Carbon fluxes and herbivory in ponderosa pines stands across a forest thinning chronosequence

Christopher E. Doughty, Andrew Abraham, Tomos Prys-Jones

***Abstract*—Forest thinning of overgrown Western US forests is becoming more common to reduce severe fire danger. Such large changes in forest structure could impact the global carbon budget, but despite being relatively well studied, there are uncertainties on how forest thinning may impact forest carbon use efficiency, carbon allocation, and herbivore abundance. In three, quarter ha plots along a forest thinning chronosequence near Flagstaff, Az, we measured total NPP (wood, fine root, and litter), total autotrophic respiration (wood, rhizosphere, and canopy respiration) and large mammal herbivory (with camera traps and dung counts) over a 2-year period. We found strong seasonality in all carbon cycling parameters and herbivory peaking during the warm, wet monsoon period. Forest thinning increased understory NPP, herbivore abundance and small tree mortality. Carbon was produced more efficiently in the thinned stands (Carbon use efficiency – CUE = 0.63 and 0.61) versus the un-thinned stand (CUE 0.39). Unexpectedly, carbon allocated towards root growth increased in the thinned stands. Overall, GPP was similar in the two thinned sites 4.3 Mg C ha-1 year-1, but was about 30 per greater in the un-thinned site (5.68 Mg C ha-1 year-1). Overall, the thinning, and the return to a more natural pre-fire suppression landscape, increased the efficiency of the forest both in terms of carbon and animals.**

I. INTRODUCTION

Recent efforts have been made to restore Western US forests to their historic lower stand density that was present before widespread fire suppression efforts. For instance, between 1637 and 1883 the historic fire return interval was 3.7 yr for all fires and 6.5 yr for widespread fires in the southwestern ponderosa pine (Pinus ponderosa) landscape [1]. These fires were previously started by lightning and possibly Native Americans [2][3]. Prior to theses fire suppression efforts, forests typically had 2 -40 trees per acre in small groups within more abundant grasses, forbs, and shrubs [4][5][6][7](Figure 1). A wide range of studies support these finding including verbal descriptions by early explorers [5], plot data by early scientists [8], and tree ring, dendrochronological, and restoration studies [9][4]. Fires have been broadly suppressed in the area since the late 19th century and this has led 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 [10][11]. Today many current Ponderosa pines germinated in 1919 when increased fire suppression and decreased herbivory prevented tree loss while favorable climatic conditions led to stand regeneration.

(Figure 1). These Ponderosa Pine stands now show decreased tree vigor and increased fuel accumulation which can lead to increased crown fire potential size and intensity. For instance, a large survey in 2012 near Flagstaff AZ indicated an extreme fire hazard potential in 71 percent of the area [12]. Following large intense wildfires there is often an increase in flooding such as a recent flood following a fire in 2010 that caused tens of millions of dollars of damage to infrastructure and private property. In response, many regions of the Southwest have begun to thin forests to reduce the possibility of large dangerous fires and flooding. In Arizona, a recent project called the Flagstaff Watershed Restoration Project (FWRP) is thinning forests to reduce the risk of high severity wildfire and subsequent flooding in two key watersheds [12]. Restoration treatments that include thinning out trees to reduce fuel load, followed by prescribed burning, has the potential to improve the ecological health of the forest. Such restoration efforts

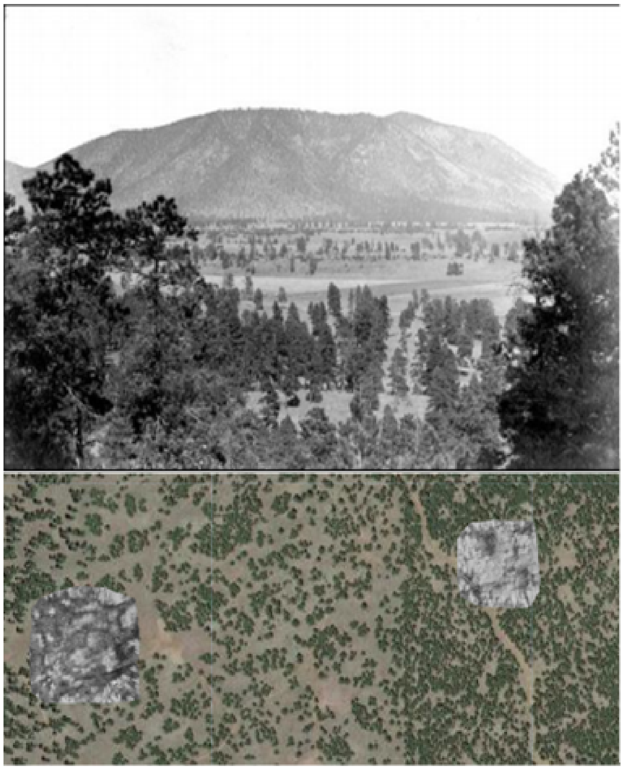

Fig. 1. (top) Historical photo from a nearby region from 1895 before widespread fire suppression efforts (from Northern Arizona University archives). (bottom) NDVI drone imagery for Plots 2 (left) and 3 (right) (greyscale) overlaid on a Google maps image showing the forest thinning. Note – Plot 3 is slightly to the right of the UAV image and does not include the trail.

