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Forest Thinning in Ponderosa Pines Increases Carbon Use Efficiency and Energy Flow From Primary Producers to Primary Consumers

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Key Points:

- Forest thinning in high elevation dry forests increased energy flow from primary producers to primary consumers
- Carbon was produced more efficiently in the thinned stands (carbon use efficiency [CUE] = 0.63 and 0.65) versus the unthinned stand (CUE = 0.38)
- Gross Primary Production was similar in the two thinned stands (~3.5 Mg C ha^{-1} yr^{-1}) but was about 30% greater in the unthinned stand (5.0 Mg C ha^{-1} yr^{-1})

Supporting Information:

- Supporting Information S1

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Abstract A better understanding of carbon use efficiency (CUE) and carbon allocation during disturbance is critical to improve simulations of the global carbon cycle and understanding future climate impacts. Forest thinning of high-stem density, high elevation dry western US forests is becoming more common to reduce severe fire danger but there are uncertainties about how forest thinning may impact forest CUE, carbon allocation and energy flow through the food chain. In three, quarter ha stands with similar soils, elevation and climate along a forest thinning gradient near Flagstaff (AZ), we measured total net primary production (NPP of wood, fine root, and leaves), total autotrophic respiration (R_a of wood, rhizosphere, and canopy respiration), gross primary production (GPP = NPP + R_a) and large mammal herbivory (with camera traps and dung counts) over a ~2-year period. We found strong seasonality in all carbon cycling variables and herbivory, peaking during the warm, wet monsoon period. Carbon was produced more efficiently in the thinned stands, with carbon use efficiency (CUE = NPP/GPP) of ~0.63, versus the unthinned stand with CUE of 0.38. GPP was similar in the two thinned stands (~3.5 Mg C ha^{-1} yr^{-1}) but was about 30% greater in the unthinned stands (5.0 Mg C ha^{-1} yr^{-1}). Finally, the thinned stand had higher understory NPP, large herbivore consumption and had triple the total energy going into primary consumers. Overall, the thinning, and the return to a more natural prefire suppression forest structure, increased the CUE and energy flow from primary producers to primary consumers.

1. Introduction

Ponderosa pine (*Pinus ponderosa*) forests account for 22% of western U.S. forests and are an important part of the US carbon stock (Powell et al., 1993). Understanding carbon cycling in these forests will give a better understanding of the North American carbon cycle and the USA's net contribution to climate change. Empirical understanding of carbon cycling in ponderosa forests beyond just photosynthesis and woody biomass is critical to inform land surface models because these models disagree widely (Friedlingstein et al, 2014). By 2,100, there is a 1,000 Pg C discrepancy in land flux among current models, which makes future global climate predictions difficult (Friedlingstein et al., 2014). Much uncertainty of these models is due to uncertainty in carbon use efficiency (CUE: total Net Primary Production [NPP]/Gross Primary Production [GPP]) and how carbon is allocated to long term pools such as wood (De Lucia et al., 2007; Malhi et al., 2011). For instance, *a* ±20% uncertainty in current estimates of CUE in land surface models (between 0.4 and 0.6) could misrepresent an amount of carbon equal to total annual anthropogenic emissions of CO_2 when scaled globally (De Lucia et al., 2007). “Bottom up” measurements of CUE and allocation are rare because they require separate monthly measurements of leaf, wood, and fine root growth (total NPP) and leaf, wood and rhizosphere respiration (total autotrophic respiration) at the same site. It is also important to make these measurements during periods of perturbation such as mega-drought (Williams et al., 2020) and disturbances such as forest thinning (Amiro et al., 2010) to provide empirical data to parameterize and test the models against.

Restoration of high-elevation dry western US forests to their historic lower stand density present before widespread fire suppression efforts is an increasingly important management goal (Covington et al., 1997). Between 1637 and 1883, the historic fire return interval was 3.7 years for all fires and 6.5 years for widespread fires in the southwestern ponderosa pine landscape (Fulé et al., 1997). The fires were previously

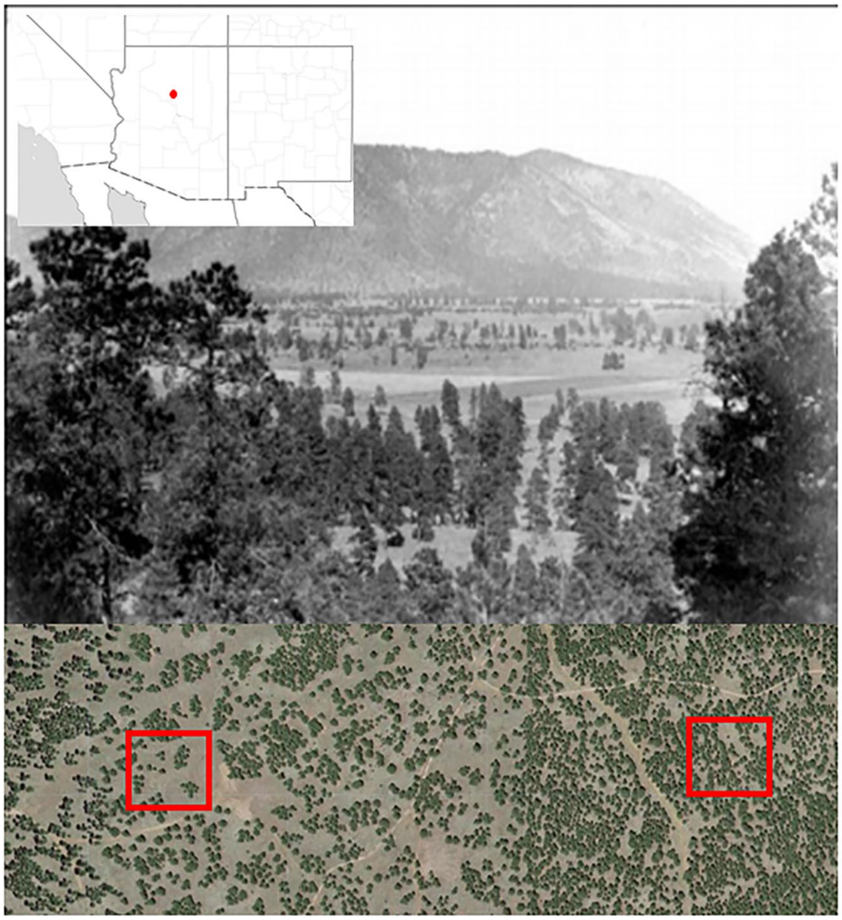

Figure 1. (Top) Historical photo from a nearby region from 1895 before widespread fire suppression efforts (from Northern Arizona University archives). (Top left) Location of our plots (bottom). Google maps image from 2016 with red outlines for stands T-15 (left) and NT (right) showing the forest thinning. Stand T-15 was thinned in 2015. We do not show stand T-17 in the image because the Google maps image was from prior to 2017 and does not show the thinning in T-17.

started by lightning and likely, Native Americans (Allen et al., 2002; Kaye & Swetnam, 1999). Prior to fire suppression efforts, forests typically had 5–100 trees per hectare in small groups and more abundant grasses, forbs, and shrubs (Abella & Denton, 2009; Cooper, 1960; Covington et al., 1997; White, 1985; Figure 1). For example, mean number of trees/ha in 15 AZ and NM stands increased from 77 in 1909 to 519 in 1997 (Moore et al., 2004). A wide range of studies support these findings including verbal descriptions by early explorers (Cooper, 1960), stand data by early scientists (Woolsey, 1911), and dendrochronological and restoration studies (Fulé et al., 1997). Fires have been broadly suppressed in the western US since the late nineteenth century leading to increased stand densities, decreased age and size class diversity, changes in successional dynamics, altered insect and disease dynamics, decreased understory productivity and diversity, and a more even-aged forest structure (Covington & Moore, 1994; Covington et al., 1997).

A review of eddy covariance studies found N. American forests generally lost carbon following a stand-replacing disturbance, but returned to a carbon sink after 10 years for most forests (Amiro et al., 2010). There have been many studies on individual components of the carbon cycle in northern Arizona ponderosa pine forests, especially aboveground biomass changes. For instance, Dore et al. (2012) found that forest carbon stocks recover quickly after thinning because of an increase in growth of residual trees and greater herbaceous production (Dore et al., 2012). Eddy covariance measurements have shown that thinning ameliorates the negative impacts of drought on forest carbon assimilation (Dore et al., 2012). Modeling studies suggest that thinning and associated prescribed burning treatments in ponderosa pine forests reduce carbon storage in the short-term, but protect and stabilize long-term storage in live large trees (Krofcheck et al., 2019; Sorensen et al., 2011). There have been fewer studies of respiration and belowground components. One study showed inconclusive results of the impact of thinning of fine root growth (Dore et al., 2010). Another study showed a reduction in total soil respiration 1 and 2 years after thinning, but soil respiration was not partitioned into autotrophic and heterotrophic components (Sullivan et al., 2008).

