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Slow carbon and nutrient accumulation in trees established following fire exclusion in the southwestern United States

Jason P. Kaye,[1,5] Margot W. Kaye,[1] Stephen C. Hart,[2] W. Wallace Covington,[3] and Peter Z. Fulé[4]

[1]*Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, Pennsylvania 16802 USA*
[2]*School of Natural Sciences and Sierra Nevada Research Institute, University of California, Merced, California 95344 USA*
[3]*Ecological Restoration Institute and School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011 USA*
[4]*School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011 USA*

Abstract. Increasing tree density that followed fire exclusion after the 1880s in the southwestern United States may have also altered nutrient cycles and led to a carbon (C) sink that constitutes a significant component of the U.S. C budget. Yet, empirical data quantifying century-scale changes in C or nutrients due to fire exclusion are rare. We used tree-ring reconstructions of stand structure from five ponderosa pine-dominated sites from across northern Arizona to compare live tree C, nitrogen (N), and phosphorus (P) storage between the 1880s and 1990s. Live tree biomass in the 1990s contained up to three times more C, N, and P than in 1880s. However, the increase in C storage was smaller than values used in recent U.S. C budgets. Furthermore, trees that had established prior to the 1880s accounted for a large fraction (28–66%) of the C, N, and P stored in contemporary stands. Overall, our century-scale analysis revealed that forests of the 1880s were on a trajectory to accumulate C and nutrients in trees even in the absence of fire exclusion, either because growing conditions became more favorable after the 1880s or because forests in the 1880s included age or size cohorts poised for accelerated growth. These results may lead to a reduction in the C sink attributed to fire exclusion, and they refine our understanding of reference conditions for restoration management of fire-prone forests.

Key words: carbon; fire exclusion; nitrogen; phosphorus; ponderosa pine; tree-rings; Arizona.

Introduction

Long-term biogeochemical records are rare, but essential for advancing understanding of how biotic responses to disturbance translate into altered element cycles. Tree-ring records of forest structure provide an opportunity to reconstruct carbon (C) and nutrient storage in trees at century timescales, especially where dead wood is well-preserved in semi-arid regions with fire exclusion (Moore et al. 2004). One of the most widespread characteristics of the dendroecological record in the southwestern USA is a dramatic increase in tree density following fire exclusion after the 1880s (Fulé et al. 1997). However, the biogeochemical information embedded in these tree-ring records has only been exploited in two locations and only for C analysis (Hicke et al. 2004, North et al. 2009). The goal of our present study is to use tree-ring reconstructions from >300 plots at five contrasting sites across northern Arizona to gain a large-scale and long-term view of changes in live tree C, nitrogen (N), and phosphorus (P) storage that accompany fire exclusion.

It is now well documented, through multiple intersecting lines of evidence, that tree density in ponderosa pine (*Pinus ponderosa* P. and C. Lawson var. *scopulorum*

Engelm.)–bunchgrass ecosystems of the southwestern USA increased dramatically following fire exclusions that became effective and pervasive at the onset of the 20th century (Covington and Moore 1994). While the change in tree density is well established, its impact on regional C budgets is not. Because tree biomass is an exponential function of diameter, C accumulating in many small trees may not balance C losses from harvesting or mortality of larger trees (Fellows and Goulden 2008). Some calculations suggest that tree establishment in intercanopy spaces (i.e., infilling) that were formerly dominated by bunchgrasses and shrubs in many ponderosa pine forests could constitute a significant fraction of the U.S. C sink in recent decades (Houghton et al. 2000). However, the C accounting that lead to this conclusion was based on model estimates, not field data, and Houghton et al. (2000) considered their early estimate for infilling to be an upper bound. Subsequent field studies have shown that fire exclusion may not have increased C storage in many California wilderness areas (Fellows and Goulden 2008) and one old-growth forest (North et al. 2009), and rates in Colorado ponderosa pine forests were variable and much lower than model estimates (Hicke et al. 2004). A synthesis of research in other vegetation types with woody plant encroachment suggested that C balance varies across gradients in precipitation (Barger et al. 2011) and highlighted the need to understand what causes variation in C balance following increases in

woody plant density. Thus, more than a decade after Houghton et al. (2000) piqued interest in this C sink, it remains one of the most uncertain terms in the North American C budget (King et al. 2015). Tree-ring reconstructions of forest structure provide an opportunity to test model results against field data in the southwestern USA, constrain estimates of the role of fire exclusion in the regional and U.S. C budgets, and to improve C offset accounting.

