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Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada

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ABSTRACT

We investigated the impacts of a thinning prescription commonly used to reduce fuel loads in mature ponderosa pine forests of the northern Sierra Nevada Mountains on the distribution of carbon among functionally distinct pools, and on the component fluxes of net ecosystem production (NEP). The biomass of wood, foliage, and roots was highest in the unthinned control stands, lowest in stands measured 3 years after thinning, and intermediate in the stands measured 16 years following the same prescription. While total wood net primary production (NPP) followed the same pattern as biomass across treatments, an apparent doubling of shrub foliage NPP in the 3 years following overstory thinning reduced the impacts of thinning on total foliage NPP. Similarly, reductions in coarse root NPP associated with tree removal were largely offset by increases in fine root production. Compensatory NPP by shrubs and fine roots increased the light use efficiency of thinned stands 60% over that of unthinned plots. Both soil respiration and the decomposition of aboveground dead wood appeared conserved across all treatments. Results suggest that when modeling the influence fuel reduction treatments on regional carbon dynamics, it may be necessary to consider the compensatory responses of understory vegetation as such shifts in growth form can effect meaningful changes in the capture and allocation of carbon in the ecosystem.

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1. Introduction

To fully understand the role forest landscapes play in regional, continental, or global carbon dynamics it is necessary to consider constraints on biogenic carbon fluxes, the impacts of disturbance on the stocks of live and dead biomass, and the interactions between disturbance and biogenic carbon fluxes. Our understanding of leaf and tree-level physiology is built into a variety of process models and can be convincingly applied across a broad range of environmental conditions (Running, 1994; Aber et al., 1993). Furthermore, the influence of stand replacing disturbances can be accounted for by including forest age class distribution in spatially distributed models (Law et al., 2004; Turner et al., 2007). However, the influence of partial disturbance, such as forest thinning, is overlooked in most spatially distributed process models aside from its implicit contribution to forest type classification.

In the northern Sierra Nevada Mountains, thinning has been a major form of forest disturbance for over five decades. As a silvicultural tool, thinning is widely used to increase tree-level wood production, reduce fire risk, increase resistance to pests, restore old-growth structure, and to a lesser degree, supply biofuels for local energy plants. With growing concern over wildfire and increasing demand for domestic energy sources it seems likely that the extent of thinning will increase in the region.

The response of tree and stand-level bole wood production to thinning is well documented in the region (Oliver, 1972) and there is a growing body of literature documenting the effects of various thinning and underburning prescriptions on growth efficiency (Law et al., 1992), understory growth (Riegel et al., 1992; Cochran and Barrett, 1999; Thomas et al., 1999; Metlen et al., 2004; Bewley, 2007) and soil carbon dynamics (Concilio et al., 2005, 2006; Tang et al., 2005). By design, thinning functions to alter the structure and composition of these forests. However, questions remain as to how much and for how long these apparent alterations impact gross primary production (GPP), the allocation of GPP among functionally different growth forms and plant component (i.e. roots, stem, and leaves), and the subsequent magnitude of ecosystem respiration (Re) and net ecosystem production (NEP).

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For instance, if vegetation-level homeostasis prevails following such disturbances, even substantial alterations of forest structure and composition through thinning may have minimal impacts on GPP or Re, greatly simplifying regional modeling efforts. However, if either GPP or Re is substantially affected by thinning induced shifts in forest structure or composition, then it will be difficult to accurately simulate carbon dynamics across the Sierra Nevada Mountains, or any other region affected by partial disturbance, without accounting for such impacts (see Ernest and Brown, 2001; Lavorel and Garnier, 2002; Enquist et al., 2007).

In this study we set out to quantify the impacts of a thinning prescription commonly used to reduce fuel loading in mature ponderosa pine forests of the northern Sierra Nevada Mountains on the distribution of carbon among functionally distinct pools, and on the component fluxes of NEP. Our specific questions were:

1. To what degree, if any, were recent biomass removals from the overstory compensated by biomass gains in the understory?
2. To what degree, if any, did partial removal of trees affect production traits such as the allocation among foliage, wood, and roots?
3. To what degree, if any, did partial removal of trees affect respiration rates, such as the soil respiration and dead wood decomposition?
4. How did the distribution of biomass, production, and respiration change in 16 years after thinning?

2. Methods

2.1. Study site

The study site is located in the Forest Hill Ranger District of the Tahoe National Forest in the western foothills of the northern Sierra Nevada Mountains (Fig. 1). At a latitude of 39°N, and an elevation 1000 m, this location experiences an average annual air temperature of 12 °C, an average annual precipitation of 950 mm, and an average frost free period of 150 days. Soils at this location vary from well-drained loams to well-drained clay-loams derived volcanic substrates. With site indexes of 70–80 (50 years growth; mixed conifer; Dunning and Reineke, 1933) this area is considered more productive than most within the range of ponderosa pine. Native forests here are composed of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and California black oak (*Quercus kelloggii*) growing over a shrub layer comprised chiefly of Sierra coffeeberry (*Rhamnus rubra*), deerbrush (*Ceanothus integerrimus*), and manzanita (*Arctostaphylos* spp.). However, the stands used in this study were nearly pure plantations of ponderosa pine planted following the stand replacing Volcano Fire of 1961. After the fire, the area was salvage harvested followed by intensive site preparation which included root raking and debris windrowing. The thinning activities investigated in this study were the first such prescriptions applied to these fully stocked stands. Trees were thinned from below (larger crown classes retained) to achieve a final tree spacing of about 7.6 m and resulted in an