High-stem density ponderosa pine stands have high amounts of fuel accumulation which can lead to increased crown fire potential size and intensity. For instance, a survey in 2012 near Flagstaff, AZ, indicated an extreme fire hazard potential in 71% of the area (Stewart, 2014). Following large intense wildfires, there is often an increased risk of flood damage. For example, a recent flood following a fire near Flagstaff, AZ, in 2010 caused tens of millions of dollars of damage to infrastructure and private property (Stewart, 2014). In response, many regions of the southwestern US have begun to thin forests to reduce the possibility of large dangerous fires and subsequent flooding. In Arizona, a recent project called the Flagstaff Watershed Protection Project (FWPP) is thinning forests to reduce the risk of high-severity wildfire and subsequent flooding in two key watersheds (Stewart, 2014). Restoration treatments that include tree thinning to reduce fuel load, followed by prescribed burning, have the potential to improve the ecological health of the forest. However, other studies have found complex relationships between forest thinning and wildfires (Banerjee, 2020).

Such restoration efforts may be even more important in the future as climate change is expected to further increase the likelihood of severe wildfires (Westerling et al., 2006) and drought-related forest die-offs (Van Mantgem et al., 2009). Some climate models predict that the average forest drought stress by the 2050s will exceed that of the most severe droughts in the past 1,000 years (Williams et al., 2013). Climate change in the North American Southwest is predicted to decrease winter precipitation (Seager & Vecchi, 2010) which is the most important water source for mature trees (Kerhoulas et al., 2013). Unusually high-tree mortality has been reported in the North American Southwest during recent droughts, even in unburned forests (Ganey & Vojta, 2011). Productivity of the herbaceous understory in the region's forests is limited by drought, but can be increased by forest restoration treatments like thinning (Moore et al., 2006).

A potential impact of forest thinning is that it will increase light and water availability in the forest understory, which increases understory plant growth (Dore et al., 2012; Moore et al., 2006) and herbivore populations. The most abundant large herbivores in the FWPP region are mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and elk (*Cervus canadensis*). Arizona Game and Fish Department provides annual population trends for these game species and these have been used to predict that forest thinning will increase foraging habitat quality and quantity for elk, have little impact on mule deer populations, and unknown impacts on pronghorn (Stewart, 2014). Here, we propose to address the impact of perturbations like forest thinning on energy flow through the trophic food chain. For instance, thinning may decrease GPP and increase herbivory, but it is unclear how the ratio of herbivory to GPP will change.

As far as we are aware, no studies have measured total NPP, total autotrophic respiration (R_a), and herbivory at the same time and place in N. American forests. Therefore, to better understand the impacts of forest thinning on carbon cycling and herbivore abundance, we investigated three stands in the FWPP (one not thinned, one thinned in 2015, and one thinned in 2017) that have similar soils and climate using a protocol where we measured NPP (leaf, wood and fine root NPP) and autotropic respiration (leaf, wood, and rhizosphere respiration) (Doughty et al., 2015) (detailed methods in Tables 1 and 2). Two previous studies have explored aspects of CUE and carbon allocation in ponderosa pine forests (Dore et al., 2012; Law et al., 1999) but each used different methodologies, did not include herbivory, and only one was along a thinning gradient in high-elevation, dry ponderosa forests. These terms are often poorly parameterized in global models (Malhi et al., 2011) making future climate impact predictions difficult in this region. Such thinning efforts are widespread across regions of the world (Sohn et al., 2016), making it vital to understand how these changes might affect the global carbon cycle. In addition, by estimating herbivory on the same stands we can better quantify impacts of the FWPP on herbivores and see how such changes impact total energy flows and food webs.

The hypotheses tested in this study are threefold:

(1) Forest thinning will increase CUE
(2) Forest thinning will increase carbon allocated to wood
(3) Forest thinning will increase energy flow from primary producers to primary consumers

Table 1
Methods for Intensive Studying of Carbon Dynamics on the Three Ponderosa Pine Stands Near Flagstaff, Arizona

	Component	Description	Sampling period	Sampling interval
Above-ground net primary productivity (NPP_{AG})	Above-ground coarse wood net primary productivity (NPP_{ACW})	Forest inventory: All trees censused to determine growth rate of existing surviving trees and rate of recruitment of new trees. Stem biomass calculated using the Law et al. (2001) allometric equation for ponderosa pines. We measured tree height for every tree once using a laser rangefinder and trigonometry.	November 2017–September 2019	Every 3 months
	Litterfall net primary productivity ($NPP_{litterfall}$)	Litterfall production of dead organic material was estimated by collecting litterfall in 1 m^2 (1 × 1 m) litter traps placed on the ground at the center of each of the six subplots in each stand. We did not account for decay prior to collection as the dry climate makes for slow decomposition rates in pine needles.	July 2018–September 2019	Every month
	Leaf area index (LAI)	Canopy images were recorded with a digital camera and hemispherical lens near the litter trap of each of the six subplots in each stand, at a standard height of 1 m, and during overcast conditions or in a tree shadow.	November 2017–September 2018	Every month
	Herbivory ($Herb_{camera}$ and $Herb_{dung}$)	We used 1–2 camera traps per stand and measured dung fallen in the area of the litter traps to estimate large herbivore herbivory. $Herb_{dung}$ is estimated with dung from the ground litterfall traps.	April 2018–September 2019	Every month
	Understory Net primary production NPP_{under}	We removed all vegetation in 1 m^2 (1 × 1 m) areas immediately adjacent to each of the six littertraps in each stand.	Collected October 2018	Every year

2. Methods

Site description: Our three, quarter ha stands are within ~2 km of each other and have similar soils, climate, and elevation (characteristics compared in Table 3). Soils are shallow, very stony and classified as Mollic eutroborralfs and Lithic eutroborralfs. The climate class is low sun cold and the soil temperature class is frigid (classifications based on Keys to Soil Taxonomy, Eighth Edition, 1998). They are on flat homogenous basalt substrate caused by a lava flow ~300,000 years ago (Duffield, 1997) near Flagstaff AZ at ~2,260 m elevation. The stands are on top of a flat plateau with 0 slope and aspect (<2 m change per 100 m). The thinning was part of the Flagstaff Watershed Protection Project (Figure 1; Stewart, 2014). The vegetation community near our stands is dominated by ponderosa pines (*P. ponderosa*) which occur at elevations ranging from 2,130 to 2,800 m. Understory grasses in the area are typically Arizona fescue (*Festuca arizonica*), pine dropseed (*Blepharoneuron tricholepis*), mountain muhly (*Muhlenbergia montana*), and Kentucky bluegrass (*Poa pratensis*). Average (between 1913 and 1993) precipitation in the region is 577 mm yr^{-1} falling ~half as snow and ~half as summer monsoonal rains, with a mean annual temperature of ~8°C (Savage et al., 1996; Schubert, 2015).

Thinning treatment: Stand T-17 (−111.679024, 35.218921, elevation 2,260 m) was thinned in 2017 and we started measurements a few months after thinning was completed. Stand T-15 (−111.689168, 35.207406,

Table 1
Continued

	Component	Description	Sampling period	Sampling interval
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{coarse\ roots}$)	This component of productivity was not measured directly and was estimated by assuming that coarse root productivity was 0.25 of above-ground woody productivity, based on published values from Law et al. (2001).	n/a	Not directly measured
	Fine root net primary productivity ($NPP_{fine\ roots}$)	Three ingrowth cores (mesh cages 14 cm diameter, installed to ∼30 cm depth) were installed in stands 1 and 3. Cores were extracted and roots were manually removed from the soil samples in three 5 min time steps and the pattern of cumulative extraction over time was used to predict root extraction to 45 min. Root-free soil was then re-inserted into the ingrowth core. This process was repeated for each measurement thereafter.	July 2018–September 2019	Every 3 months
Autotrophic and heterotrophic respiration	Total soil CO_2 efflux (R_{soil})	Total soil CO_2 efflux was measured using a closed dynamic chamber method, near the litterfall trap of each of the 6 subplots in each stand with an infra-red gas analyzer (IRGA; EGM-5) and soil respiration chamber (SRC-1) in the soil.	November 2017–September 2019	Every month
	Soil CO_2 efflux partitioned into autotrophic ($R_{rhizosphere}$) and heterotrophic ($R_{soilhet}$) components	At three points, at each corner of the stand, we placed long collars (40 cm depth) to exclude both roots and mycorrhizae. We did not use the first three months of data to account for the effects of root severing and soil structure disturbance that occurs during installation.	July 2018–September 2019	Every month
	Canopy respiration (R_{leaves})	We did not directly measure leaf dark respiration but used the value for ponderosa pines from Law et al. (1999) (normalized to 10°C) of 0.20 μmol m^{-2} s^{-1}.		Not directly measured
	Above-ground live wood respiration (R_{stems})	Bole respiration was measured using a closed dynamic chamber method, from 6 trees, one per subplot at ∼1.3 m height with an IRGA (EGM-5) and soil respiration chamber (SRC-1) connected to a smoothed part of the tree bole surface.	April 2018–September 2019	Every month

elevation 2,264 m) was thinned in 2015 and we started measurements 2 years after thinning was completed. Stand NT (−111.681604, 35.208055 elevation 2,259 m) was not thinned. Stand NT is 636m from Stand T-15 and 1,170 m from Stand T-17. The area had been previously logged (sawtimber harvest) in 1919, 1925, and 1972. The forest thinning in our stands was done by crews on foot with chainsaws to remove the excess