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may be even more important in the future as climate change and continued fire suppression are hypothesized to further increase the likelihood of severe western wildfires [13][14]. Some climate models predict that the average forest drought stress by the 2050s will exceed that of the most severe droughts in the past 1000 years [15]. Droughts between 2002 to 2007 led to a tree mortality rate of 22 percent in ponderosa pine trees greater than 28 inches diameter at Breast Height (DBH) [16]. Climate change in the North American southwest is predicted to lead to decreased winter precipitation [17], which could decrease herbaceous cover dependent on winter precipitation, although herbaceous productivity in the southwest is primarily controlled by summer precipitation delivered by the North American monsoon (NAM). The effect of climate change on the NAM, which accounts for roughly half the precipitation in the region, is uncertain.

Another potential impact of forest thinning is that it will increase light availability in the forest understory, which could increase understory NPP and herbivore populations. The most abundant large herbivores in the region are mule deer (Odocoileus hemionus), pronghorn (Antilocapra Americana), and Elk (Cervus canadensis). It has been predicted that FWRP will open the canopy, thereby increasing foraging habitat quality and quantity for elk, which have already been increasing in the area [12]. In contrast, deer have been generally declining, but no impact on deer population is anticipated [12]. The forest-wide Pronghorn population trend is stable and FWRP is expected to increase habitat and habitat quality for pronghorn [12]. However, the increase in habitat quality is too small to alter forest-wide population trends.

To better understand the impacts of the FWRP on carbon cycling and herbivore abundance, we have set up three carbon cycling plots (one not thinned, one thinned 4 years ago, and one thinned 2 years ago) following a protocol where we measure all Net Primary Production (NPP) (leaf, wood and fine root NPP) and autotropic respiration (leaf, wood and rhizosphere respiration) [18]. Even in well studied forests like Ponderosa pines, there is still uncertainty in what drives changes in carbon use efficiency (CUE) and carbon allocation. These terms are often not well parameterized in global models[19] and this will make future climate predictions difficult in this region. Such thinning efforts are widespread across regions of the world, making it vital to understand how these changes might affect the global carbon cycle. In addition, by estimating herbivory at the same plots we can better quantify impacts of the FWRP on herbivores and see how such changes impact total energy flows and food webs. The hypotheses tested in this paper are threefold. Firstly, the removal of dense stands would allow trees more space for growth and we hypothesize trees will take advantage of this and 1) Forest thinning will increase CUE. Next, with more space, there might be a selective advantage to gaining height and we hypothesize that 2) Forest thinning will increase carbon allocated to wood. Finally, there will be more light available to understory plants after the thinning and we hypothesize 3) Forest thinning will increase understory NPP and herbivore abundance.

II. METHODS

A. Site information

Our three, quarter ha plots are on homogenous basalt substrate caused by a lava flow 300,000 years ago [20] near Flagstaff AZ at 7000 ft elevation. Plot 1 (-111.679024, 35.218921) was thinned in 2017 and we started measurements a few months after thinning was completed, Plot 2 (-111.689168, 35.207406) was thinned in 2015 and we started measurements 2 years after thinning was completed, and Plot 3 (-111.681604, 35.208055) was not thinned. The thinning was part of the Flagstaff Watershed restoration project (Figure 1) [12]. The vegetation community near our plots is dominated by ponderosa pines (Pinus ponderosa) with the occasional oak, juniper and aspen which occur at elevations ranging from 7,000 to 9,200 feet. Ponderosa pine forests are the most widely distributed pine in North America accounting for 22 percent of western U.S. forests [21]. In our plots, there were 124 stems ha-1 in Plot 1 (thinned 2 years ago), 116 ha-1 in Plot 2 (thinned 4 years ago), and 400 ha-1 in Plot 3 (not thinned). All trees were Ponderosa Pines. Mean and median DBH of the trees in Plot 1 was 32 and 35 cm, Plot 2 was 30 and 34 cm, and Plot 3 was 30 and 30 cm. Our plots have a mean annual temperature of 7.6^{o}C and mean annual precipitation of 750 mm yr-1.

B. Carbon Fluxes

We estimate ecosystem C flux components within the quarter ha plot (divided into 6, 20m by 20m subplots) using protocols similar to those developed by the RAINFOR – GEM network (Doughty et al., 2015). 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 SI Tables 1 and 2, respectively. We calculated net primary production (NPP) using the following equation:

$$EQ1 : NPP = NPP AboveGroundWood(ACW)$$

$$+NPP litterfall + NPP fineroots + NPP coarseroot$$

This neglects several small NPP terms, such NPP lost as volatile organic emissions and litter decomposed in the canopy. Total autotrophic respiration - Ra is estimated as

$$EQ2 : Ra = Rcanopy + Rstems + Rrhizosphere$$

Here we count root exudates and transfer to mycorrhizae as a portion of Rrhizosphere rather than as NPP. In quasi-steady state conditions (and on annual timescales or longer where there is no net change in plant non-structural carbohydrate storage), GPP should be approximately equal to the sum of NPP and Ra. Hence, we estimated GPP as

$$EQ3 : GPP = NPP + Ra$$

We estimated the CUE as the proportion of total GPP invested in total NPP:

$$EQ4 : CUE = NPP/GPP$$

C. 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 – 2 per plot). To estimate herbivory with camera traps, we counted numbers of Mule deer, Elk and Pronghorn using photos which were triggered every 10 seconds. We estimate that their presence represented a metabolic rate based on eq 5 over 10 second (repeat time of camera traps) over an area of 672 m2 or 1/15th of a ha (field of view 34.7 degrees and 36m deep). We estimate metabolic needs for each animal over that 10 second period using the following equation from [22] Wolf et al 2013:

$$EQ5 : Metabolicrate = 0.021 * M^{0}.716kgDM/ind/day$$

We sum all individual elk, deer, and pronghorn photographed each month. M is mean weight which we estimate is M= 81 kg for mule deer (males 65 to 135 kg, females 45 to 80 kg) and M= 47 kg pronghorn (males 40 to 65 kg, females 34–48 kg), M=160 kg for elk (males 171 kg, females 150 kg) and coyote M=14kg (males 8 to 20 kg , females 7 to 18 kg). Each photo of an animal represents 10 seconds of metabolic cost. We therefore convert the 10 seconds to a day by dividing by 6*60*24. We multiply by 15 to convert the area to ha and by 30 to convert to months. We estimate DM=50percent carbon and animal assimilation efficiency of food is 50percent. This converts our camera trap abundance numbers to Mg C ha-1 mo-1 and we call this Herbcamera. We crosscheck these values by comparing them to the dried weight of dung fallen in our ground based litter traps each year in six, 1 m2 areas per plot. We dried and weighed the dung in a manner similar to the litterfall and we call this Herbdung. We found roughly similar values for both methods (Table 1).

D. Climate

In each plot, we used the TMS-4 soil measurement system to measure soil moisture and temperature at 3 levels, in a depth of -6, +2 and +15cm [23]. 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 volume soil humidity and assumed soil type to be Sandy Loam B.

III. RESULTS

A. Climate

Soil temperature was warmer in the un-thinned Plot 3 than the thinned Plot 1 (the sensor in Plot 2 was damaged by herbivores), although this difference decreased towards the late afternoon (Figure 2a). Air temperature was warmer at night in Plot 3 but was similar to Plot 1 during the daytime (Figure 2b). Volumetric water content was higher in Plot 1 than 3 possible because the greater temperatures in Plot 3 increased evaporative demand (Figure 2c).

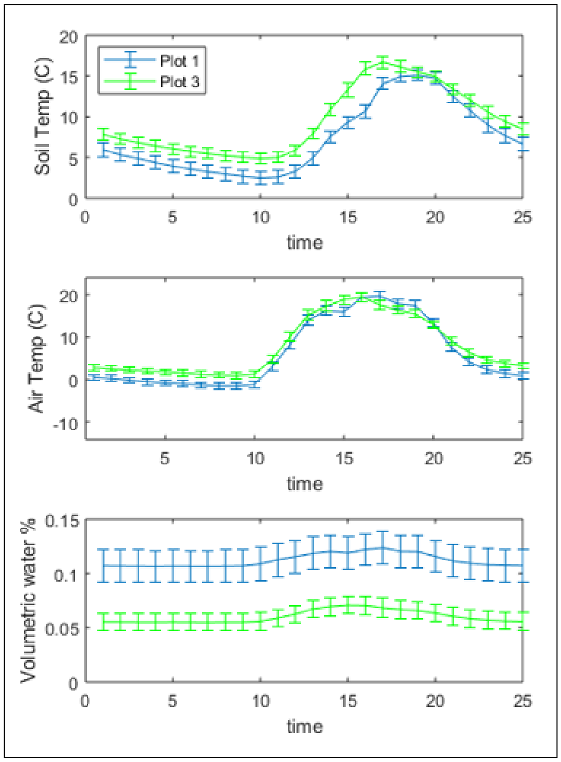

Fig. 2. (top) Soil temperature at 6 cm belowground, (middle) air temperature at 12cm, and (bottom) volumetric water content (percent) for Plots 1 (blue) and 3 (green) over a 24-hour period from 3 months of data (Sept to Dec).

B. Net Primary Production

Above-ground woody NPP - Total stand level above-ground biomass in 2017 was 17.5 Mg C ha-1 (Plot 1- thinned 2 years ago), 14.5 Mg C ha-1 (Plot 2- thinned 4 years ago) and 43.0 Mg C ha-1 (Plot 3 - un-thinned). Total stem number in plot 3 was about four-fold greater (400 ha-1, vs 120 stems ha-1) than the other plots, but total Above Ground Biomass (AGB) was only about 2.5 times as most large trees remained after the logging. We measured the DBH of all stems every three months from Nov 2017 to Sept 2019, and NPPACW at Plot 1 was 0.09 Mg C ha1 year1, 0.19 Mg C ha1 year1 in Plot 2, and in Plot 3 was 0.33 Mg C ha1 year1. However, individual trees in Plot 2 grew fastest (3percent) followed by plot 3 (1.8percent) and plot 1 (1.1 percent). There was a strong seasonality in tree growth rate with most growth during the summer monsoon seasons (Figure 3a). Dividing the above-ground wood biomass by the above-ground wood biomass productivity, we estimated stem biomass residence times of 204, 76, and 132 years for the three plots respectively. We estimated coarse root NPP as 25 percent of stem NPP and therefore plot 1 was 0.02 Mg C ha1 year1, plot 2 was 0.05 Mg C ha1 year1, and plot 3 was 0.08 Mg C ha1 year1.