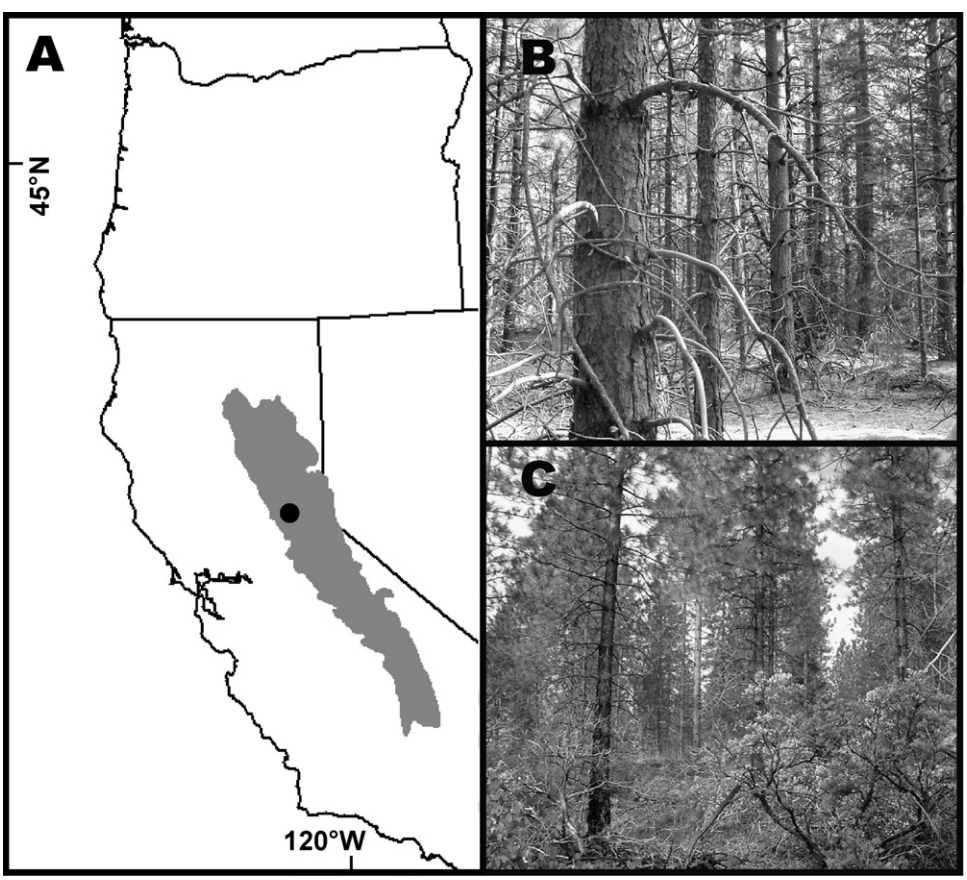

Fig. 1. Map and images from the study site. The study site was located at 1000 m of elevation in the western foothills of the northern Sierra Mountains of California (A). Study site (black circle) is shown within the greater Sierra Nevada ecoregion (shaded area). Prior to thinning (B), these ponderosa pine plantations were characterized by a closed canopy, and understory shrub cover. Sixteen years following thinning without underburning (C), the overstory was open and shrub cover was notably denser.

Table 1
Stand characteristics across thinning treatments.

Parameter	Unthinned control	Thinned 3 years earlier	Thinned 16 years earlier
Importance factor of ponderosa pine[a]	98 ± 2	96 ± 4	80 ± 25
Average age of overstory trees (years)	36 ± 1	37 ± 1	37 ± 2
Quadratic mean stem diameter (DBH in cm)	34 ± 9	33 ± 4	39 ± 10
Density of trees overstory trees (stems ha^{-1})	554 ± 265	186 ± 46	191 ± 58
Basal area of overstory trees (m^2 ha^{-1})	42 ± 9	16 ± 5	23 ± 11
Canopy height (m)[b]	19 ± 4	18 ± 3	20 ± 3
Live shrub cover (ground area fraction)[c]	9 ± 4	32 ± 8	22 ± 9

[a] Percentage of tree basal area that is ponderosa pine (*Pinus ponderosa*); compositional balance made up largely of incense-cedar (*Calocedrus decurrens*).
[b] Average height of dominant and co-dominant trees.
[c] Shrub layer composed primarily of Sierra coffeeberry (*Rhamnus rubra*), deerbrush (*Ceanothus integerrimus*), manzanita (*Arctostaphylos* spp.). Overstory trees defined as trees >10 cm DBH. Uncertainties are the standard deviation of the mean of four replicate plots.

average reduction of basal area from 40 to 20 m^2 ha^{-1} (see Table 1). Mechanized harvest afforded consolidation of slash into few large piles which were then burned. The area covered by the original planting and subsequent thinning was about 800 ha. Quantitative stand structural characteristics for unthinned plots, plots thinned 3 years earlier, and plots thinned 16 years earlier, including the understory composition, are given in Table 1. All measurements in this study were taken in the growing season of 2005. Thinning prescriptions for ponderosa pine forests vary in basal area reduction, leave tree selection, and slash treatment depending on the management objectives and resource availability. The thinning activities investigated in this study represent only one such prescription but are not atypical of the region.

2.2. Study design

The experimental unit in this study is a 1-ha plot. Twelve such plots were placed in twelve separate management units, four of which were unthinned control units, four of which were units thinned 3 years earlier, and four of which were units thinned 16 years earlier (i.e. a sample size of 4 plots per treatment). The selection of management units to be thinned was made prior to the study, based largely on logistical considerations, and showed no overt bias toward landform or site condition. We assume the managements units, and hence the single study plots within each, to be independent based on their distance from one another (greater than 1 km) and interspersion with alternative management units. The exact placement of each study plot within a management unit was arbitrary with deliberation only to avoid edge influence including the few locations where large slash piles were burned. The localized nature of the slash piles (much fewer than one pile per ha) was such that their burning did not influence plot-level measurements and, like harvested bole wood, burned slash was considered an export from the perspective of the study plot. Described in detail below, plot-wide measurements were performed through sub-sampling at various spatial frequencies specific to the parameter being quantified.

2.3. Aboveground biomass

Aboveground tree wood mass, was estimated for each plot using species-specific allometric equations that predict mass from stem diameter and height which was recorded for approximately 20% of the trees in the 1-ha study plots (all trees in each of four 220 m^2 subplots). Tree height and DBH were used to estimate stem wood mass of ponderosa pine using an equation developed by Wenzel (1977) from ponderosa pine 25–160 cm DBH growing in northern California and an assumed wood density of 0.37 (Maeglin and Wahlgren, 1972), while branch and bark mass for ponderosa pine was estimated from DBH alone using equations developed by Gholz et al. (1979) from ponderosa pine 15–80 cm DBH growing in northern Arizona. The stem wood of incense-cedar and California black oak (which together amounted to less than 6% of the total aboveground biomass) was estimated by the same methods using equations developed by Wenzel (1977) and Pillsbury and Kirkely (1984), respectively and assumed wood densities of 0.35 and 0.56, respectively (Waddell and Hiserote, 2005). For incense-cedar, branch and bark mass was estimated from DBH using equations developed by Gholz et al. (1979). For California black oak, branch and bark mass were assumed to be contained in the estimate of stem wood mass. The same allometric equations were used across all treatments. As such, reported differences in tree wood biomass among treatments reflect only differences in stem volume and frequency and do not resolve any treatment-specific apportionment among bole, branch and bark.

Tree foliage mass was estimated as the product of plot-wide leaf area index (see methods below) and specific leaf mass (SLM) determined from needles taken from five branches collected from mid-canopy on each plot (see Table 2). While SLM is known to vary as a function of exposure, we assumed these samples to representative of the entire canopy, in part, since the coefficient of variation for SLM among all samples across all treatments was less than 0.10.

The wood and foliage biomass of the understory (here after referred to as shrubs) was estimated using allometric equations developed on site that predict wood and foliage biomass from shrub volume (operationally defined as an ellipsoid cylinder where volume equals the product of π, minimum horizontal radius, maximum horizontal radius, and height). These allometric relationships are shown in Fig. 2. Harvests were conducted separately for each of the three predominant species present (Sierra coffeeberry, deerbrush, and manzanita). Upon analysis, it was determined that species distinctions were not warranted and common equations for wood and foliage mass were applied to all shrubs encountered in the survey. To determine plot-level shrub biomass, shrub volumes were measured on four 80 m^2 subplots per plot.

