80 (28.49)	5.73 (0.73)	154.00 (27.91)	77.92 (21.04)	18 892 (3148)	59.6 (3.1)	0.63 (0.15)
Unthinned	0	28.70 (6.21)	175.98 (54.23)	1.75 (0.12)	44.50 (15.50)	0.00 (0.00)	12 566 (3740)	70.0 (14.0)	4.34 (0.05)

Note: The reported values are means (standard errors).

^aTotal cubic stem volume of live trees.

^bCubic volume periodic annual increment (PAI) is for the period of stand age 48–62 years (ages 38–62 years for unthinned plots).

^cMerchantable cubic volume to a 11.4 cm (4.5 in.) top.

^dMerchantable cubic volume to a 15.2 cm (6 in.) top.

^eRelative density was calculated with the methods of Drew and Flewelling (1979). Stand density index (SDI) maximum was calculated using a stochastic frontier model (Kimsey 2013).

^fAnnual mortality rates for the period of 2001 to 2015 (1991 to 2015 for unthinned plots). Percentage calculated using an annual compounding equation.

(Reukema 1979; Peet and Christensen 1987; Marshall and Curtis 2002; Harrington et al. 2009).

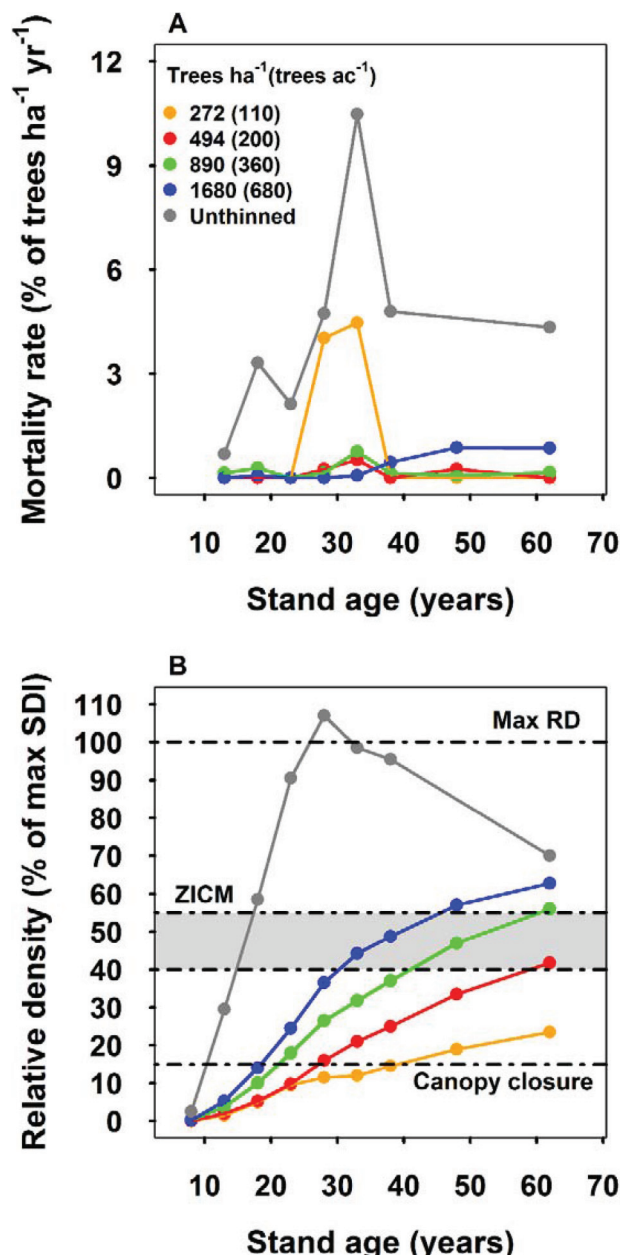
4.2. Tree size and form

Over the entire range of thinning treatments, top height was sensitive to competitive history (Fig. 6). When the stands were thinned directly to the three target densities in 1961, top height was not significantly sensitive to density (Fig. 6). However, stands that took multiple entries to reach the target density experienced much higher levels of competition early in stand development than stands that were thinned directly to the target density in one entry (Fig. 2). Top height can be significantly affected by extremes of stand density (Sjolte-Jorgensen 1967; Lanner 1985) and shade-intolerant species such as *Pinus radiata*, *Pinus resinosa*, *Pinus sylvestris*,

and *Pseudotsuga mesziesii* have shown greater height reductions at high densities than shade-tolerant species such as *Picea abies* (Sjolte-Jorgensen 1967). Top height growth was adversely affected in 14-year-old *Pinus contorta* at densities greater than 15 000 tree·ha⁻¹ (Mitchell and Goudie 1997). The densities of the intermediate thinning (up to 6700 trees·ha⁻¹; Fig. 2) in this study may represent density levels in which *Larix occidentalis* height growth is reduced and certainly the densities of the unthinned plots (up to 63 000 trees·ha⁻¹) cause height growth repression (Fig. 6).