Table 2
Data Analysis Techniques

Component		Data processing details
Above-ground net primary productivity (NPP_{AG})	Above-ground coarse wood net primary productivity (NPP_{ACW})	Stem biomass calculated using the (Law et al., 2001) allometric equation for ponderosa pines >5 cm dbh: AGB = 4141.644 + 14.509*((D$^{\wedge 2}$)*H) where AGB is aboveground biomass (g), *D* is dbh (cm), and *H* is height (m). To convert biomass values into carbon, we assumed that dry stem biomass is 50% carbon.
	Litterfall net primary productivity ($NPP_{litterfall}$)	$NPP_{litterfall}$ is calculated as follows: $NPP_{litterfall} = NPP_{canopy}$ over annual timescales. Litterfall is oven dried at 70°C to constant mass and weighed. Litter is estimated to be 50% carbon.
	Leaf area index (LAI)	LAI estimated using 6 hemispherical photos taken in each subplot monthly following code developed in Hemiphot.R: Free R scripts to analyze hemispherical photographs for canopy openness, leaf area index and photosynthetic active radiation under forest canopies (ter Steege, 2018).
	Herbivory ($Herb_{camera}$ and $Herb_{dung}$)	The herbivory ($Herb_{camera}$) rate was an estimate of the number of elk, deer, and pronghorn present multiplied by estimated metabolic cost over a time period (10 s) and area. See methods for details. $Herb_{dung}$ is estimated with dung from the ground litterfall traps.
	Understory Net primary production (NPP_{under})	We removed all vegetation in 1 m^2 (1 × 1 m) areas immediately adjacent to each of the 6 littertraps in each stand. Vegetation is oven dried at 70°C to constant mass and weighed. Vegetation is estimated to be 50% carbon.
Below-ground net primary productivity (NPP_{BG})	Coarse root net primary productivity ($NPP_{coarse\ roots}$)	Coarse root production (25% of wood production) following Law et al. (2001).
	Fine root net primary productivity ($NPP_{fine\ roots}$)	Roots were oven dried at 70°C to constant mass and weighed. Roots were manually removed from the soil samples in three 5 min time steps, according to a method that corrects for underestimation of biomass of hard-to-extract roots and used to predict root extraction beyond 15 min (45 min) (Metcalfe et al., 2007); we estimate that there was an additional 26% correction factor for fine roots not collected within 15 min. Due to very rocky soils we did not correct for fine root productivity below 30 cm depth.
Autotrophic and heterotrophic respiration	Soil CO_2 efflux partitioned into Heterotrophic ($R_{soilhet}$) components	The partitioning experiment allows estimation of the relative contributions of soil organic matter by estimating soil respiration with the long tube to exclude all $R_{rhizosphere.}$
	Soil CO_2 efflux partitioned into autotrophic ($R_{rhizosphere}$) components	The partitioning experiment allows estimation of the relative contributions of roots and mycorrhizae by subtracting $R_{soilhet}$ from R_{soil}.
	Canopy respiration (R_{leaves})	To scale to whole-canopy respiration, we multiplied mean dark foliage respiration normalized to 10°C which was 0.20 $\mu mol\ m^{-2}\ s^{-1}$ from Law et al. (1999), by our monthly estimates of LAI. 10°C is close to the measured average air temperature of our stands (~8°C). To account for light inhibition of dark respiration we multiplied our result by 0.67 (Malhi et al., 2009).
	Above-ground live wood respiration (R_{stems})	To estimate stand-level stem respiration tree respiration per unit bole area was multiplied by bole surface area (SA) for each tree, estimated with the equation for a cylinder: $SA = 2\pi\ (DBHb/2) * H + 2\pi r^2$, where H is tree height, and DBHb is bole diameter at 1.3 m height.

density of intermediate trees in the most abundant size class so as to develop uneven-aged structure and a mosaic of openings and tree groups of varying sizes. Openings occupy ~25% of the treatment area (Stewart, 2014) and felled trees were removed from the area. Further details of the thinning are available in an online supplement (SI). In our stands, there were 124 stems ha^{-1} in Stand T-17 (thinned in 2017), 116 stems ha^{-1} in Stand T-15 (thinned in 2015), and 400 stems ha^{-1} in Stand NT (not thinned) including all trees. All trees were ponderosa pines. Mean DBH (>10 cm) was 37 cm (5 trees <10 cm dbh) in Stand T-17, 36 cm (6 trees <10 cm dbh) in Stand T-15, and 30 cm (0 trees <10 cm dbh) in Stand NT. Thinned stands (T-15 and T-17) have more trees at the extremes of height and DBH compared to stand NT (Figure 3).

Carbon fluxes: We estimate ecosystem C flux components (detailed methods in Tables 1 and 2) within the quarter ha stand (divided into 6, 20 m by 20 m subplots) using protocols similar to those developed by the Global Ecosystem Monitoring network (Doughty et al., 2015; Malhi et al., 2021). A detailed description is available online for download (http://gem.tropicalforests.ox.ac.uk). Summaries of the different components quantified, and the field methods and data processing techniques used, are presented in Tables 1 and 2, respectively. Error propagation was carried out for all combination quantities using standard rules of quadrature, assuming that uncertainties were independent and normally distributed. We calculated NPP using the following equation:

$$\mathrm{NPP} = \mathrm{NPP}_{\mathrm{Above\ Ground\ Wood(ACW)}} + \mathrm{NPP}_{\mathrm{litter\ fall}} + \mathrm{NPP}_{\mathrm{fine\ roots}} + \mathrm{NPP}_{\mathrm{coarse\ roots}} + \mathrm{NPP}_{\mathrm{understory}} + \mathrm{Herb}_{\mathrm{dung}} \quad (1)$$

This neglects several small NPP terms, such as NPP lost as volatile organic emissions and litter decomposed in the canopy, but these terms are likely to be small (<5%) (Malhi et al., 2009). Total autotrophic respiration, R_a (detailed methods in Tables 1 and 2) was estimated as

$$R_a = R_{\mathrm{canopy}} + R_{\mathrm{stems}} + R_{\mathrm{rhizosphere}} \quad (2)$$

Here, we count root exudates and transfer to mycorrhizae as a portion of $R_{\mathrm{rhizosphere}}$ rather than as NPP. In quasisteady-state conditions (and on annual timescales or longer where there is no net change in plant nonstructural carbohydrate storage), *GPP* should be approximately equal to the sum of NPP and R_a. Hence, we estimated GPP (detailed methods in Tables 1 and 2) as

$$\mathrm{GPP} = \mathrm{NPP} + R_a \quad (3)$$

We estimated the *CUE* (detailed methods in Tables 1 and 2) as the proportion of total GPP invested in total NPP:

$$\mathrm{CUE} = \mathrm{NPP} / \mathrm{GPP} \quad (4)$$

Herbivory measurements: We estimated large herbivore (mule deer, elk and pronghorn) herbivory in similar units to our carbon cycle measurements (Mg C ha^{-1} yr^{-1}) in two ways, with dung counts and camera traps (Bushnell Trophy Cam HD Essential E2 12MP Trail Camera, two per stand over 18 months). We also estimated carnivore (coyote and bobcat) occurrence with camera traps. We estimated herbivory with camera traps by counting numbers of mule deer, elk and pronghorn in photos which were triggered every 10 s (detailed methods in Tables 1 and 2). We calculated the metabolic needs of the animals observed in each of the photos (10 s snapshot) over an area of 672 m^2 (~1/15 ha) (Bushnell user guide) using the following equation from Wolf et al. (2013):

$$\mathrm{Metabolicrate} = 0.021 * \mathrm{M}^{\wedge 0.716}\mathrm{kgDM} / \# / \mathrm{day} \quad (5)$$

We summed all individual elk, deer, and pronghorn photographed each month. M is mean weight which we estimated at $M = 81$ kg for mule deer (males 65–135 kg, females 45–80 kg) and $M = 47$ kg pronghorn (males 40–65 kg, females 34–48 kg), $M = 160$ kg for elk (males 171 kg, females 150 kg) and coyote/bobcat $M = 14$ kg (males 8–20 kg, females 7–18 kg) (we did not observe any larger carnivores like mountain lions or bears). Each photo of an animal represented 10 s of metabolic cost. We therefore converted the 10 s to a day by dividing by 6 × 60 × 24. We multiplied by 15 to convert the area to ha and by 30 to convert to months. We estimated DM = 50% carbon and animal assimilation efficiency of food is 50% (Chapin et al., 2012). This converted our camera trap abundance numbers to Mg C ha^{-1} mo^{-1} and we call this $\mathrm{Herb}_{\mathrm{camera}}$. We cross

Table 3
Stand Characteristics

	Stand T-17	Stand T-15	Stand, NT
Elevation	2,260 m	2,264 m	2,259 m
Stem density (stems ha^{-1})	124	116	400
Mean DBH (>10 cm)	37	36	30
Total Basal Area (m^2 ha^{-1})	12.4	10.3	30.4
Tree height (m) (>10 cm)	14.6	13.0	14.0
Woody surface area (m^2 ha^{-1})	1,847	1,426	5,426
Slope/aspect	0/0	0/0	0/0
Rocks/Sand/Silt-clay (%)	22/70/8	11/64/5	23/74/3
P parts per thousand (ppt)	0.031 ± 0.008	0.021 ± 0.003	0.026 ± 0.004
Ca (ppt)	1.25 ± 0.24	1.03 ± 0.20	1.20 ± 0.09
Mg (ppt)	0.94 ± 0.19	0.96 ± 0.26	1.01 ± 0.13
K (ppt)	1.66 ± 0.12	1.69 ± 0.09	1.75 ± 0.11

Errors are sd. DBH, diameter at breast height

checked these values by comparing them to the dried weight of dung (50% carbon) fallen in our ground-based litter traps each month in six, 1 m^2 areas per stand. We dried and weighed the dung in a manner similar to the litterfall and we call this $Herb_{dung}$. We found roughly similar values for both methods (Table 4).