Forb and grass biomass was estimated by multiplying ocular cover estimates forbs and grass an assumed mass of 4.0 g m^{-2} of leaf cover (Table 2). This crude conversion was based on a cross-taxa average compiled from Means et al. (1994) and was not specific to the site, however given the very low levels of grass and forbs on these sites (rarely exceeding 0.5% of shrub mass) even large errors in their estimate would have negligible influence in perceived patterns of biomass distribution.

2.4. Leaf area index

Plot-wide overstory leaf area index (LAI) was determined optically with a LAI2000 Plant Canopy Analyzer (Li-Cor Biosciences,

Table 2
Ecosystem parameters used in estimation of biomass, production, and decomposition.

Parameter	Value[a]	Source[b]
Overstory LMA (mg projected m^{-2})		
Unthinned control plots	11.7 ± 0.3	1
Plots thinned 3 years earlier	12.3 ± 0.2	1
Plots thinned 16 years earlier	11.3 ± 0.8	1
Overstory foliage production (fraction of total mass)		
Unthinned control plots	0.56 ± 0.03	1
Plots thinned 3 years earlier	0.61 ± 0.08	1
Plots thinned 16 years earlier	0.49 ± 0.04	1
Fine root turnover (yr^{-1})		
Unthinned control plots	0.53 ± 0.01	1
Plots thinned 3 years earlier	0.68 ± 0.08	1
Plots thinned 16 years earlier	0.30 ± 0.03	1
Dead wood density (g cm^{-3})		
Decay class 1	0.336	2
Decay class 2	0.330	2
Decay class 3	0.264	2
Decay class 4	0.228	2
Decay class 5	0.192	2
Dead wood decay constants (yr^{-1})[c]		
Standing stems (snags)	0.011	3
Downed dead wood >7.6 cm diameter	0.030	4
Downed dead wood 2.5–7.6 cm diameter	0.040	4
Downed dead wood 1.0–2.5 cm diameter	0.050	4
Dead coarse roots	0.011	5
Grass and forb biomass (g m^{-2} of ground cover)	4.0	6
Shrub foliage turnover time (yr^{-1})		
Arctostaphylos spp.	2.7	7
Ceanothus integerrimus and *Rhamnus rubra*	1.2	8
Other semi deciduous species	2.0	1
Fraction of total fine roots found in top 20 cm	0.79	9
Carbon concentration of wood (mass fraction)	0.50	10
Carbon concentration of foliage (mass fraction)	0.49	1
Carbon concentration of forest floor (mass fraction)	0.40	11

[a] Uncertainties are the standard error of values measured in four replicate study plots; actual plot-specific values were used in computations.
[b] Sources are: (1) this study; (2) Harmon and Sexton (1996); (4) adapted from McIver and Ottmar (2007) and Harmon (personal communication); (3) Bull (1983); (5) Harmon et al. (2004); (6) Means et al. (1994); (7) Karlsson (1992); (8) Ackerly (2004); (9) Law et al. (2003); (10) Law et al. (2001); (11) Campbell et al. (2007).
[c] Lower decay constants were used for dead wood from incense-cedar and black oak, but the low volume of this wood rendered such adjustments negligible to overall decomposition rates.

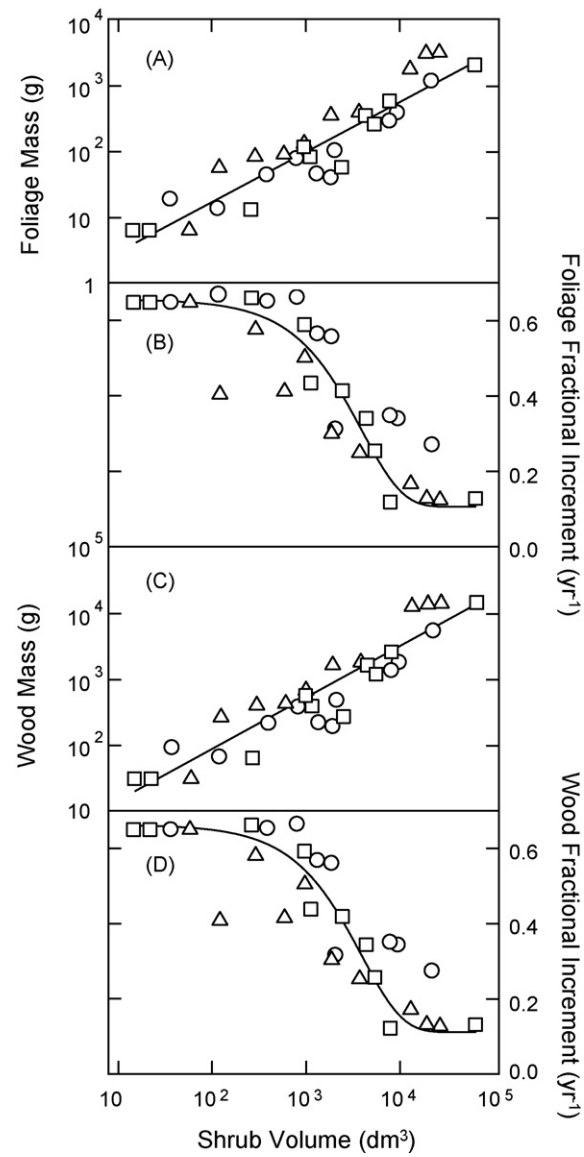

Fig. 2. Allometric relationships between shrub volume and foliage mass (A) where $y = 0.606 \times {}^{0.770}$, $R^2 = 0.78$; annual foliar increment, as fraction of total (B) where $y = 0.180 + 0.455e^{-0.0004x}$, $R^2 = 0.79$; wood mass (C) where $y = 2.418 \times {}^{0.779}$, $R^2 = 0.93$; and annual wood increment, as fraction of total (D) where $y = 0.178 + 0.453e^{-0.0004x}$, $R^2 = 0.79$. Triangles denote Sierra coffeeberry (*Rhamnus rubra*), circles denote deerbrush (*Ceanothus integerrimus*), and squares denote manzanita (*Arctostaphylos* spp.). Shrub volume is defined as an ellipsoidal cylinder where volume = $\pi \times$ maximum horizontal radius $\times$ minimum horizontal radius $\times$ height.

Lincoln, NE). Plot-wide values were computed as the average of 16 point measurements stratified regularly through out the plot and corrected for tree-level clumping, shoot-level clumping, and wood area according to the methods of Law et al. (2001). Understory LAI (used only to compute total LAI, not understory foliage mass) was also determined optically with a LAI2000 Plant Canopy Analyzer at up to 16 points per plot determined to have 100% shrub cover and then multiplied by the estimate of plot-wide shrub cover. Considering the measurement uncertainties inherent to this approach and the relatively small contribution of shrub LAI to total LAI, no corrections were attempted for shoot-level clumping and wood area of shrubs as these would have likely amounted to false accuracies.