In all three plots, we only noted two instances of tree mortality and both were in Plot 2 of small trees (¡5cm) with signs of bark removal from herbivores. There were only eight trees ¡5cm DBH in all plots and both were in Plots 1 and 2, none in Plot 3. 20 percent of trees ¡5cm DBH died over our 2-year study period.

Litterfall NPP – Total canopy NPP was an average from six, 1 m2 ground litter traps per plot with Plot 1 averaging 0.64 Mg C ha-1 yr-1, Plot 2 averaging 0.34 Mg C ha-1 yr-1, Plot 3 averaging 0.87 Mg C ha-1 yr-1. All sites peaked in total litterfall in October with 0.19 Mg C ha-1 month-1 in Plot 1, 0.06 Mg C ha-1 month-1 in Plot 2 and 0.28 Mg C ha-1 month-1 in Plot 3.

Fine root NPP - In the initial excavation of the 3 ingrowth cores per plot, we measured fine root stocks and found stocks for Plot 1 (6.1 2.3 Mg C ha-1) and Plot 3 (5.4 2.8 Mg C ha-1). Plot 1 had more total fine root NPP, averaging 1.86 0.23 Mg C ha-1yr-1 than Plot 3 averaging 0.92 0.26 Mg C ha-1yr-1. Dividing the above-ground wood biomass by the above-ground wood biomass productivity, we estimated fine root biomass residence times of 3.3 and 5.8 years for the two plots. We did not measure root growth and biomass in Plot 2 and assume it is similar to Plot 1 for our total NPP calculations. There is a strong seasonality to all NPP components generally peaking during the warm wet monsoon period (Figure 3).

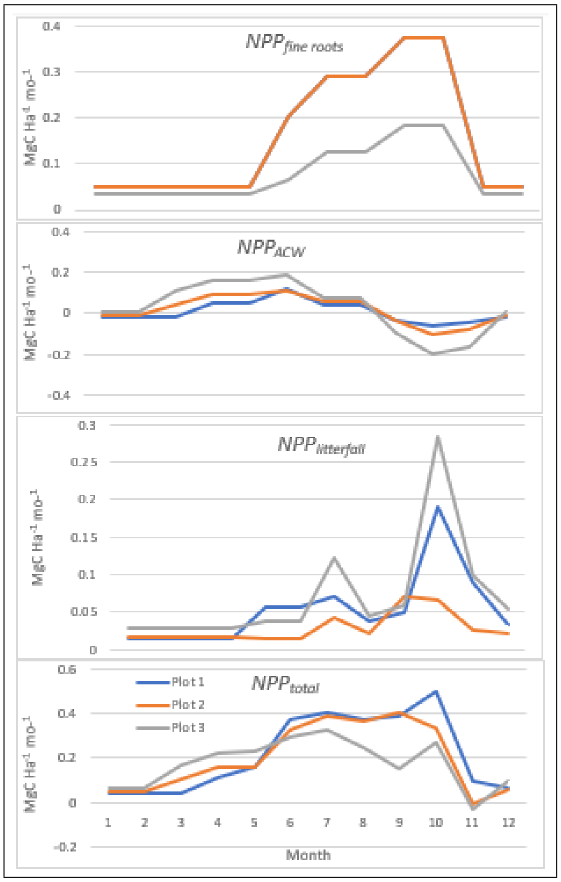

Fig. 3. (a) Fine root NPP from 3 ingrowth cores in Plots 1 and 3 collected every three-six months over a 15-month period. (b) Woody NPP from measuring every tree per plot with a DBH tape every 3 months over a 2-year period. (c) Sum of the monthly collections from 6 litter traps per plot of total litter in a 1 m2 area over a 1-year period. (d) Total NPP is the sum of the fine root, wood and litter NPP. All units are Mg C ha1 mo1

C. Respiration

Soil heterotrophic and rhizosphere respiration - Total annually averaged soil respiration averaged 7.6 3.4 Mg C ha-1 year-1 at Plot 1, 11.0 4.0 Mg C ha-1 year-1 at Plot 2 and 9.2 4.7 Mg C ha-1 year-1 at Plot 3. However, we apply a temperature correction because the average temperature when our measurements were taken was 20.4^{o}C but the average temperature at our site was 7.6^{o}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 Rsoiltotal = 0.0144*soil temp - 0.0695 (R2 = 0.28). Based on this relationship, total soil respiration taken at the mean annual temperature (7.6^{o} C) would be 1.4 Mg C ha-1 year-1 at Plot 1, 2.0 Mg C ha-1 year-1 at Plot 2 and 1.7 Mg C ha-1 year-1 at Plot 3. There is a strong seasonality to soil respiration peaking during the warm wet monsoon period (Figure 4).