Climate: In each stand, we used the TMS-4 soil measurement system to measure soil moisture at a depth of 10 cm and temperature at three depths, −6 (soil), +2 and +12 cm (air) (Wild et al., 2019). We used a conversion tool at http://tomst.com/web/en/systems/tms/software/ to convert data of humidity collected from TMS stations into real values of volumetric soil moisture content and assumed soil type to be sand based on our measurements described below (~95% rocks/sand and ~5% silt/clay).

Soils: We collected soil from three locations per stand (two corners and the center in a line) from the top 5 cm after scraping away the top organic layer. We dried the soils for three days at 70°C. We then measured soil texture with a series of filters (2, 1, 0.25, 0.063 mm) shaking for ~1 min. We defined texture as >2 mm as rock, between 0.063 and 2 mm as sand and below 0.063 mm as silt/clay. We measured chemical composition on each dried, homogenized (<0.25 mm) sample three times with a Bruker Tracer five XRF with a soil calibration which measures all elements with an atomic mass heavier than sodium.

3. Results

Climate: Averaged soil temperature in the unthinned stand NT during 2019/2020 was cooler by several degrees than the thinned stand T-17 for several afternoon hours but similar for the rest of the day (Figure 2a). Unfortunately, the sensor in stand T-15 was damaged by herbivores. Air temperature showed a similar, but reduced pattern (Figure 2b). Volumetric water content was higher in Stand T-17 than NT possibly because of the greater evapotranspiration in Stand NT from more trees (Figure 2c). There was strong seasonal variability in both air temperature and soil moisture at all stands (Figures 2d and 2e)

Soils: Soils across the three stands were similar and very sandy (~95% rocks/sand and ~5% silt/clay) due to the recent substrate (300,000-year old lava flow) (Table 3). Soil chemical composition was broadly similar with some minor variations between stands, such as slightly less phosphorus in Stand T-15 and slightly more cations (Ca, Mg, and K) in Stand NT. Slope and aspect were similar across stands.

Forest Structure: The forest thinning greatly impacted forest structure with the thinned stands having higher structural diversity. Stands T-15 and T-17 have more trees at the taller and shorter and bigger and smaller DBH range than stand NT (Figure 3). Total stand level above-ground biomass in 2017 was 17.9 Mg C ha^{-1} (Stand T-17- thinned in 2017), 14.3 Mg C ha^{-1} (Stand T-15- thinned in 2015) and 42.0 Mg C ha^{-1} (Stand NT,

Table 4

Total Yearly Averaged Aboveground Coarse Wood (ACW), Litterfall Net Primary Production (NPP), Fine Root NPP, Coarse Root NPP, Understory NPP, Total NPP, Large Herbivore Herbivory From Camera Traps and Dung Counts, Wood Respiration, Canopy Respiration, Rhizosphere Respiration, Total Autotrophic Respiration, Total Heterotrophic Soil Respiration, Gross Primary Production (GPP) and Carbon Use Efficiency (CUE) for 1–2 years of Data for Stands T-17, T-15, NT

	Stand T-17	Error	Stand T-15	Error	Stand -NT	Error
$\mathrm{NPP}_{\mathrm{ACW}}$	0.06	0.01	0.14	0.01	0.23	0.02
$\mathrm{NPP}_{\mathrm{litter\ fall}}$	0.64	0.39	0.34	0.19	0.85	0.31
$\mathrm{NPP}_{\mathrm{fine\ roots}}$	1.42	0.55	1.42	0.55	0.72	0.26
$\mathrm{NPP}_{\mathrm{coarse\ root}}$	0.01	0.00	0.03	0.00	0.06	0.01
$\mathrm{NPP}_{\mathrm{under}}$	0.09	0.01	0.12	0.01	0.04	0.00
Total NPP	2.27	0.67	2.15	0.58	1.90	0.40
$\mathrm{Herb}_{\mathrm{camera}}$	0.037	0.004	0.103	0.008	0.006	0.001
$\mathrm{Herb}_{\mathrm{dung}}$	0.021	0.002	0.028	0.003	0.014	0.001
R_{stems}	0.61	0.27	0.52	0.18	1.93	0.77
R_{canopy}	0.35	0.24	0.23	0.15	0.52	0.35
$R_{\mathrm{rhizosphere}}$	0.54	0.25	0.67	0.32	0.70	0.34
R_{a}	1.50	0.51	1.42	0.51	3.16	0.51
R_{soilhet}	0.79	0.36	0.99	0.47	0.92	0.45
GPP	3.63	0.84	3.32	0.72	4.96	1.07
CUE	0.63	0.20	0.65	0.19	0.38	0.10

Units are all Mg C ha^{-1} yr^{-1} except for CUE. Errors are standard error and error is propagated with quadrature.

unthinned). Total number of stems in stand NT was about 4-fold greater (400 ha^{-1} vs. ~120 stems ha^{-1}) than the other stands, but total above ground biomass (AGB) was only about 2.5 times greater as most large trees remained after the thinning.

3.1. Net Primary Production

Above-ground woody NPP: Based on measurements of DBH of all stems every three months from November 2017 to September 2019, $\mathrm{NPP}_{\mathrm{ACW}}$ at stand T-17 was 0.06 Mg C ha^{-1} yr^{-1}, at stand T-15 was 0.14 Mg C ha^{-1} yr^{-1}, and at stand NT was 0.23 Mg C ha^{-1} yr^{-1}. However, individual trees in stand T-15 grew fastest (by an average of 0.44 cm circumference growth over the measurement period) followed by similar growth in stand NT (0.22 cm) and stand T-17 (0.20 cm). There was a strong seasonality in tree growth rate with most growth occurring during the summer monsoon seasons, whereas drought related shrinkage occurred during dry periods (Figure 4a). Dividing the above-ground wood biomass by the above-ground wood biomass productivity, we estimated stem biomass residence times of 183 years for the NT stand. In all three stands, we only noted two instances of tree mortality (but these were 20% of trees <5 cm DBH) with signs of bark removal by herbivores. There were only eight trees <5 cm DBH in all stands and both were in stands T-15 and T-17.

Litterfall NPP: Total canopy NPP was calculated from six, 1 m^2 ground litter traps per stand and was greatest in stand NT, followed by stand T-17 and stand T-15. All stands peaked in total litterfall in October with 0.19 Mg C ha^{-1} mo^{-1} in stand T-17, 0.06 Mg C ha^{-1} mo^{-1} in stand T-15 and 0.28 Mg C ha^{-1} mo^{-1} in stand NT (Figure 4b).

Fine root NPP: In the initial excavation of the three ingrowth cores per stand, fine root stocks were 6.1 ± 2.3 Mg C ha^{-1} for stand T-17 and 5.4 ± 2.8 Mg C ha^{-1} for stand NT. Stand T-17 had almost double the total fine root NPP as stand NT (Figure 4c). Dividing the root biomass by the root productivity, we estimated a fine root biomass residence time of 7.5 years for the NT stand. We did not measure root growth and biomass in stand T-15 and assume it is similar to stand T-17 for our total NPP calculations. There is a strong seasonality to all NPP components generally peaking during the warm wet monsoon period or mid-June to the end of September (Figure 4).

3.2. Respiration

Soil heterotrophic and rhizosphere respiration: Total annually averaged soil respiration peaked in stand T-15 followed by stand NT and stand T-17 (Figure 5a). However, we apply a temperature correction because the average soil temperature (taken at the time and point of each measurement by the PP Systems soil temperature and moisture probe) when our measurements were taken was ~20°C but the average soil temperature at our site was ~8°C. We plotted all our soil respiration data against soil temperature measured at the same time and found a positive linear relationship explained by the relationship $R_{\mathrm{soiltotal}} = 0.0144 *$ soil temp-0.0695 ($R^2 = 0.28$, note this equation is for units grams [CO$_2$] m^2 hr^{-1}). Based on this relationship, total soil respiration taken at the mean annual temperature (8°C) would be 1.3 Mg C ha^{-1} yr^{-1} at stand T-17, 1.7 Mg C ha^{-1} yr^{-1} at stand T-15 and 1.6 Mg C ha^{-1} yr^{-1} at stand NT. There is a strong seasonality to soil respiration peaking during the warm wet monsoon period (Figure 5a).