2.5. Aboveground production

Bole wood increment cores taken on 20 trees in each plot (stratified by bole diameter) were used to build plot-specific regressions that predict annual radial growth based on current tree diameter. With the same allometric equations used to estimate current biomass, annual radial growth of bole, branch, and bark was estimated for each tree by the difference between current and previous biomass (Hudiburg et al., in review). Tree foliage production was calculated as total overstory foliage biomass multiplied by the fraction of total foliage mass that grew that year, which was determined from the separation of needle cohorts on five branches collected on each plot (see Section 2.3 above).

Using stem radial increment measured on 35 shrubs throughout the study area combined with allometric equations relating stem diameter to foliage and stem mass (as per harvest described above) it was determined that annual biomass increment of shrubs ranged from 10 to 80% for stem wood and 20 to 70% for foliage and was most strongly dependent on shrub volume; with the smaller shrubs aggrading biomass more rapidly than larger ones. As shown

in Fig. 2, this afforded the estimation of annual increment (annual growth as a fraction of total biomass) from field measurements of shrub volume. By equating wood production to wood increment, wood production was computed for each shrub encountered in the plot surveys as its allometrically estimated wood mass multiplied by an estimate of fractional annual increment (see Fig. 2D). By equating foliage production to the sum of annual increment and mortality (annual leaf fall), shrub foliage production was computed for each shrub encountered in the plot surveys as its allometrically estimated foliage mass multiplied by an estimate of fractional annual increment (see Fig. 2B) plus estimated foliage mass multiplied by an estimate of leaf turnover time (see Table 2). Grasses and forbs were assumed to be annuals, so that annual production was equivalent to late-season standing biomass.

2.6. Detritus

The volumes of standing dead wood (snags) and stumps were surveyed coincident with the live tree survey described above. Downed dead wood was inventoried on each plot using the line intercept method (Harmon and Sexton, 1996) on a total of 300 m of transects per plot (arranged as four cardinally directed 75 m transects originating at plot center). Wood fragments 1–7.6 cm diameter were sampled along 120 m, and wood fragments >7.6 cm diameter were sampled along all 300 m. For all fragments >2.5 cm diameter, a decay class (1–5) was recorded for the purpose of assigning wood density values. Dead wood volume per unit ground area (geometrically extrapolated from inventories) was converted to mass and decay rate based on densities and decomposition constants shown in Table 2. Forest floor (litter and duff) were sampled at 16 locations at each plot using corers measuring 15 cm in diameter. Oven-dry forest floor masses were converted to carbon mass according to Table 2.

2.7. Roots mass and production

The mass of coarse roots (roots >1 cm in diameter) was determined using the allometric equation of Santantonio and Hermann (1985) relating DBH to coarse root mass of Douglas-fir. Due to the paucity of equations predicting coarse root mass, this equation is widely applied to conifers throughout the North America. Nonetheless, we have no practical way to test the accuracy of this equation when applied trees in this study. Since the same allometric equation was used across all treatments, reported differences in coarse root biomass among treatments reflect only differences the size and frequency of tree stems.

The production of coarse roots attached to living trees was determined using the same equation parameterized with annual radial stem increment (either measured through coring or modeled from diameter). The decomposition of coarse roots attached to snags and stumps was computed as the coarse root mass multiplied by a class-specific decay constant (see Table 2).

Fine roots (roots ≤2 mm diameter) present in the top 20 cm of soil was sampled by soil coring once during June in each plot and also in May, July, and September in half of the plots (two per thinning treatment). In each sample period, 32 regularly spaced soil cores were taken per plot (6.4 cm in diameter × 20 cm deep). Fine roots were dry sieved from the mineral soil, washed with a hydropneumatic elutriator (Gillison's Variety Fabrication, Inc., Benzonia, MI), and then manually sorted to exclude non-root material. While most fine roots in ponderosa pine forests are in the top 20 cm of soil, a standard correction factor was applied to convert the mass of fine roots measured in the top 20 cm to an estimate of the total mass of fine roots per unit ground area based on profile data from Law et al. (2003) (Table 2). An index of fine root turnover (shown in Table 2) was computed as the difference between maximum fine root mass (attained in the June measurement cycle) and the minimum fine root mass (attained in the September measurement cycle) divided by the maximum fine root mass (see Fig. 3 and Table 2).

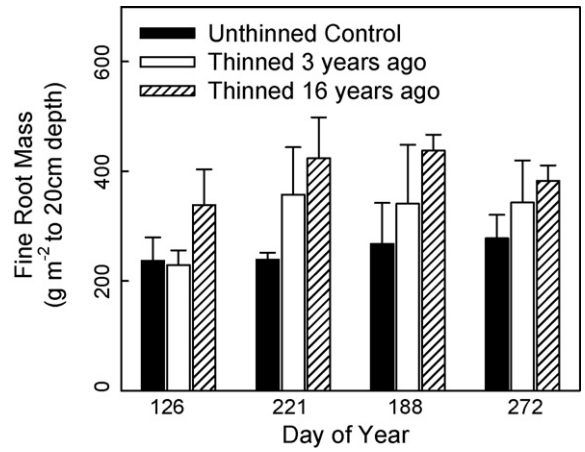

Fig. 3. Growing season phenology of total fine root mass across thinning treatments. Values shown are the means of four plots per treatment with error bars showing the standard error of the mean. Each individual 1 ha plot was sampled for roots at 32 regularly stratified locations.

2.8. Soil respiration

Soil respiration (soil surface CO_2 efflux) was measured on half of the plots (two per thinning treatment) using a LiCor-6400 portable infrared gas analyzer coupled to a LiCor-6400-09 soil respiration chamber (Li-Cor Biosciences, Lincoln, NE). During measurements, the chamber sat on permanently installed plastic collars. Efflux measurements were made at 12 points regularly stratified throughout each 1 ha plot (three points 2.8 m apart from one another in each of four subplots 35 m from one another). All plots were measured on a single rain-free day between the hours of 10 a.m. and 2 p.m. first in May and again June, July and September.

2.9. Net ecosystem production

The component ecosystem carbon fluxes described above can be combined to estimate aggregate ecosystem fluxes such as ANPP (total aboveground net primary production), BNPP (total belowground net primary production), R_h (total heterotrophic respiration) and NEP according to various different computational schemes each of which require a different suite of assumptions, and produce different values. In this study we employ two such methods (see Table 3).

The chief assumption of method one is that soil respiration is balanced annually with litterfall, gross root carbon allocation, and any accumulation (or loss) of carbon in the roots and soil (Raich and Nadelhoffer, 1989; Van Tuyl et al., 2005). As such, measurements of soil respiration do not enter the calculations. By contrast, method two does not enforce a balance between soil respiration and belowground inputs. In method two, the fraction of measured soil respiration believed to be of heterotrophic origin is applied directly to estimates of R_h, which in turn are subtracted from net primary production (NPP) for an estimate of NEP. For method two, we assumed 60% of total soil respiration was from heterotrophic sources with the balance attributed to living roots. This partitioning was based on trenching experiments conducted in similar-aged Ponderosa pine forests in central Oregon (Irvine et al., in review).