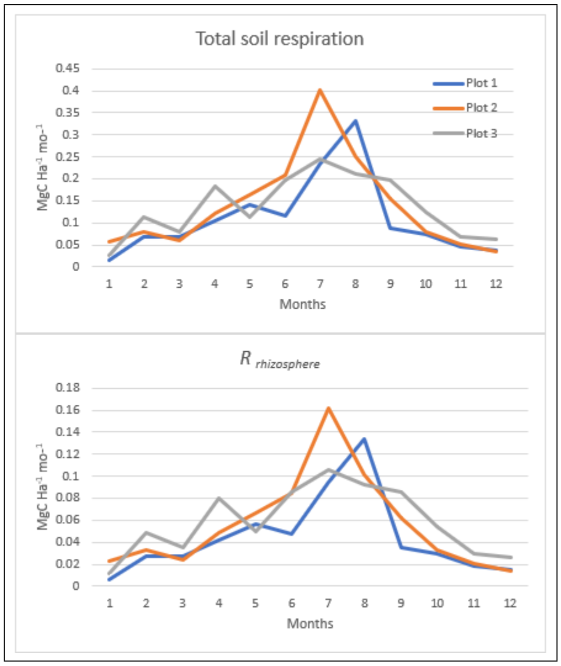

Fig. 4. (top) Total soil respiration and (bottom) autotrophic respiration measured at 6 locations per plot monthly over a 2-year period for Plot 1 (blue), Plot 2 (orange) and Plot 3 (grey) near Flagstaff Az, USA. Autotrophic respiration was determined by an exclusion experiment (N = 3 per plot), where respiration was measured from tubes after roots and mycorrhizae had been removed. All values are in units of Mg C ha1 mo1.

We calculated the average percentage respiration attributable to the rhizosphere by subtracting monthly values of tubes excluding rhizosphere respiration from those including rhizosphere and heterotrophic respiration. Averaged monthly values of rhizosphere respiration at Plot 1 were 34 percent of soil respiration and 43 percent of soil respiration at Plot 3. We applied the percent rhizosphere respiration value from Plot 1 to Plot 2. Total annually averaged rhizosphere respiration averaged 0.56 Mg C ha-1 year-1 at Plot 1, 0.8 Mg C ha-1 year-1 at Plot 2 and 0.72 Mg C ha-1 year-1 at Plot 3. Total annually averaged heterotrophic respiration averaged 0.81 Mg C ha-1 year-1 at Plot 1, 1.18 Mg C ha-1 year-1 at Plot 2 and 0.94 Mg C ha-1 year-1 at Plot 3.Total soil respiration varied seasonally with a strong peak during the warm wet monsoon period in July-Sept with these values greater than 5 fold higher than the rest of the year.

Wood respiration - Total estimated woody surface area of trees at Plot 1 was 1887 m2 ha-1, Plot 2 was 1535 m2 ha-1 and 5745 m2 ha-1 for Plot 3. Average tree respiration was 0.13 0.06 grams (CO2) m2 Hour-1 at Plot 1, 0.16 0.06 at Plot 2, and 0.14 0.06 at Plot 3. There was a seasonal cycle in wood respiration with respiration peaking in the wet warm monsoon months (Fig 3). To scale these measurements to the plot level we multiplied total plot woody surface area by our scaled woody respiration fluxes. However, we apply a temperature correction because the average temperature of our measurements was 22.8°C but the average temperature at our site was 7.6°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 Rwood = 0.0025*soil temp + 0.084 (R2 = 0.04). Based on this relationship, our measurements taken at the mean annual temperature (7.6° vs 22.8°C), total annual woody respiration would be 0.66 Mg C ha-1 year-1 at Plot 1, 0.75 Mg C ha-1 year-1 at Plot 2 and 2.2 Mg C ha-1 year-1 at Plot 3. There is a moderate seasonality to wood respiration peaking during the warm wet monsoon period (Figure 5).

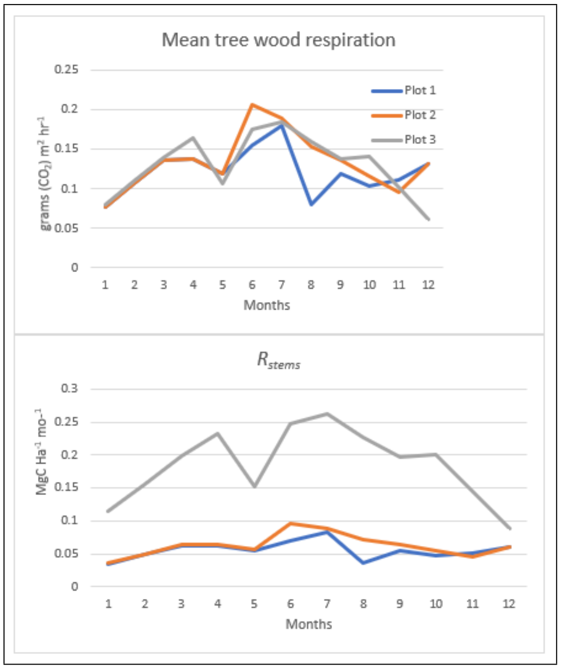

Fig. 5. (top) Average tree above-ground wood respiration from 6 trees per plot measured every month and (bottom) multiplied by the total woody surface area of the plot over a 16-month period. Top values are in units of grams (CO2) m2 hr-1 and bottom values are in units of Mg C ha1 mo1.