Fire exclusion is also likely to impact nutrient cycles, yet we are unaware of any studies that have used tree-ring reconstructions of forest structure to examine pre-fire exclusion nutrient storage in trees. Foliage is a larger fraction of total tree biomass in small trees compared to larger trees (Jenkins et al. 2003), and foliage has a higher concentration of N and P than woody tree components (Vitousek et al. 1988). Together, these patterns suggest that infilling with hundreds of small trees per ha (as occurs in our study area) could lead to an increase of N and P in live tree biomass (Covington et al. 2001). Furthermore, the N and P storage in new tree biomass is likely greater than N and P in the bunchgrass biomass that was replaced by infilling trees (Kaye et al. 2005). It is unclear whether the transfer of N and P to infilling tree biomass is large enough to deplete soil pools and affect nutrient supply. However, if new biomass N and P storage are significant relative to annual plant uptake, then C sequestration from infilling could ultimately be constrained by soil nutrient availability.

In prior research, we used tree rings to document changes in forest structure that accompanied fire exclusion throughout northern Arizona (Table 1). We draw on these stand structure data to conduct a spatially expansive analysis of historical and contemporary tree element storage in northern Arizona and ask (1) How has fire exclusion and the subsequent forest infilling changed tree C, N, and P storage over 120 years? (2) How do reconstructions of N and P accumulation in trees compare to literature estimates of soil nutrient availability and annual plant demand? and, (3) How do our reconstructions of C accumulation in trees compare to model estimates used to build regional and U.S. C budgets? In addition to gaining a richer understanding of the past, this rare glimpse of century-scale ecosystem change may provide insights into controls on long-term forest dynamics that can guide projections and management of C and nutrients as drought, fire, and pests potentially lead to declines in tree density in the coming century.

Methods

We used tree-ring reconstructions from five sites throughout the Colorado Plateau in Arizona (Table 1). The original goal of the reconstructions was to guide ecological restoration, so the sites were not randomly located, but rather were selected due to the desire of the land managers to emulate stand conditions prior to fire exclusion. Nevertheless, the sites are dispersed across

TABLE 1. Characteristics of the ponderosa pine dominated ecosystems in northern Arizona, USA, used in carbon and nutrient storage reconstructions.

Site name	Year sampled	Year of last fire	Fires since 1880	Harvest history	No. plots	Plot size (ha)	Sampling grid (m)	Elevation (m)	Soil types	Parent material	Source
Camp Navajo	1994	1883	0	harvested	62	0.04	300	2130	Argiborolls and Eutroboralfs	basalt	Fulé et al. 1997
Kaibab National Forest	1998	1887	0	harvested	23	0.1	300	2260	Vertic paleustalfs and Haplustalfs	calcareous sandstone	Fulé et al. 2002b
Grandview	1998	1887	0	not harvested	67	0.1	300	2260	Udic Haplustalfs	calcareous sandstone	Fulé et al. 2002a
Mt. Trumbull	1996	1870	0	harvested	117	0.04	60	1670–2620	Vitrandic Haplustepts	basalt	Waltz et al. 2003
North Rim	1998	...	5–12	not harvested	76	0.1	300	2250–2350	Typic Paleustalfs	limestone	Fulé et al. 2002a, 2003

Note: Sampling grid size describes the distance between plot centers in a rectangular grid.

Northern Arizona, and each site represents tens to hundreds of hectares of sampling area. Furthermore, the inclusion of harvested and unharvested sites with and without fires enabled us to evaluate controls on C accumulation over the past 120 years. Thus, we expect that the 345 plots used in this study provide a strong basis for inference about ponderosa pine-dominated ecosystems in the southwestern USA.

Three sites (Camp Navajo, Kaibab National Forest, and Mt. Trumbull) are typical of the region in that fire exclusion began in the 1880s and continued to the present, and initial harvesting occurred within 50 yr following fire exclusion. After the initial harvesting event, these three sites also had subsequent periodic logging, and the Kaibab National Forest site had a notably heavy harvest to control a mistletoe outbreak. Two sites (Grandview and North Rim) were never logged. One of the unharvested sites (North Rim) did not experience complete fire exclusion over the past century, with 5–12 surface fires (considering all trees scarred; Fulé et al. 2003) since the 1880s.

Sampling plot origins were located from a systematic grid placed over each sampling site. Plot sizes were 0.04 ha (circular, 22.56 m diameter) or 0.1 ha (rectangular, 20 × 50 m), and plot areas were corrected for slope. Tree diameter at breast height (DBH; 1.37 m above the ground) was measured on all live trees in the 0.04-ha plots. In the 0.1-ha plots, all trees with a DBH >15 cm were measured on the entire plot and trees between 2.5 and 15 cm DBH were measured on one quarter of each plot. We did not include trees with DBH <2.5 cm in our analysis. Previous research in northern Arizona showed that trees established prior to the 1880s could be identified in the field by bark color or DBH. Specifically, sampling ponderosa pines with DBH >37.5 cm or ponderosa of any size with yellowed bark (White 1985, Mast et al. 1999), and oaks, junipers, and pinyon trees with DBH >17 cm (Barger and Ffolliott 1972) ensures that all trees established prior to 1880 were sampled. All living trees meeting these field criteria (from 0 to 32 per plot) for pre-1880 establishment were cored at 40 cm above ground level. In addition, 10% of all post-1880 live trees were also cored.