Table 3
Aggregate ecosystem carbon fluxes in g C m^{-2} yr^{-1} as estimated by three alternate mass balance methods.

Flux parameter and method	Unthinned Control	Thinned 3 years earlier	Thinned 16 years earlier
Method 1			
ANPP (∑all wood and foliage production)	435 ± 69	216 ± 60	341 ± 129
BNPP ((fine root mass × turnover) + live coarse root increment)	167 ± 13	129 ± 49	134 ± 38
R_h (ANPP + BNPP − NEP)	308 ± 33	238 ± 59	220 ± 24
NEP (ANPP − litterfall − dead wood decomposition + Δroot + Δsoil C)	294 ± 53	107 ± 48	256 ± 152
Method 2			
ANPP (∑all wood and foliage production)	435 ± 69	216 ± 60	341 ± 129
BNPP ((fine root mass × turnover) + live coarse root increment)	167 ± 13	129 ± 49	134 ± 38
R_h ((R_s − fraction attributed to roots) + dead wood decomposition)	464 ± 47	447 ± 40	510 ± 61
NEP (ANPP + BNPP − R_h)	93 ± 76	−61 ± 125	−160 ± 50

ANPP is aboveground net primary production, BNPP is belowground net primary production, R_h is heterotrophic respiration, NEP is net ecosystem production, and R_s is soil respiration. ΔRoot is calculated as live coarse root increment minus dead coarse root decomposition (assuming steady stasis in fine root mass). See Campbell et al. (2004) for full derivation of NEP equation. All values were estimated through field measurement except the fraction of R_s attributed to roots which was assumed to be 0.60 and Δsoil C which was assumed to be zero. Sample size was two independent study plots for computations involving soil respiration and four for computations not involving soil respiration. Uncertainties are the standard deviation among replicate study plots, not the propagated uncertainties associated with component measurements.

This estimate is also consistent with seasonal measurements made with portable chambers and root excision in a variety of forest types (Law et al., 2001).

Solely for the purposes of estimating NEP (method 2), cumulative annual soil respiration was estimated for each plot as follows: (1) mid-day measurements were converted to 24-h averages using a diel correction factor developed for similar forests in Oregon (Martin, unpublished data), this correction had the effect of reducing measured fluxes by an average of seven percent which is within one% of a correction computed from diel measurements made in a ponderosa pine plantation in the Northern Sierra Nevada Mountains by Xu and Qi (2001); (2) winter-time efflux rates of 0.5 μmol CO_2 m^{-2} s^{-1} were assumed to persist from December through March (based on measurements by Campbell and Law, 2005); (3) daily flux rates were linearly interpolated between measurement dates; and (4) daily flux rates were then integrated over the course of the year.

3. Results

3.1. Carbon pools

The distribution of biomass among plant components (i.e. roots, stem, and leaves), and growth form (overstory and shrubs) across treatments are shown in Fig. 4. Three years after prescribed thinning, total overstory aboveground biomass (wood and foliage) is, on average, 0.37 of that measured in unthinned stands. Sixteen years after the same thinning prescription, total overstory biomass recovered an average of about 0.62 of that measured in unthinned stands. Patterns in aboveground shrub biomass are inverse to that of tree wood mass with total average shrub biomass 2.7 times higher in plots measured 3 years after thinning than in unthinned plots and 2.4 times higher in plots measured 16 years after thinning than in unthinned plots.

The response of belowground biomass to thinning is similar to that of the aboveground pools since live large coarse roots are lost to dead pools in direct proportion to the removal of tree stem wood. Considering the substantial loss of live tree root systems to thinning, the observation that total fine root mass (in the top 20 cm) remains similar among treatments is notable. However, with among-plot coefficients of variation (standard deviation/mean) in our estimate of fine root mass approaching 0.30 it is unclear how much of this apparent conservation of fine root mass across thinning treatments is due to additional fine root mass of shrubs, the expansion of roots by retained vegetation, or type two statistical error.

Despite differences in the proportion of tree and shrub biomass among treatments, the ecosystem-level root:wood:foliage biomass ratios are remarkably conserved at 30:60:10 across all treatments. This conservation of component proportions at the ecosystem level is afforded in part by shrubs on these plots having only marginally higher foliage fractions than trees (0.19 and 0.14 for shrubs and tree, respectively) and also due to biomass being dominated by trees even in plots having the most shrubs.

Patterns of detrital mass across the thinning treatments are shown in Fig. 4. The mass of forest floor is highest in the unthinned plots but is only marginally less in the thinned stands. The total amount of dead wood is largely conserved across treatments as the

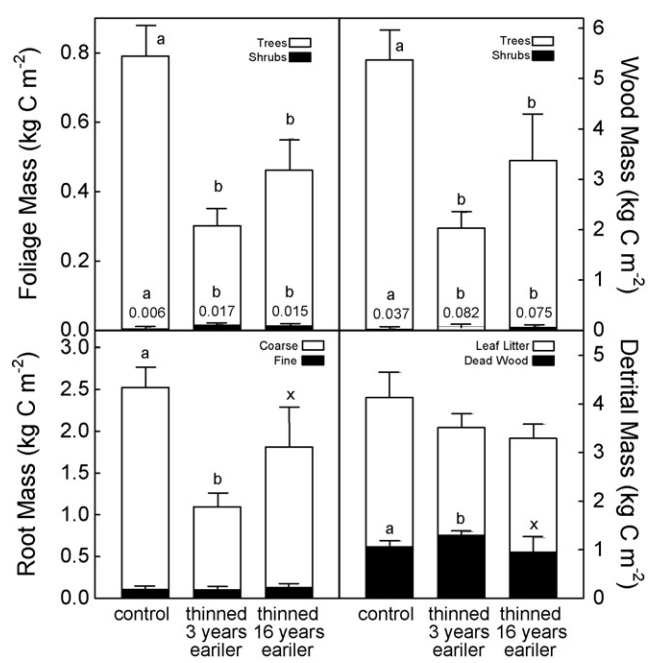

Fig. 4. Distribution of biomass among ecosystem pools and across thinning treatments. Stacked bars show the mean value of four plots within each treatment; values are shown above bars for shrub masses; error bars show the standard error; lower case letters distinguish among statistically different groups for each parameter, the letter x is used when a treatment is not different from either a or b ($p < 0.05$ one-tailed Students *T*-test). Tree wood mass, tree leaf area, and total coarse root mass decline substantially with thinning showing some recovery after 16 years. Declines in tree leaf area associated with thinning are partially compensated for by increases in shrub foliage. Shrub wood mass, fine root mass, and detrital masses are by comparison largely conserved across treatments.

increase in stump mass associated with thinning (small in this case due to mechanized harvesting) is offset by the removal of standing dead trees (small in this case due to stand age and overall vigor).