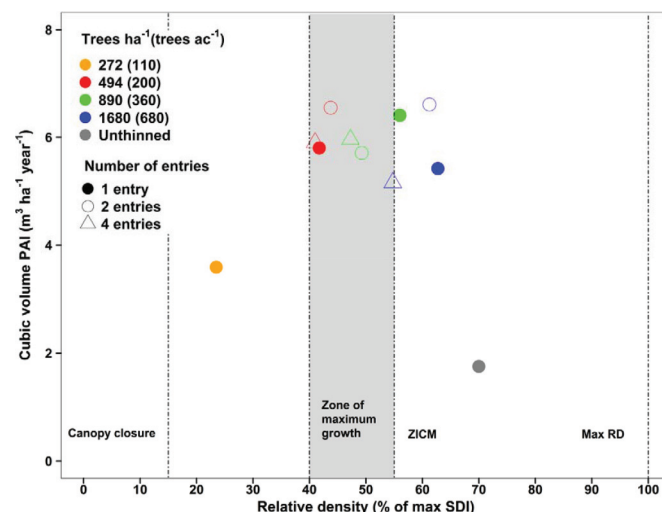
We propose two potential explanations for why we found a significant effect of density on top height: (i) *Larix occidentalis* height growth is more sensitive to competition than some other conifers, and (ii) decreases in top height at high densities were

Fig. 11. (A) Annual mortality rate for stands thinned once in percentage of stems $\text{ha}^{-1}\text{year}^{-1}$ calculated via annual compounding. (B) Relative density for stands thinned once calculated as percentage of maximum stand density index. Note that the increase in the mortality rate of the 1680 trees ha^{-1} density increases as it passes into the zone of imminent competition mortality (ZICM; sensu [Drew and Flewelling 1979](#)), which begins at a relative density of 55%. The canopy closure line indicates the beginning of intertree competition ([Drew and Flewelling 1979](#)). The gray band, between relative densities of 40% and 55%, identifies the zone of maximum stand volume growth. [Colour online.]



partially the result of high $H:D_{200}$, leading to elevated levels of top breakage. There is evidence from past work examining the effect of stand density on *Larix occidentalis* that height growth is sensitive to competition ([Schmidt and Seidel 1988](#); [Schmidt 1997](#); [Martin and Barber 1995](#); [McLeod 2012](#)); this is particularly clear in studies in which thinning manipulated density early in stand development. By contrast, when thinning is delayed to later stand ages, the effects of density are conflated with the effects of thinning.

Fig. 12. The relationship of 2015 relative density (RD, calculated as percentage of maximum stand density index (SDI)) to periodic annual increment (PAI) of total cubic volume for the period from 2001 to 2015. The clustering of points of the three tested densities (494, 890, and 1680 trees ha^{-1}) around a PAI of $6 \text{ m}^3\text{ha}^{-1}\text{year}^{-1}$ across the zone of maximum growth (RDs of 40% to 55%) show constant volume growth across stand densities during the most recent measurement interval ($5.42\text{--}6.41 \text{ m}^3\text{ha}^{-1}\text{year}^{-1}$; $P > 0.05$). The lower value of the 272 trees ha^{-1} and unthinned treatments show lower volume growth at RDs below 40% or above 55%. [Colour online.]



Top height of *Larix occidentalis* was not affected by density in studies in which PCT was delayed past stand age 30 years ([Cole 1984](#); [Seidel 1987](#); [Cochran and Seidel 1999](#); [Barber 2007](#)). In a study in which thinning did not occur until stand age 50 years, there were no differences in top height among stands of differing densities, rather trees in all densities showed very slow height growth, roughly $7.6 \text{ cm}\text{year}^{-1}$, suggesting that all trees in the study were experiencing reduced height growth due to past competition ([Barber 2007](#)). In contrast, in a study in which *Larix occidentalis* was thinned at age 7 years, by age 13 years, top height was lower in unthinned stands and stands with high density (12 000 trees ha^{-1}) than in stands thinned to lower densities ([Martin and Barber 1995](#)). In the same study, at age 36 years, there were large differences in top height among treatments, with unthinned and high-density stands having shorter top heights by over 6 m compared with low-density stands ([McLeod 2012](#)).

Reduced top height at higher levels of competition may result in part from $H:D_{200}$. High $H:D_{200}$ has been connected to increased risk of stem breakage due to wind and snow loading ([Cremer et al. 1982](#); [Wilson and Oliver 2000](#); [Wonn and O'Hara 2001](#)), and an $H:D_{200}$ of 80 has been suggested as a threshold above which there is increased risk of stem breakage for *Larix occidentalis* ([Wonn and O'Hara 2001](#)). The time period when differences in top height occurred in this study aligned with a region-wide late-season heavy snow event in 1996 ([Wonn and O'Hara 2001](#)), and stands with target densities of 890 and 1680 trees ha^{-1} exceeding the $H:D_{200}$ of 80 ([Fig. 7A](#)). Many of the tallest trees in 1680 trees ha^{-1} density plots experienced stem breakage, whereas little damage occurred to trees in low-density plots. Therefore, the decrease in top height may not be entirely a direct result of intertree competition but also the indirect effect of high-density plots producing trees of lower stability ([King 1986](#)).