We calculated the average percentage of respiration attributable to the rhizosphere by subtracting monthly soil respiration values of tubes excluding rhizosphere respiration from those including rhizosphere and heterotrophic respiration. Averaged monthly values of rhizosphere respiration at stand T-17 were 40% of soil respiration and 43% of soil respiration at stand NT. We applied the percent rhizosphere respiration value from stand T-17 to stand T-15 (Figure 5b). Both total annually averaged rhizosphere respiration and heter-

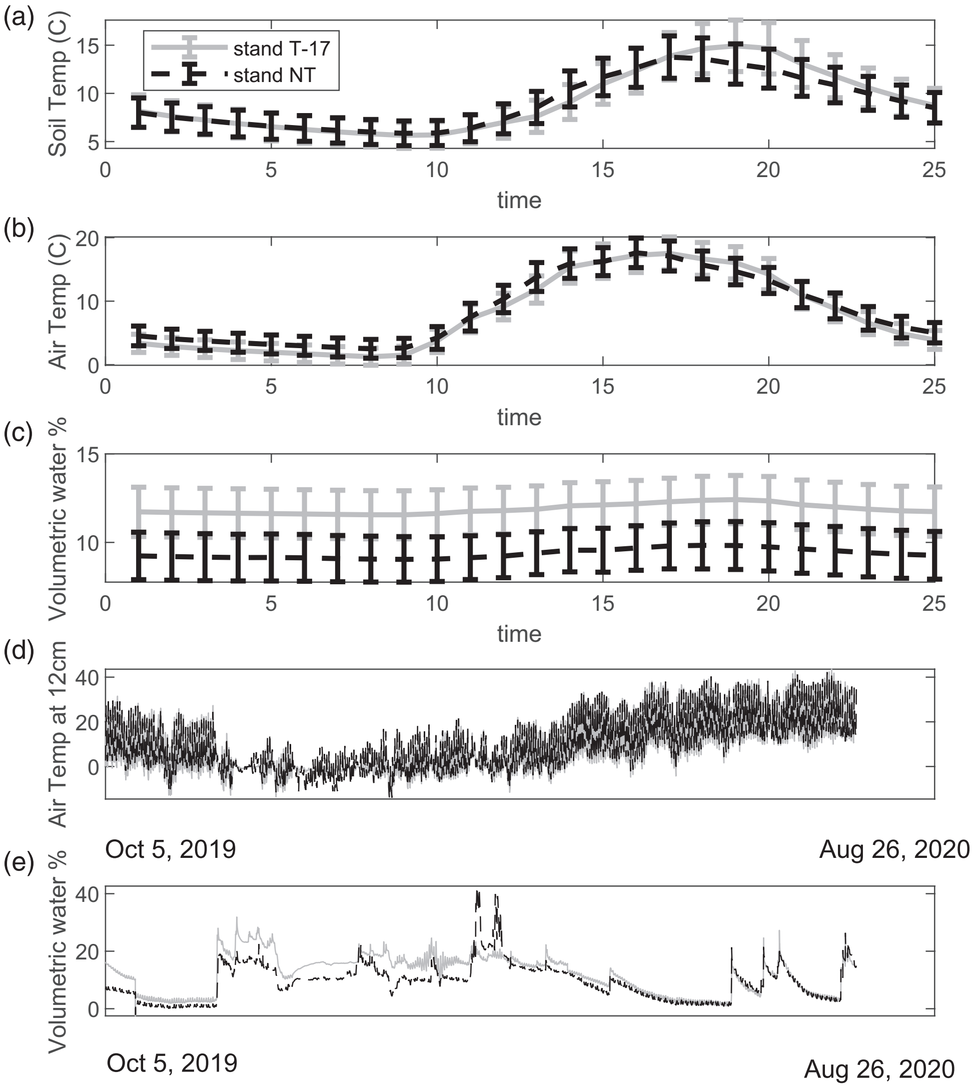

Figure 2. (a) Diurnal soil temperature at 6 cm belowground (error bars are standard errors), (b) diurnal air temperature at 12 cm aboveground, (c) diurnal volumetric water content (%), (d) annual air temperature at 12 cm and (e) annual volumetric water content (%) for stands T-17 (gray) and NT (black) over a 24-h period for ~1 year of data (October 2, 2019–August 26, 2020). Error bars are sd. Stands T-17 is thinned while NT is unthinned.

otrophic respiration was greatest at Stand T-15 followed by Stand NT and Stand T-17. Total soil respiration varied seasonally with a strong peak during the warm wet monsoon period in ~July-September with these values >5-fold higher than the rest of the year (Figure 5a).

Wood respiration: Average tree respiration was greatest at stand T-15 followed by stand NT and stand T-17. There was a seasonal cycle in wood respiration with respiration peaking in the wet warm monsoon months (Figure 5c). To scale these measurements to the stand level, we multiplied total stand woody surface area by our scaled woody respiration fluxes. We estimated total woody surface area of trees at stand T-17 as 1,847 m^2 ha^{-1}, stand T-15 as 1,426 m^2 ha^{-1}, and stand NT as 5,426 m^2 ha^{-1}. We acknowledge this may overestimate surface area as it does not account for tree taper with height increase. However, we apply a temperature correction because the average soil temperature of our measurements was 23°C but the average temperature at our site was ~8°C. We plotted all our wood respiration data against soil temperature measured at the same time and found a positive linear relationship explained by the relationship $R_{\text{wood}} = 0.0025 * \text{soil temp} + 0.084$ ($R^2 = 0.04$)

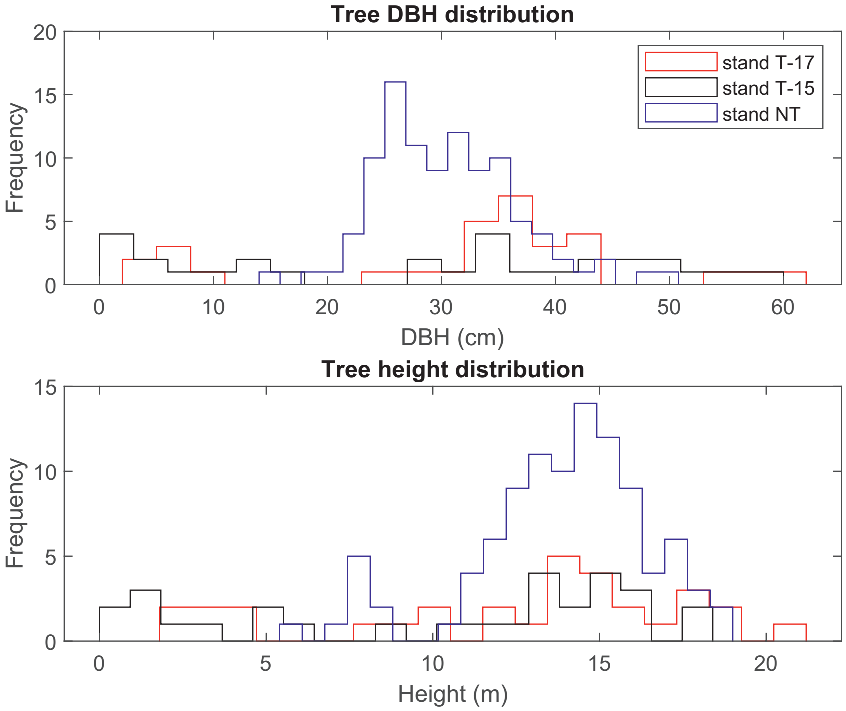

Figure 3. Histograms for diameter at breast height (DBH) (top) and tree height (bottom) between the stands.

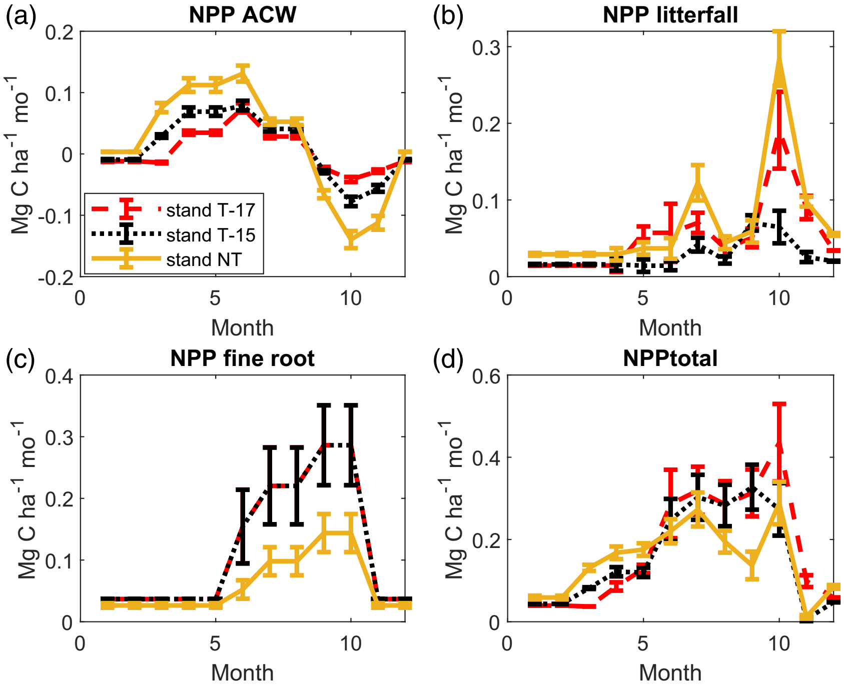

Figure 4. (a) Woody NPP from measuring every tree per stand with a diameter at breast height (DBH) tape every 3 months over a 2-year period for stand T-17 (red dashed), stand T-15 (black dotted) and stand NT (orange). (b) Fine root NPP from three ingrowth cores in Stands T-17 and NT collected every three-six months over a 15-month period. (c) Sum of the monthly collections from 6 traps per stand of total litter in a 1 m^2 area over a 1-year period. (d) Total NPP is the sum of the fine root, wood and litter NPP and here does not include NPP components such as understory, herbivory, or coarse roots because we have no seasonal data on these components. All units are Mg C ha^{-1} mo^{-1} and errorbars are standard errors. Stands T-15 and T-17 are thinned while NT is unthinned. NPP, net primary production.