3.2. Production

Estimates of NPP of foliage, wood, and roots are shown in Fig. 5. In unthinned plots, total wood NPP is about equal to total foliage NPP (approximately 0.2 kg C m^{-2} yr^{-1}) and about 25% more than the estimated NPP of roots (approximately 0.16 kg C m^{-2} yr^{-1}). In plots measured 3 years after thinning, both wood and foliage NPP are 50% that of unthinned stands. NPP measured on plots 16 years after the same thinning prescription suggests a recovery of overstory wood production, partial recovery of overstory foliage production and a stabilization of wood and foliage production by shrubs at levels approximately twice that of the unthinned controls.

Estimates of coarse root NPP in plots measured 3 years after thinning were about one third of that measured in unthinned plots but largely compensated for by a near doubling of fine root NPP such that total root NPP was only 22% lower than that of unthinned plots. Total root production in plots measured 16 years after thinning was no different from that measured in unthinned plots due mostly to a substantial recovery of coarse root production (see Fig. 5). Since fine root mass was largely conserved across treatments, the differences observed in fine root production among treatments were largely the result of differential turnover rate (see Table 2).

The distribution of total NPP among root, wood and foliage did vary somewhat with thinning treatment but due almost entirely to the increases in root production in plots 3 years after thinning. The proportioning of aboveground production between wood and foliage was largely conserved across plots despite shifts between overstory and shrubs since both allocated approximately 40% of their aboveground NPP to foliage versus wood.

3.3. Light use efficiency

As shown in Fig. 6, overstory LAI in plots measured 3 years after prescribed thinning is, on average, only 20% that of unthinned stands.

However, due to a more than doubling of shrub leaf area, total LAI in plots measured 3 years after prescribed thinning is, on average, 33% of unthinned stands. Measurements of LAI on plots thinned 16 years earlier suggest a slight recovery of overstory LAI and a stabilization of shrub LAI.

As shown in Fig. 6, average light use efficiency (computed here as total NPP divided by total LAI) for plots measured 3 years and 16 years after thinning was 0.21 compared to 0.13 for unthinned stands. In other words, thinning induced reductions in NPP were disproportionably less than thinning induced reductions in LAI. While overstory production per unit leaf area increased slightly, more than 50% of the observed increase in light use efficiency is attributable to increases in fine root production and 40% is attributable to increases in shrub production.

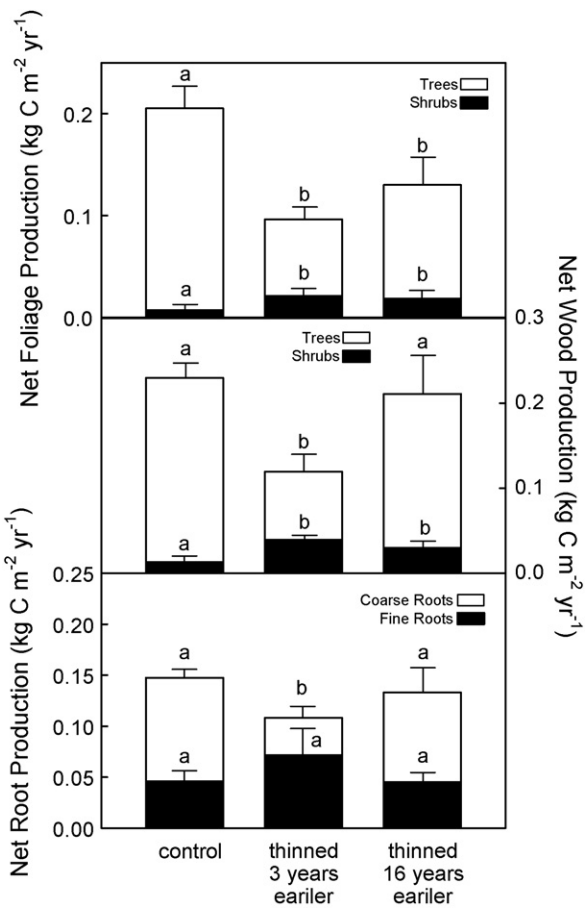

Fig. 5. Distribution of net primary production among ecosystem pools and across thinning treatments. Stacked bars show the mean value of four plots within each treatment, error bars show the standard error, lower case letters distinguish among statistically different groups for each parameter ($p < 0.05$ one-tailed Students *T*-test). Initially wood production declines proportional to tree removals but appears to recover dramatically after 16 years. The decline foliage and wood production by trees associated with thinning is moderated by the stimulation of shrub growth. Similarly, short-term declines in coarse root production are partially compensated by increases in fine root production.

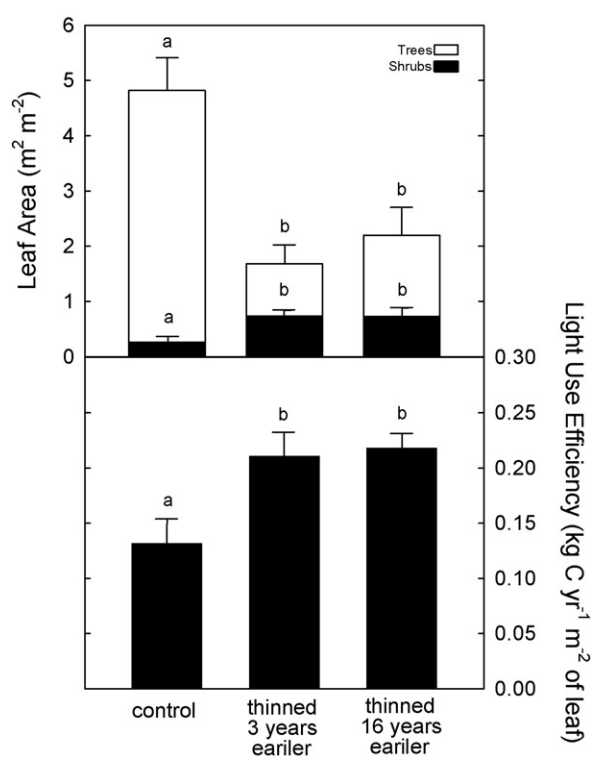

Fig. 6. Leaf area index and light use efficiency across thinning treatments. Light use efficiency is calculated as total NPP/total LAI. Stacked bars show the mean value of four plots within each treatment, error bars show the standard error, lower case letters distinguish among statistically different groups for each parameter ($p < 0.05$ one-tailed Students *T*-test).

3.4. Respiration

Daytime soil respiration averaged 3.3, 5.1, 4.7, and 3.2 μmol m^2 s^{-1} for day of year 126, 188, 221, 272, respectively, and did not vary significantly among treatments (Fig. 7). Respiratory fluxes arising from decomposition of aboveground dead wood, and decomposition of dead coarse roots are also shown in Fig. 7. Generally speaking, these respiratory fluxes are conserved across treatments with the exception of decomposition from dead coarse roots which is three times higher in the thinned stands (where stumps are prevalent) than in the in unthinned stands (where dead roots are associated only with the few dead trees). The seasonality of soil respiration was similar across all treatments with maximum rates of 4–5 μmol CO_2 m^{-2} s^{-1} occurring in the June measurement period.