Leaf respiration - Leaf Area Index (LAI) measured with six hemispherical photos per plot per month averaged 0.68 0.49 m2 m-2 at Plot 1, 0.37 0.43 at Plot 2 and 1.01 0.38 m2 m-2 at Plot 3. There was not a seasonal cycle in LAI at the plots. We did not directly measure leaf dark respiration but used the value from Law et al 2001 (normalized to 10C) of 0.20 mol 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 0.35 Mg C ha-1 year-1 at Plot 1, 0.23 Mg C ha-1 year-1 at Plot 2, 0.51 Mg C ha-1 year-1 at Plot 3.

TABLE I

Total yearly averaged fine root NPP, litterfall NPP, aboveground coarse wood (ACW) NPP, coarse root NPP, understory NPP, total NPP, large herbivore herbivory from camera traps and dung counts, rhizosphere respiration, canopy respiration, wood respiration, total autotrophic respiration, total heterotrophic soil respiration, GPP and CUE for 1-2 years of data for Plots 1-3 and an average of all three plots in Flagstaff AZ, USA. Units are all Mg C ha-1 year-1.

	Plot 1	Plot 2	Plot 3	Mean
$NPPfineroots$	1.86	1.86	0.92	1.55
$NPPlitterfall$	0.64	0.34	0.87	0.62
$NPPACW$	0.09	0.19	0.33	0.20
$NPPcoarseroot$	0.02	0.05	0.08	0.05
$NPPunder$	0.09	0.12	0.04	0.08
NPP	2.70	2.56	2.23	2.50
$Herbcamera$	0.06	0.11	0.01	0.06
$Herbdung$	0.02	0.03	0.01	0.02
$Rrhizosphere$	0.56	0.67	0.72	0.69
$Rcanopy$	0.35	0.19	0.51	0.35
$Rstems$	0.66	0.75	2.22	1.21
Ra	1.57	1.65	3.45	2.26
$Rsoilhet$	0.81	1.18	0.94	0.97
GPP	4.27	4.21	5.68	4.75
CUE	0.63	0.61	0.39	0.54

D. Total productivity, autotrophic respiration and CUE

We added annually averaged fine root NPP, above-ground woody NPP, understory NPP, canopy NPP, and estimated coarse root NPP (25percent of above-ground woody NPP) to estimate a plot level NPP of 2.70 Mg C ha-1 year-1 for Plot 1, 2.56 Mg C ha-1 year-1 for Plot 2 , 2.23 Mg C ha-1 year-1 for Plot 3 (Figure 6). We added annually averaged rhizosphere respiration, woody respiration, and leaf respiration to estimate total autotrophic respiration at 1.57 Mg C ha-1 year-1 for Plot 1, 1.65 Mg C ha-1 year-1 for Plot 2, 3.45 Mg C ha-1 year-1 for Plot 3. We added total autotrophic respiration to total heterotrophic respiration to estimate total GPP at 4.27 Mg C ha-1 year-1 for Plot 1, 4.21 Mg C ha-1 year-1 for Plot 2, 5.68 Mg C ha-1 year-1 for Plot 3. We divided total NPP from total GPP to estimate carbon use efficiency (CUE) at 0.63, 0.61 and 0.39. There is a strong seasonality to GPP (or more accurately plant carbon expenditure -PCE) peaking during the warm wet monsoon period (Figure 6). Seasonality is less pronounced in total autotrophic respiration and carbon use efficiency increases almost linearly until October when it drops.

E. Total productivity, autotrophic respiration and CUE

We estimated large herbivore (deer, elk, and pronghorn) herbivory in two ways: with camera traps and with dung counts. Using 1-2 camera traps per plot, we estimate the metabolic cost of being in the frame for all animals per month (Figure 7) and year and sum this to 0.06 Mg C ha-1 year-1 for Plot 1, 0.11 Mg C ha-1 year-1 for Plot 2, and 0.01 Mg C ha-1 year-1 for Plot 3 (Table 1). We compare this to dung count estimates of 0.02 Mg C ha-1 year-1 for Plot 1, 0.03 Mg C ha-1 year-1 for Plot 2, and 0.01 Mg C ha-1 year-1 for Plot 3. We note a general good agreement between the two methods with both methods estimating Plot 2 having the highest herbivory. However, we also note these values seem high compared with our understory NPP estimates and average