Our results for temporal trends of height differentiation ([Fig. 8](#)) are strikingly similar to those recently reported for long-term *Pinus ponderosa* spacing trials in eastern Oregon and Washington, USA ([McGown et al. 2016](#)). The unthinned plots exhibited the

classic predicted trend for high-density stands undergoing self-thinning due to asymmetrical competition (Fig. 8): an initial increase in height differentiation followed by a subsequent decrease in CV_{ht} due to differential mortality of the smallest trees (Weiner and Thomas 1986; Brand and Magnussen 1988; Knox et al. 1989). The mortality and relative density trajectories for the unthinned stands (Fig. 11) corroborate this interpretation. In contrast, the CV_{ht} was lower in all thinned stands and declined through time, with no initial peak (Fig. 8). We attribute the subtle increase in CV_{ht} between the 1991 and 2001 measurements (Fig. 8) to a region-wide late-season heavy snow event in 1996 (Wonn and O'Hara 2001), which caused top breakage (without mortality) of many trees across our experimental units. CV_{ht} at the 2015 measurement was positively correlated with relative density (Fig. 8D; cf. fig. 7 in McGown et al. 2016), indicating greater size variability at higher levels of competition, which is predicted by theory (Weiner and Thomas 1986; Bonan 1988) and consistent with recent long-term spacing trial results in *Pinus ponderosa* stands (McGown et al. 2016). Declining CV_{ht} through time in thinned stands cannot be explained by self-thinning mortality, because mortality was very low in those treatments (Fig. 11). Rather, in the once-thinned plots, this trend is most clearly explained by converging growth rates (Stoll et al. 1994). In the multiple-entry treatments, the intermediate thinnings also contributed to declining CV_{ht} through time, because subordinate and damaged trees were targeted for removal, reducing size variation in the residual population. Thinned stands are obviously experiencing competition because mean tree size decreased (Fig. 5) while CV_{ht} increased (Fig. 8D) with increasing stand density. However, the CV_{ht} trajectories (declining to stable) for all thinned treatments are indicative of relatively weak competition overall (especially in low-density treatments) and of a dominant role of symmetrical competition, most likely for belowground resources (Brand and Magnussen 1988; Stoll et al. 1994).

5. Management implications and conclusions

This study shows the strong and long-lasting effects of thinning *Larix occidentalis* early in stand development. Our results complement other studies that have found that *Larix occidentalis* responds weakly or not at all to thinning treatments applied later in stand development (Roe and Schmidt 1965; Cochran and Seidel 1999; Martin and Barber 1995; Barber 2007). Individual-tree size is maximized at lower density. We did not detect a stand density (competition) threshold below which no additional increases in individual-tree size occurred (sensu Drew and Flewelling 1979); trees in the 272 trees·ha⁻¹ treatment were substantially larger than trees in the 494 trees·ha⁻¹ treatment. If a rotation age of 62 years is used to manage *Larix occidentalis*, the maximum merchantable volume is realized in the one-entry 890 trees·ha⁻¹ PCT treatment, but the differences are not large enough to be significantly different from the other thinned densities if a high utilization standard is used (11.4 cm top). Stand densities lower than 494 trees·ha⁻¹ may be appropriate for some landowner objectives, for example, if rapid growth of individual large-diameter trees is prioritized over maximizing stand-level wood production. Densities below 494 trees·ha⁻¹ may fail to fully occupy the site, and densities above 890 trees·ha⁻¹ may result in mortality before many trees reach merchantable size, particularly if larger top diameters are required to meet merchantability specifications. There is no evidence of a benefit of multiple precommercial thinning entries.

Our results support the conclusion that at densities as low as 494 trees·ha⁻¹, the increase in individual-tree growth and stability will eventually compensate for lower initial stand growth and yield relative to higher density stands. Across the tested range of densities, the primary effect of early thinning is to control whether volume is concentrated on few large, stable trees or spread over

many small, unstable trees. At lower densities, tree stability increases, indicating that volume, as well as volume increment, may continue to stay high. We also found that top height was affected by a broad range of initial densities (up to 6700 trees·ha⁻¹), which has strong implications for long-term stand yield. Increasing tree instability ($H:D_{200}$) may also increase mortality, which will lead to decreased yield at higher densities. Said simply, the long-term effect of lower stand density was to produce trees of larger size and greater stability while not sacrificing stand yield.

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