3.5. Net ecosystem production

Table 3 shows the average estimates of ANPP, BNPP, R_h, and NEP for each of the thinning treatments, as computed by two alternate methods. If one is willing to assume that soil carbon is in equilibrium so that soil respiration is necessarily balanced by estimates of leaf litter input, live root input, and loss from decomposing dead coarse roots (method 1) then it appears that after 3 years, thinning treatments had the effect of reducing NEP one third from a sizable sink of ~300 g C m^{-2} yr^{-1} to a marginal sink of ~100 g C m^{-2} yr^{-1} and that NEP had returned to unthinned levels by 16 years after thinning. If one prefers not to assume equilibrium in soil carbon, and couples heterotrophic respiration directly to measured soil respiration (method 2), then it appears that NEP is slightly negative in the unthinned controls and becomes increasingly negative up to ~−200 g C m^{-2} yr^{-1} with time since thinning.

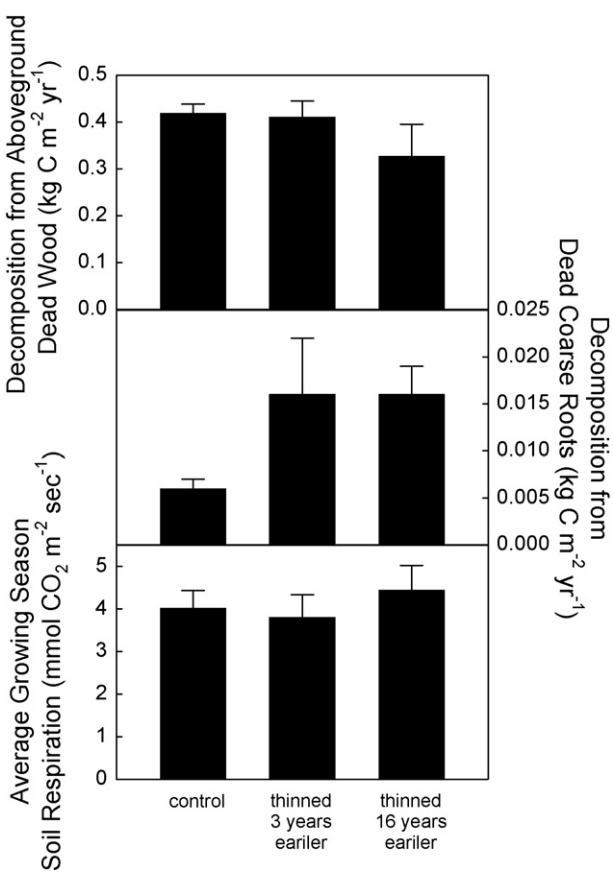

Fig. 7. Respiratory fluxes across thinning treatments. Soil respiration is the average of periodic measurements taken in 2005 day of year 126, 188, 221, and 272. With the exception of dead coarse root decomposition, which reflects generation of stumps by thinning, respiratory fluxes are largely conserved between thinning treatments.

4. Discussion

4.1. Thinning and component carbon fluxes

Historically, thinning has been one of the primary means by which foresters have manipulated the growth and yield of timber producing forests. Countless empirical studies, demonstrate that the partial removal of stems functions initially to reduce overall stand production while increasing the productivity of the remaining trees. However, given enough time, density manipulations result in little difference in stand level productivity. The simple explanation is that the resource supply of the environment dominates the rate at which stand members grow, and ultimately sets the limit to yield irrespective of density, i.e. the Law of Constant Final Yield (Kira et al., 1953; Harper, 1977). The remarkable consistency with which woody ecosystems rearrange their basal area in response to perturbation has been the basis for developing universal scaling laws relevant to all forms of biological vascularization (Enqiust et al., 1998; Enquist and Niklas, 2001). The thinning prescriptions considered in this study were implemented primarily to reduce fire hazard but also functioned to reduce stand-level productivity and increase stem-level productivity. While this result was predictable, understanding the effects of such thinning on the ecosystem-level carbon balance requires one to consider additional factors such as compensatory responses of understory vegetation, shifts in allocation among foliage, stem, and root, and impacts on heterotrophic respiration and net ecosystem production, the net of ecosystem photosynthesis and respiration.

The thinning prescriptions considered in this study appear to have resulted in a substantial increase in the mass and production of understory shrubs. While the magnitude of this response is likely to depend on the level of overstory thinning, this response has been observed by others studying ponderosa pine thinning and attributed to reduced competition for light and water (Simonin et al., 2006, 2007). Assuming pine density is high enough to warrant thinning in the first place, potential increases in the biomass of shrubs in response to thinning prescriptions is likely to be small relative to either the biomass of overstory removed or left behind. Where the compensatory responses of understory vegetation may have the largest impact on carbon dynamics involves their allocation patterns relative to that of trees. For instance, as a growth form, shrubs often allocate a greater proportion of their gross production to leaves and fine roots than do full-stature trees (Law and Waring, 1994; Cornelissen et al., 1996).

Because live foliage and fine roots have higher respiratory demands and higher turnover rates when dead than does wood, a shift toward shrubs may function to decrease the proportion of net to gross primary production (Law et al., 2001a; Field, 1991; Law and Waring, 1994). Empirical relationships observed among clear-cut and mature conifer forests suggest that soil respiratory rates per unit foliage mass may be as much as two to ten times more for open-grown shrubs than for trees across the same stands (Campbell et al., 2004; Law et al., 2001b). In Law et al. (2001a), a shrub-dominated young ponderosa pine forest had about half the NPP of a mature forest, but similar soil respiration, such that it was a net source of CO_2 to the atmosphere.

In this study, the semi-deciduous broad shrubs that made up the majority of the understory allocated production and standing

biomass to foliage and wood in almost exactly the same proportions as the pine overstory. As such, thinning induced shifts in growth form did not affect the fractional allocation to foliage. However, thinning induced increases in shrub abundance may be responsible for commensurate increases in fine root turnover which contributed substantially to the increased light use efficiency of thinned plots.

The apparent conservation of soil respiration across treatments in this study is consistent with the findings of Kobziar and Stephens (2006) and Kobziar (2007) who found that prescribed thinning of a ponderosa pine forest in the Sierra Nevada Mountains had a negligible effect on soil respiration.

A study conducted by Vesala et al. (2005) in a southern Finland Scotts pine forest also found soil respiration to be unaffected by a routine thinning prescription. However, our findings are inconsistent with the observations Concilio et al. (2005) who reported a 43% increase in soil respiration 2 years following selective thinning of a mixed-conifer forest in the Sierra Nevada Mountains. While type II statistical error makes it difficult to prove the absence of an effect, given that the within treatment coefficient of variation of soil respiration was only 0.15, any undetected effects of thinning on soil respiration in this study were necessarily small.