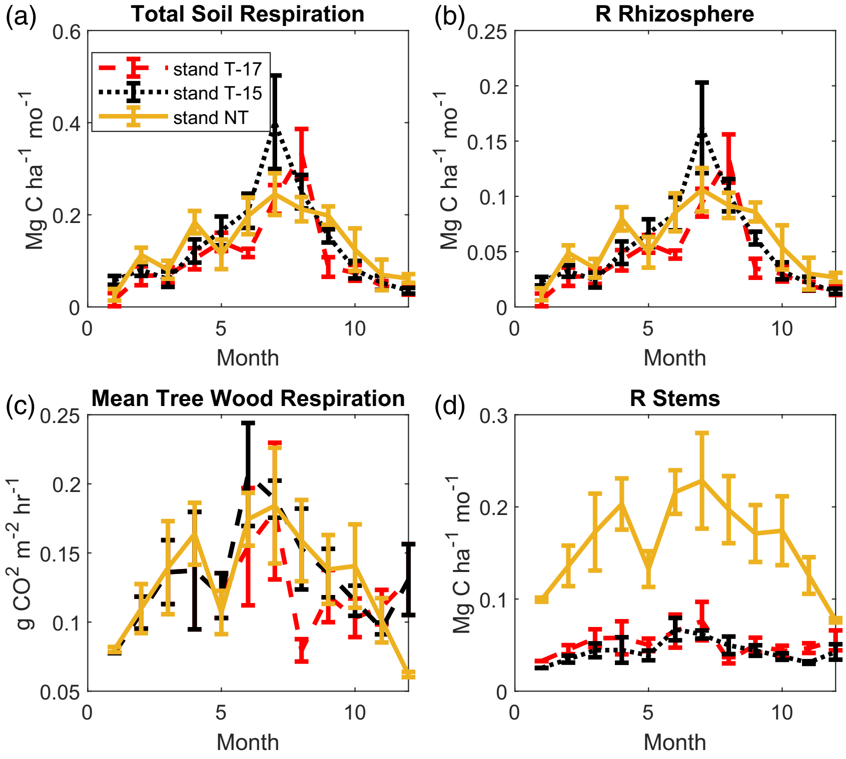

Figure 5. (a) Total soil respiration and (b) autotrophic soil respiration measured at six locations per stand monthly over a ~2-year period for stand T-17 (red dashed), stand T-15 (black dotted) and stand NT (orange) near Flagstaff, Arizona, USA. Autotrophic respiration was determined by an exclusion experiment ($N = 3$ per stand), where respiration was measured from tubes after roots and mycorrhizae had been removed. (c) Average tree above-ground wood respiration from six trees per stand measured every month and (d) multiplied by the total woody surface area of the stand over a 16-month period, (c) are in units of grams (CO$_2$) m^2 hr^{-1} and (d) is in units of Mg C ha^{-1} mo^{-1} and error bars are standard errors. Rhizosphere respiration is assumed to be a constant fraction of total soil respiration. Stands T-15 and T-17 are thinned, while NT is unthinned.

(although the R^2 is low, the fit is significant [$P < 0.05$]). Based on this relationship, our measurements taken at the mean annual temperature (8° vs. 23°C), total annual woody respiration would be 0.61 Mg C ha^{-1} yr^{-1} at stand T-15, 0.52 Mg C ha^{-1} yr^{-1} at stand T-15 and 1.9 Mg C ha^{-1} yr^{-1} at stand NT. There is a moderate seasonality to wood respiration with a peak during the warm, wet monsoon period (Figures 5c and 5d).

Leaf respiration: Leaf Area Index (LAI) measured with six hemispherical photos per stand per month averaged 0.68 ± 0.49 m^2 m^{-2} at stand T-17, 0.37 ± 0.43 at stand T-15 and 1.01 ± 0.38 m^2 m^{-2} at stand NT. There was not a seasonal cycle in LAI in the stands. We did not directly measure leaf dark respiration but used the value from Law et al. (2001) (normalized to 10°C which is close to the average air temperature measured at our site of 8°C) of 0.20 µmol m^{-2} s^{-1}. To account for light inhibition of dark respiration we multiplied our result by 0.67 (as in Malhi et al., 2009). Based on these results, we estimate total annual canopy respiration averaged was greatest at stand NT followed by stand T-17 and stand T-15 (Table 4).

Total productivity, autotrophic respiration and CUE: We added annually averaged fine root NPP, above-ground woody NPP, understory NPP, canopy NPP, herbivory NPP, and estimated coarse root NPP (25% of above-ground woody NPP) to estimate a stand level NPP of 2.27 Mg C ha^{-1} yr^{-1} for stand T-17, 2.15 Mg C ha^{-1} yr^{-1} for stand T-15, and 1.90 Mg C ha^{-1} yr^{-1} for stand NT (Figure 6a and Table 4). We added annually averaged rhizosphere respiration, woody respiration, and leaf respiration to estimate total autotrophic respiration at 1.50 Mg C ha^{-1} yr^{-1} for stand T-17, 1.42 Mg C ha^{-1} yr^{-1} for stand T-15, and 3.16 Mg C ha^{-1} yr^{-1} for stand NT. We added total autotrophic respiration to total NPP to estimate total GPP at 3.63 Mg C ha^{-1} yr^{-1} for stand T-15, 3.32 Mg C ha^{-1} yr^{-1} for stand T-17, and 4.96 Mg C ha^{-1} yr^{-1} for stand NT (Figure 6b). We divided total NPP from total GPP to estimate CUE at 0.63, 0.65, and 0.38. There is a strong seasonality to

GPP (or more accurately plant carbon expenditure, PCE) peaking during the warm wet monsoon period (Figure 6c). Seasonality is less pronounced in total autotrophic respiration and CUE increases almost linearly until October when it drops.

Herbivory: We estimated herbivory due to larger species (deer, elk, and pronghorn) in two ways: with camera traps and with dung counts. Using 1–2 camera traps per stand and Equation 5, we calculated the energy expended by the animals when in frame and averaged this per month (Figure 7) and per year. We find that herbivory was greatest at stand T-15 followed by stand T-17 and stand NT (Figure 7a; Table 4). Dung count estimates had a similar pattern between the stands. We note a reasonable agreement between the two methods with both methods estimating stand T-15 having the highest herbivory. This amount is 48% of understory NPP with the camera trap method and 28% using the dung count method. We estimate carnivore biomass as a percent of herbivore biomass to average 0.04% for all three stands and slightly higher in stand NT at 0.06% (Table 5). There is a strong seasonality to herbivory that matches seasonality of other carbon fluxes (Figures 6 and 7). Thinning tripled energy flow into primary consumers (herb/GPP) with herbivores consuming 0.28% of GPP in the unthinned stand (NT) and 0.71% in the thinned stands (average of T-15 and T-17).

4. Discussion

Forest thinning affected the ponderosa forest in some expected ways, such as increasing understory NPP and herbivore abundance. It also increased the CUE of the forest in the thinned stands (0.63 and 0.65) versus the unthinned stand (0.38) (Table 4 and Figure 8). There were also some unexpected changes, such as higher NPP allocation to root growth in the thinned stands than the unthinned stand. Overall, GPP was similar in the two thinned stands ~3.5 Mg C ha^{-1} yr^{-1} but was about 30% greater in the unthinned stands (5.0 Mg C ha^{-1} yr^{-1}). There was not a clear trend in growth rates of individual trees in our stands (T-15 grew fastest, followed by stand NT and stand T-17). Past studies have documented greater growth rates of "big trees" like those in T-15 and T-17 in even-aged and uneven-aged stands (Blanche et al., 1985; O'Hara, 1988; Waring et al., 1980). The increase in understory growth (~0.06 Mg C ha^{-1} yr^{-1}) did not offset the loss of tree photosynthetic area following thinning in terms of total carbon fixed.

Our estimates of GPP are lower than from other ponderosa pine stands in the US. Near our stands in Flagstaff AZ, thinning of a ponderosa pine forest from 472 stems/ha to 143 stems/ha (vs. 400 and ~120 at our stands) reduced GPP (measured by eddy covariance) from 9.1 to 8.3 Mg C ha^{-1} yr^{-1} (vs. 5.0 and 3.5 at our stands), and reduced NPP from 2.45 to 2.41 Mg C ha^{-1} yr^{-1} (vs. 2.2 and 1.9 at our stands) (Dore et al., 2010). LAI in the Dore et al. (2010) study was reduced from 1.5 to 0.9 m^2/m^2 (vs. ~1.0 and ~0.55 m^2/m^2 at our stands). Therefore, in our stands, both GPP and LAI are ~55% of the Dore et al. (2010) study, but NPP is similar for both studies which suggests between site variability in CUE. In contrast, the differences in GPP could be partially methodological (eddy covariance vs. bottom up scaling), although previous work has found similar GPP estimates between these methods (Doughty et al., 2015). In another study, a young ponderosa pine forest in central Oregon had a GPP of 8.0 Mg C ha^{-1} yr^{-1} and a NPP of 3.6 Mg C ha^{-1} yr^{-1} and a relatively undisturbed old-growth forest Oregon had a GPP of 10.4 Mg C ha^{-1} yr^{-1} and a NPP of 4.7 Mg C ha^{-1} yr^{-1} (Law et al., 2001). These values are more than double our estimates of GPP (~3.5 Mg C ha^{-1} yr^{-1} in the thinned and 5.0 Mg C ha^{-1} yr^{-1} in the unthinned). CUE was similar between the Oregon stands (~0.45) and the average for our stands (~0.50 average). The Law et al. (2001) study reported similar carbon allocation of NPP (60% roots, 20% wood, and 20% leaves) to our study (57% roots, 7% wood, and 30% leaves) with most fixed carbon going toward roots. Therefore, average CUE and carbon allocation were similar between our Arizona site and the Law et al. (2001) Oregon site even though our GPP was ~half of GPP in Oregon. Carbon fluxes at our site were greater during the two-month warm, wet monsoon period (Figures 4–6); low activity in other seasons due to cold and aridity likely limits total annual GPP. Nutrient limitation due to young soils (~300 K years) (Duffield, 1997) at our stands also could also limit GPP.