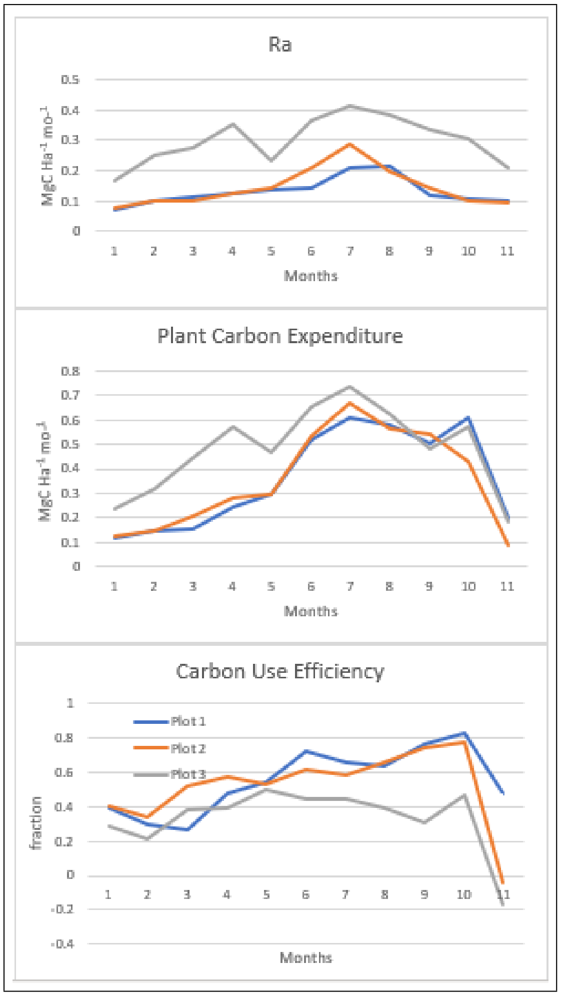

Fig. 6. Total autotrophic respiration (top), total plant carbon expenditure (NPP + Ra) (middle) and carbon use efficiency (bottom) at a monthly timescale for the three plots. All values are in units of Mg C ha1 mo1, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP.

60 percent of understory NPP with the camera trap method and 28 percent using the dung count method. We estimate carnivore abundance as a percent of herbivores to average 0.04 percent for all three plots and slightly higher in plot 3 at 0.06 percent (Table 2). There is a strong seasonality to herbivory that matches seasonality of other carbon fluxes (Figure 6 and 7).

TABLE II

Patterns of carbon NPP allocation, large herbivore consumption of understory NPP, total carnivore mass divided by total herbivore mass and partitioning of autotrophic respiration for 1-2 years of data for Plots 1-3 and the mean for all plots near Flagstaff AZ, USA. Units are all percentages.

	Plot 1	Plot 2	Plot 3	Mean
$NPPfineroots$	69	73	41	61
$NPPlitterfall$	24	13	39	25
$NPPACW$	4	9	18	11
$Herbcamera$	64	93	23	60
$Herbdung$	23	24	37	28
$Carn/Herb$	0.04	0.03	0.06	0.04
$Rrhizosphere$	35	46	21	34
$Rcanopy$	22	11	15	16
$Rstems$	42	43	64	50

Fig. 7. Camera trap estimated herbivory as measured in each plot (top) and by species (bottom) over a yearly cycle. All values are in units of Mg C ha1 mo1. The high Elk value in December is likely anomalous as there was a stationary herd near the camera one day.

IV. DISCUSSION

Forest thinning affected the Ponderosa forest in some expected ways like increasing understory NPP, herbivore abundance and small tree mortality. It also increased the efficiency of the forest and carbon was produced more efficiently in the thinned stands (0.63 and 0.61) versus the dense stand (Plot 3 – CUE 0.39) (Figure 8). There were also some unexpected changes such as increasing carbon allocated towards root growth in the thinned stand. Overall, GPP was similar in the two thinned sites 4.3 Mg C ha-1 year-1, but was about 30 percent greater in the unthinned site (5.68 Mg C ha-1 year-1). Therefore, the increase in understory growth (0.15 Mg C ha-1 year-1) did not offset the loss of tree photosynthetic area following thinning in terms of total carbon fixed.

Our estimates of GPP and NPP are lower than from other Ponderosa Pine sites in the US. For instance, a young ponderosa pine forest in central Oregon had a GPP of 8.0 Mg C ha-1 year-1 and a NPP of 3.6 Mg C ha-1 year-1 and a relatively undisturbed old-growth forest Oregon had a GPP of 10.4 Mg C ha-1 year-1 and a NPP of 4.7 Mg C ha-1 year-1 (B E Law et al., 2001). These values are more than double our estimates of GPP 4.3 Mg C ha-1 year-1 in the thinned and 5.68 Mg C ha-1 year-1 in the unthinned. Carbon use efficiency was similar between the Oregon sites (0.45) and the average for our sites (0.54 average). The Law et al 2001 study had similar carbon allocation to our study with most fixed carbon going towards roots (60 percent roots, 20 percent wood, and 20percent leaves) versus (60 percent roots, 25 percent wood, and 15 percent leaves at our site [24]. Therefore, average CUE and carbon allocation numbers were similar between our site and the Law et al 2001 work even though our GPP was half the values of the Oregon plots. Our lower total GPP estimates may indicate a more challenging environment for Ponderosa. Although average temperatures are similar (7.6^{o}C vs 8^{o}C) and Flagstaff get more precipitation (750mm rain (a third in snowfall) versus 550mm yr-1), these averages mask very cold winters and very dry spring and early summers at our site. Our site seems to be mainly active (Figure 3-6) during the two-month warm, wet monsoon period which likely will limit total photosynthesis. Nutrient limitation due to young soils (300K years)[20] could also limit photosynthesis.