4.2. Thinning and net ecosystem production

Limited by our inability to directly measure either GPP or total belowground carbon allocation, conclusions regarding how thinning (or any other conditional treatment) influence forest NEP are largely restricted to the component fluxes that are actually measurable. For instance, conditions that function to increase NPP can be said to contribute positively to NEP while conditions that function to increases soil respiration can be said to contribute negatively to NEP regardless of what the value of NEP may actually be. Never the less, if one is willing to make certain assumptions, crude estimates of NEP can be made from field data; which, in many cases, compare favorably with independent estimates of NEP arrived at through eddy covariance techniques (Loescher et al., 2006). Moreover, even if ground-based estimates of NEP include unknown assumptional biases, there is some value in comparing their relative magnitude among treatments

If one is willing to assume that soil carbon is in equilibrium (method 1) then it appears that after 3 years, thinning treatments had the effect of reducing NEP one third from a sizable sink of $\sim$300 g C m^{-2} yr^{-1} to a marginal sink of $\sim$100 g C m^{-2} yr^{-1} and that NEP had returned to unthinned levels by 16 years after thinning. This response is logical, assuming (1) live biomass is accumulating in all three treatments, (2) thinning initially reduces the amount of photosynthesizing tissue without immediately interrupting soil heterotrophic respiration, (3) shrubs store less mass per unit carbon assimilated than do the trees they partially replace (i.e. lower carbon use efficiency), and (4) tree productivity is restored over time, though among fewer stems than before thinning. Understand that since these estimates of NEP do not explicitly include measurements of soil respiration they, by definition, do not account for any possible stimulation or retardation of soil heterotrophic respiration that may have resulted from the punctuated mortality of fine roots or the sudden reduction rhizospheric carbon priming.

If one prefers not to assume equilibrium in soil carbon, and couples heterotrophic respiration directly to soil respiration (method 2), then it appears that NEP is slightly negative in the unthinned controls and becomes increasingly negative up to $\sim$−200 g C m^{-2} yr^{-1} with time since thinning. Considering that all of these forests are aggrading aboveground biomass, for these numbers to be accurate, legacy soil carbon must by respiring from these plots at rates up to 200 g C m^{-2} yr^{-1} which we feel is unlikely since the total stock of carbon in these soils was estimated to be only 16 kg C m^{-2} (based on total soil carbon from 4 cores per plot to depths up to 80 cm). A better assessment of annual soil fluxes through continuous measurement over multiple years could resolve this inconsistency. Never the less, these high rates of soil respiration we detected from periodic measurements can not be entirely ignored since across various forest types the most important factor driving cumulative annual soil respiration is base rates during the growing season (Campbell and Law, 2005).

4.3. Relevance to regional modeling

While plot-level studies such as this one can be valuable in elucidating the processes by which disturbance affects forest carbon dynamics, it is only at the regional or continental scale that these processes are relevant to issues of atmospheric CO_2 concentrations and associated global change. For that reason it is important to discuss findings in the context of process models capable of simulating forest carbon dynamics across large spatial domains. Process models are beginning to incorporate dynamic vegetation growth, including early successional vegetation as well as regrowth of trees. These models have the capability of simulating understory components of thinned forests, but it has been thought that this is unnecessary because shrubs generally account for a small portion of the total biomass. Yet, there has been uncertainty in how photosynthesis and respiration change with more carbon partitioned to shrubs versus trees in thinned forests.

When simulating carbon fluxes following partial canopy removal, the first question that arises is whether or not ecosystem production should scale with tree canopy retention. The results of this study suggest this is not the case since ecosystem-level light use efficiency was almost 60% higher in thinned plots than in unthinned ones. Moreover, if a process model is parameterized with a measure of post-disturbance leaf area which excluded understory canopies, production capacity would be further underestimated.

The second question that arises is whether or not carbon allocation patterns and thus production and respiration are similar before and after a partial disturbance. In distributing ecosystem process models over large regions it seems obvious that plant physiological traits should vary across environmental gradients. It may also be appropriate to adjust vegetation physiology according successional stage (i.e. pioneer verses climax plant assemblages growing in the same edapoclimatic space). A reliable, quantitative answer to this question will require more detailed autecological information than this particular study has to offer. However, it does appear that differences in the amount of foliage, wood, and root production among the thinning treatments considered in this study did not scale in fixed proportion to tree removal and seemed to shift away from wood and foliage and toward root production in the most recently thinned stands. Even transient shifts vegetation traits associated with partial disturbance may have important consequences in the carbon dynamics of a region where such disturbance is spatially extensive (see Steffen et al., 1996).

The third question regarding the modeling of partial forest disturbance is how best to properly simulate the mass of and decomposition from dead wood left on site following the event. Unfortunately, unlike the autotrophic responses discussed above, the generation of dead wood depends more on the specific nature of the disturbance and less so than on the intrinsic behavior of vegetation. The thinning prescriptions studied here employed a pile-and-burn approach to remove the branch slash left behind by mechanized thinning. As such, the respiration fluxes arising from

post-thinning debris were limited largely to stumps and the dead coarse roots attached to them. For modeling purposes, it seems reasonable to account for the generation of dead coarse roots at a minimum and assign additional volumes of dead decomposing wood according to the specific disturbance mode.

4.4. Future work

Understanding the quantitative influence of forest disturbance on regional carbon dynamics requires consideration of partial tree removal. This is because thinning, insect mortality, and mixed-severity fire affect much more forested area than do stand replacing forms of these disturbances. With climate change functioning to increase mortality from pests and fire there is a need to improve ways of modeling these partial disturbances. The results from this study point toward the need to consider changes in the relative dominance of growth forms (i.e. tree verses shrub) and how these changes may alter the flow and allocation of carbon in the ecosystem from that of either the unthinned condition or a hypothetical condition where trees are removed but composition remains unchanged. Assuming the frequency and type of forest thinning can be accurately quantified through remote detection and or forest inventory data, properly scaling the impacts of thinning on regional carbon dynamics will require continued research on three fronts.

Firstly, stand-level studies like this one need to be carried out over a broader range of forest types and thinning prescriptions and for longer time periods. The scope of inference in this study is limited to a relatively small set of site conditions. The regional range of responses are certain to be dependent on the composition of growth forms prior to thinning, the level and type of thinning, the resource availability that dictates competition, and any post-thinning treatments such as mastication, underburning, or planting. Moreover interannual variability in climate could reveal patterns different than those documented in a single growing season. As evidenced in other studies conducted in the Sierra Nevada Mountains (Kobziar, 2007), thinning can influence the sensitivity of soil respiration to temperature and moisture which may have influenced soil respiration during periods of the day or year not explicitly accounted for in this study.

Secondly, more autecological studies are needed to better characterize the underpinnings of growth form-specific production efficiencies and carbon allocation patterns. While general tendencies in these behaviors have been acknowledged for some time, the conifer-centric approach to forest physiology in western North America has left many important shrub species understudied.

Thirdly, sensitivity analysis preformed on process models wherein growth form-specific production efficiencies and carbon allocation patterns can be specified could help set limits on just how important growth form composition may be across a range of thinning conditions. The results of these analyses would not only help constrain the importance of such vegetation responses but could also guide efforts in future field studies.

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