Our thinned stands produced carbon more efficiently (CUE ~0.63) than the unthinned stand (CUE ~0.38). The thinned stands are as efficient as the unthinnned stands during the dormant season, but more efficient during the growing season (Figure 6c). The thinned stands have similar total NPP to the unthinned stand during the dormant season and slightly more total NPP during the growing season (mainly due to increased root growth) than the unthinned stand (Figure 4) while R_a is uniformly lower in the thinned

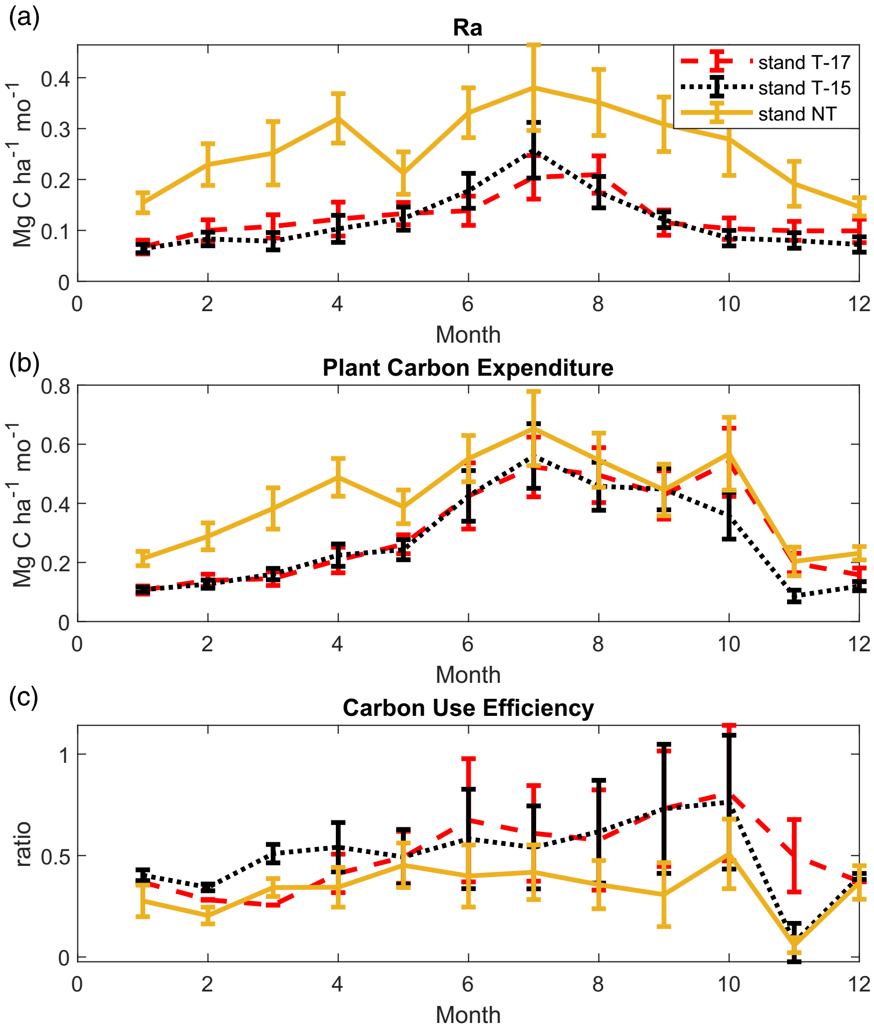

Figure 6. Total autotrophic respiration (a), total plant carbon expenditure (PCE = NPP + Ra) (b) and carbon use efficiency (c) at a monthly timescale for Stand T-17 (red dashed), Stand T-15 (black dotted) and Stand NT (orange). PCE is a proxy for GPP. All values are in units of Mg C ha^{-1} mo^{-1}, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP and errorbars are standard errors. Stands T-15 and T-17 are thinned, while NT is unthinned. NPP, net primary production; GPP, gross primary production; PCE, plant carbon expenditure.

than unthinned stands. The thinned stands have lower R_a than the unthinned stand mainly due to higher R_{stems} in the unthinned stand. Per tree respiration is similar between the stands, but the threefold increase in stem density increases R_{stems} threefold in the unthinned stand. Therefore, it is the lower respiratory cost (R_a per total NPP) of maintaining biomass during the dormant season that appears to make the thinned stands more efficient. Thinning at another nearby site also showed similar (but smaller) trends in CUE to our stands (Dore et al., 2010). CUE can vary widely in forests and previous studies in temperate, boreal (Goulden et al., 2011) and Amazonian forests (Doughty et al., 2018) have found less carbon allocation to growth in older forests. However, it is important to note that forests can also change their CUE by becoming more efficient (increase CUE) during times of stress. For instance, a tropical site reduced autotrophic respiration rates during a major drought period (Doughty et al., 2015). Therefore, we intend to continue to monitor CUE to see if the change was temporary or more permanent.

The forest thinning surprisingly led to more growth allocated toward fine roots. This result differs from most previous studies (e.g., Dore et al., 2010). Forest thinning may increase soil compaction and decrease soil macroporosity due to the use of heavy machinery (Han et al., 2009), although this is unlikely in our study as most thinning was done with hand crews and chain saws. One possibility is the increased animal

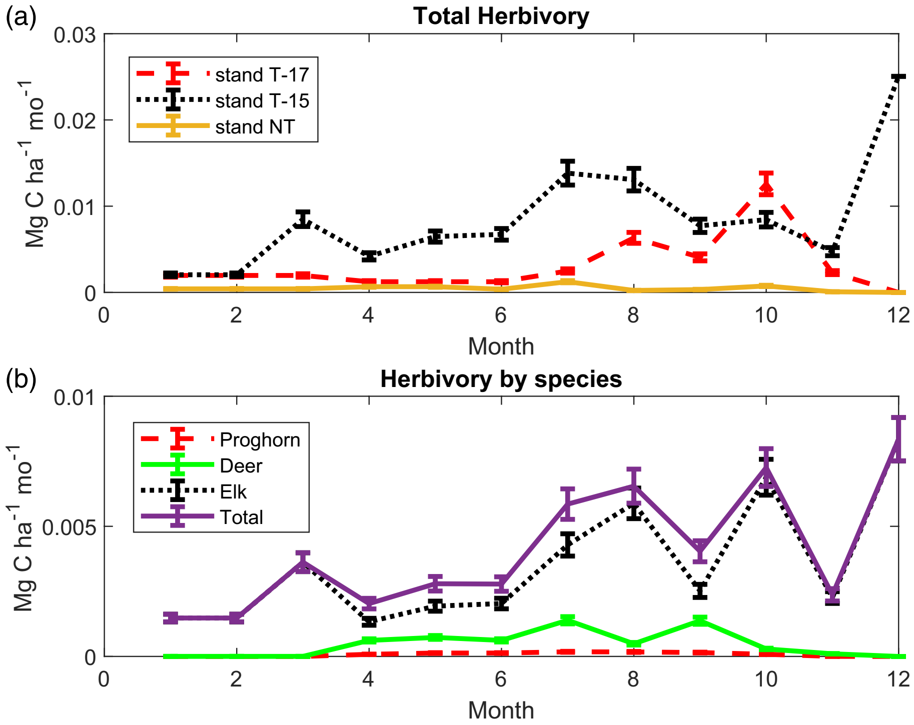

Figure 7. Camera trap estimated herbivory as measured in each stand (a) for Stand T-17 (red dashed), Stand T-15 (black dotted) and Stand NT (orange) and by species (b) over a yearly cycle. All values are in units of Mg C ha^{-1} mo^{-1} and errorbars are standard errors. The high Elk value in December is likely anomalous as there was a stationary herd near the camera on a single day. Stands T-15 and T-17 are thinned, while NT is unthinned.

dung in the thinned stands triggered an increase in root growth to access nutrients in dung. Other studies found an increase in woody NPP compared with leaf NPP following logging but no change in root allocation (Anderson-Teixeira et al., 2016; Riutta et al., 2018). The Law et al. (2001) study found similar fine root NPP at both a young and old site. Why was more carbon allocated belowground both absolutely and as a percentage in the thinned stands (Table 5)? One possibility is that reduced tree water stress and higher leaf-level photosynthesis in the thinned stands provided more carbon for growth of the organ responsible for capturing the most limiting resource, which is root growth in a semi-arid forest where water is the most limiting resource. However, this result must be considered tentative because of our low ingrowth core sample size ($N = 6$) and thus requires future evaluation.

Plots T-15 and T-17 were thinned two years apart, but our study did not show large differences between these two plots. There were, however, large differences between the thinned plots and unthinned plots, which suggests that there are immediate changes (<3 months) and possibly longer-term changes (>5 years), but fewer medium-term changes (~2 years) to these forests following thinning. Future studies will need to address these longer term changes to vegetation structure as well as, for example, how competition/succession of nonwoody vegetation will affect tree growth in the thinned stands.