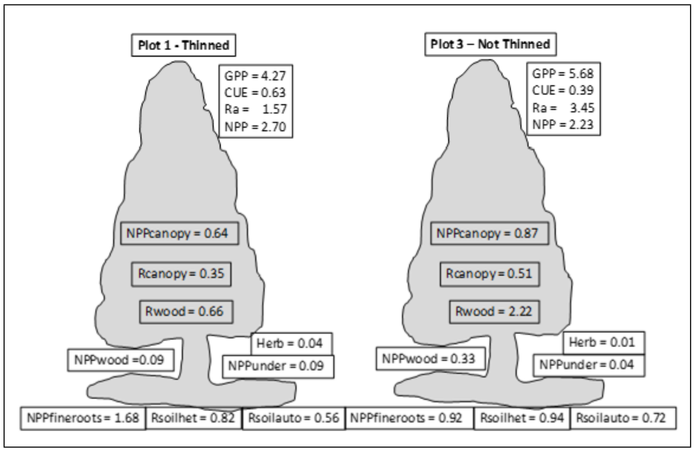

Fig. 8. (Diagram showing the magnitude and pattern of key carbon fluxes for Plot 1 the thinned stand (left) and Plot 3 the un-thinned stand (b) near Flagstaff, AZ, USA. Components with prefixes R, NPP denote respiration, and net primary production terms respectively. Herb is the average large mammal herbivory estimate of the dung and camera trap methods. Detailed descriptions of C flux components measured are presented in SI Tables 1-2. All values are in units of Mg C ha1 year1, with the exception of carbon use efficiency (CUE) which is calculated as total NPP/GPP.

Our thinned stands produced carbon more efficiently (CUE 0.6) than the unthinned stands (CUE 0.4). We initially hypothesized that we might see the opposite because the thinning preferentially removes the smaller trees that grow more and respire less while keeping the larger trees that grow little and respire more. For example, previous studies have found that less carbon was allocated to growth in older forests in temperate, boreal [25][26] and Amazonian forests [27]. However, it was also hypothesized that the thinning could increase CUE because removal of dense stands would allow trees more space for growth. We found evidence for this second hypothesis and more efficient forests following the thinning. However, it is important to note that existing forests can also change their CUE becoming more efficient (increase CUE) during times of stress. For instance, a tropical site reduced autotropic respiration rates during a major drought period [18]. Therefore, we intend to continue to monitor CUE to see if the change was temporary due to the stress of the logging or a more permanent sign of increased efficiency.

The forest thinning surprisingly led to more growth allocated towards fine roots. This result differs from most previous studies. For example, forest thinning often increases soil compaction and decreases soil macroporosity due to the use of heavy machinery [28]. In previous studies, this led to reduced root growth due to increased resistance of soil to root penetration [29]. Other studies found changes in carbon allocation strategy following logging but no change in root allocation [30][31].The Law et al 2001 study found similar fine root NPP at both a young and old site. Why was more allocated belowground both absolutely and as a percentage in the thinned sites (Table 2)? One possibility suggested by game theory optimization (GTO) models is that less space for roots (more compaction) could increase root growth competition and increase allocation of carbon towards roots [32]. However, we do not want to overinterpret our results because of our low ingrowth core sample size (N=6) and we wait for future data to support this result.

We documented only two trees dying in all three plots over the 2-year observation period. Both were small trees (¡5cm DBH) in Plot 2 that had signs of bark removal by herbivores. In all plots, there were few small trees (N=8 trees ¡5cm DBH in Plots 1 and 2, none in Plot 3). 20 percent died in a 2-year period, most likely killed by herbivores in Plot 2, which had the highest rate of herbivory. Therefore, this is evidence that the thinning is a self-reinforcing process with thinning increasing 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.

We measured a 2-3 fold increase in understory NPP that was available for consumption by herbivores in the thinned plots versus the un-thinned (Table 1). There was also a 2-3 fold (using dung count) increase in herbivore abundance in the thinned plots. Increased herbaceous vegetation typically increases mammal abundance [33]. We were surprised the high percentage (between 30-60 percent) of understory NPP that was potentially consumed by large herbivores. This 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. We measured carnivore abundance with our camera traps and found a body weighted abundance percentage of 0.04 percent. This indicates very low number of carnivores in the system and carnivores too small to exert top down control on this system.

It is interesting to put herbivory in Ponderosa Pine forests into a broader context under which they existed over the past few million years with more abundant large herbivores and carnivores. For instance, the goal of the FWRP was to restore forests to how they were pre-fire suppression 200 years ago. However, for most of their evolutionary history, these forests had large megaherbivores (¿1000 kg) and megacarnivores (¿100 kg) [34]. In fact, the Americas once had the largest concentration of large carnivores [35] and one of our study species (pronghorn) co-evolved with these now extinct predators because it has exceptionally large eyes for spotting predators and great speeds, second only to cheetahs (Acinonyx jubatus), for escaping predators [36]. There is now good evidence that the presence of large herbivores can greatly impact forest structure [37][38] and possibly thin the forest in a manner similar to the FWRP. 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. Therefore, the current trophic structure with mid-sized herbivores and small carnivores (bottom up controlled) may actually recreate the trophic structure of the past with mega herbivores and large carnivores (bottom up controlled) in terms of impact on forest structure. Although there is evidence that mega-herbivores like elephants have a much larger overall impact on tree disturbance than mid-sized herbs like elk [39].

Overall, our average CUE and carbon allocation were similar to a previous study [24], but total NPP and GPP were much lower indicating a less productive system. Carbon was produced more efficiently in the thinned stands (0.63 and 0.61) versus the un-thinned stand (CUE 0.39). Unexpectedly, carbon allocated towards root growth increased in the thinned stands. The thinning more than doubled understory grass and forb NPP which led to more than a doubling of large mammal herbivory. This increased herbivory also increased small tree mortality in the thinned site. The thinning, and the return to a more natural pre-fire suppression landscape, increased the efficiency of the forest both in terms of carbon and animals.

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