We measured a 2–3-fold increase in understory NPP that was available for consumption by herbivores in the thinned stands versus the unthinned stand (Table 4) similar to previous studies in the region (Kaye et al., 2005).

Table 5
Net Primary Productivity (NPP) Allocation to Wood, Fine Roots, and Canopy

	Stand T-17	Stand T-15	Stand, NT	Mean
$\mathrm{NPP}_{\mathrm{ACW}}$	3	7	12	7
$\mathrm{NPP}_{\text{litter fall}}$	29	16	45	30
$\mathrm{NPP}_{\text{fine roots}}$	64	69	38	57
R_{stems}	41	37	61	46
R_{canopy}	23	16	16	19
$R_{\mathrm{rhizosphere}}$	36	47	22	35
$\mathrm{Herb}_{\mathrm{dung}}$	23	24	38	28
$\mathrm{Herb}_{\mathrm{camera}}$	42	86	15	48
Carn/Herb	0.04	0.03	0.06	0.04
$\mathrm{Herb}_{\mathrm{dung}}$/GPP	0.58	0.84	0.28	0.57

Notes. These do not quite equal 100% because we do not include some minor terms like NPP under. Partitioning of autotrophic respiration into stem, canopy and rhizosphere respiration. Large herbivore consumption of understory NPP, total carnivore mass divided by total herbivore mass and herbivore consumption of GPP for 1–2 years of data for stands T-17, T-15 and NT and the mean for all stands near Flagstaff AZ, USA. Units are all percentages. NPP, net primary production; GPP, gross primary production

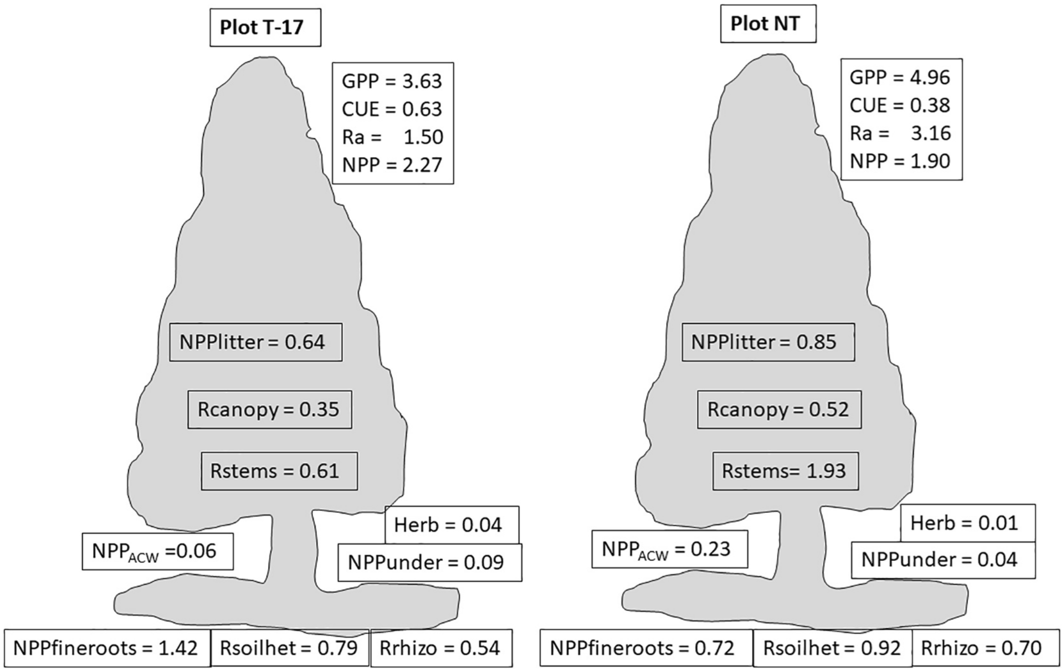

Figure 8. Diagram showing the magnitude and pattern of key carbon fluxes for Stand T-17 the thinned stand (left) and Stand NT the unthinned stand (b) near Flagstaff, Arizona, USA. Components with prefixes *R*, NPP denote respiration, and NPP terms respectively. Herb is the average large mammal herbivory estimate of the dung and camera trap methods. Detailed descriptions of C flux components measured are presented in Tables 1–4. All values are in units of Mg C ha^{-1} yr^{-1}, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP. Stand T-17 is thinned, while NT is unthinned. NPP, net primary production; GPP, gross primary production.

There was also a 2–3-fold (using dung count) increase in herbivore abundance in the thinned stands. Although our two methods (dung and camera traps) broadly agree, both were based on small sample sizes and future studies should expand sample sizes. Increased herbaceous vegetation typically increases mammal abundance (Jenness, 2000). The high percentage (between 30% and 60%) of understory (nontree) NPP that was consumed by large herbivores has been found by other studies as well. For instance, high densities of bison consumed ∼1 Mg C ha^{-1} yr^{-1} in a tall-grass Kansas prairie (Towne et al., 2005) or >50% of NPP of a typical tall grass prairie (∼1.8 Mg C ha^{-1} yr^{-1}) (Olson et al., 2013). More broadly, a review found that large herbivores reduced aboveground NPP by an average of 0.7 Mg C ha^{-1} yr^{-1} for temperate grasslands to 4.8 Mg C ha^{-1} yr^{-1} for temperate forests (Tanentzap & Coomes, 2012). However, much of this change is through herbivore impacts on plant community dynamics. The high consumption of understory NPP suggests the system is a bottom up (food limited) versus top down (predator) controlled system where an increase in food consumption will increase herbivore abundance since there are few predators in the system (there are mountain lions [Puma concolor] that eat deer and juvenile elk). We measured carnivore abundance with our camera traps and found a body weighted abundance percentage of 0.04%. This indicates very low number of carnivores in the system and carnivores too small to exert top down control on this system. Therefore, thinning appeared to increase energy flow from primary producers to primary consumers.

We documented only two trees dying in all three stands over the 2-year observation period. Both were small trees (<5 cm DBH) in Stand T-15 that had signs of bark removal by herbivores. In all stands, there were few small trees (N = 8 trees <5 cm DBH in stands T-17 and T-15, none in stand NT). Twenty percent died in a 2-year period, most likely killed by herbivores in stand T-15 (based on visual evidence of bark removal), which had the highest rate of herbivory. Therefore, this is limited evidence that the thinning is a self-reinforcing process with thinned stands having higher understory NPP, which attracts and supports more large herbivores, which then increases the mortality rate of small ponderosa trees and maintains the lower stem density forest. However, we acknowledge the stands are too small and the duration of the study is too short to get robust estimates of mortality and therefore this result needs further research for confirmation.

It is interesting to put herbivory in ponderosa pine forests into a broader historical context. Recent changes include abnormally high elk populations due to: (A) introduction of Rocky Mountain elk about a century ago, (B) creation of artificial water sources specifically to maintain high populations, (C) near extirpation of wolves from the region. Over evolutionary timescales (>12,000 years before present) there were many large herbivores and carnivores. For instance, the goal of the FWPP is to restore forests to how they were prefire suppression ~200 years ago. However, for most of their evolutionary history, this region had large megaherbivores (>1,000 kg) and megacarnivores (>100 kg) (Malhi et al., 2016). In fact, the Americas once had the largest concentration of large carnivores (Van Valkenburgh et al., 2016) and one of our study species (pronghorn) co-evolved with these now extinct predators. The pronghorn's exceptionally large eyes and great speeds, second only to extant African cheetahs (*Acinonyx jubatus*), are thought to be evolutionary adaptations to counter the extinct North American species of cheetahs (*Miracinonyx sp.*) (Geist, 2001).

There is now good evidence that the presence of large herbivores can greatly impact forest structure (Bakker et al., 2016; Doughty et al., 2016) and thin the forest in a manner similar to the FWPP. The historic large carnivores most likely did not exert much top down control on the megaherbivores since their large size makes them much less vulnerable to predation (Van Valkenburgh et al., 2016). Mega-herbivores like elephants (or likely mammoths or mastodons) have a much larger overall impact on tree disturbance than mid-sized herbivores like elk (Asner & Levick, 2012). We hypothesize that past thinning by megaherbivores could have similarly increased forest efficiency and energy flow through the trophic food chain.

Overall, CUE varied between our study and other ponderosa studies but carbon allocation was similar to these previous studies (Dore et al., 2010; Law et al., 2001). Carbon was produced more efficiently in the thinned stands (CUE 0.63 and 0.65) versus the unthinned stand (CUE 0.38). The thinning more than doubled understory grass and forb NPP which led to more than a doubling of large mammal herbivory. The thinning, and the return to a more natural prefire suppression stand structure, increased the efficiency of the forest both in terms of carbon storage and energy flow through the trophic food chain. Due to the amount of work necessary to make all the measurements, we only measured three stands, which make statistical certainty of the effect of thinning elusive. In addition, the small plot size (0.25 vs. 1 ha in most other GEM plots, Doughty et al, 2015; Malhi et al., 2021) may limit understanding, but this was justified based on the lower biodiversity of the Arizona plots. Overall, our study shows sensitivity of forest carbon balance to widespread management treatments and supports the incorporation of food chains into assessments of forest carbon cycling to obtain a more holistic understanding of ecosystem impacts.

Data Availability Statement

We have archived all our data and code in Zenodo at https://doi.org/10.5281/zenodo.4432997

Acknowledgments
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