Forest structure at the time of disruption of the frequent fire regime was reconstructed using dendroecological methods described in detail by Fulé et al. (1997). In the laboratory, tree increment cores were surfaced and visually crossdated (Stokes and Smiley 1968) with tree-ring chronologies we developed. Rings were counted on cores that could not be crossdated, especially younger trees. Diameter at breast height at the time of fire exclusion was reconstructed for all living trees by subtracting the radial growth measured on increment cores since fire exclusion. Site-specific equations were developed to predict DBH from diameter at 40 cm (where cores were collected). Dead trees and stumps that could be cored were also sampled for dendroecological analysis. For trees that no longer retained observable tree rings due to

rot, the date of death was estimated based on tree condition class using diameter-dependent snag decomposition rates (Thomas et al. 1979) or historical harvesting records for stumps. Then, to estimate the 1880s size of dead trees, we developed local species-specific models between tree diameter and basal area increment and used these equations to subtract annual increments in size to reconstruct 1880s tree diameter. An analogous process of growth estimation was used to model the past diameter of the small proportion of living pre-1880 trees for which an intact increment core could not be extracted because of rot. The final product of the field sampling and dendroecological reconstructions is a DBH estimate of every tree in the plot in the contemporary forest and in the year immediately preceding the last recorded fire. For the site without fire regime disruption (North Rim), the year 1879 was used for the reconstruction date because other nearby forests had effective fire exclusion after this date.

Biomass was calculated from the list of tree diameters using species-specific allometric equations. For ponderosa pine, equations from Kaye et al. (2005) and Omdal et al. (2001) were used for above- and belowground biomass, respectively. The belowground root biomass equations from Omdal et al. (2001) applied to coarse roots >0.6 cm in diameter, however, prior research has shown that fine roots (<0.2 cm diameter) account for <15% of total root biomass and < 2% of ecosystem C in these ecosystems (Dore et al. 2010). For Gambel oak (*Quercus gambelii* Nutt.), we used the aboveground biomass equation from Clary and Tiedemann (1987) and the generalized belowground biomass equation from Jenkins et al. (2003) derived from a synthesis of equations with minimum root diameters ranging from 0.015 to 0.5 cm. Other species were rare (Appendix S1: Fig. S1) and generalized equations from Jenkins et al. (2003) were used for both above- and belowground biomass. To convert tree biomass to C mass, we assumed that 0.48% of all tree mass was C (Kaye et al. 2005). To convert tree biomass into N or P mass, we multiplied the biomass in different tree components by the species-specific element concentration in those components. Values in Kaye et al. (2005) were used for N and P concentrations in roots and aboveground tissues for ponderosa pine and all other softwoods. Values in Tiedmann and Clary (1996) were used for N and P concentrations in roots and aboveground tissues in Gambel oak and all other hardwoods without symbiotic N fixation. Tiedmann and Clary (1996) provide different nutrient concentrations for heartwood and sapwood, so we used an archive of Gambel oak increment cores (Adams and Kolb 2005) to derive a regression equation correlating diameter with heartwood:sapwood ratios (DBH range 6.2–37.4 cm, $n = 119$, $r^2 = 0.38$). No local N tissue concentration data were available for the N-fixing New Mexican locust (*Robinia neomexicana* Gray), so we used data from Boring and Swank (1984) for black locust (*Robinia pseudoacacia* L). The mass of each element was summed across all trees in a plot and divided by slope-corrected plot area to calculate mass of

C, N, or P per ha land area. Annual element accumulation ($Mg·ha^{-1}·yr^{-1}$) in live tree biomass was calculated by dividing the difference between 1880s and 1990s mass by number of years, e.g., (1990s C – 1880s C)/time. This value is not equivalent to plant uptake because of tissue turnover, but rather, represents the annual rate of change in C, N, and P stored in live tree biomass.

We analyzed all data using repeated measures ANOVA with site as the between subjects main effect and time (pre fire exclusion or contemporary) as the within subjects repeated measure. To determine whether the change over time was significantly different among sites, we included the site × time interaction in the model. In all cases (C, N, and P), the site × time interaction was significant, so we conducted one-way ANOVAs on each time period separately, with site as the main effect. We then used paired t tests to compare C storage in the 1880s to the 1990s at each site separately; the pairs were C in a plot in 1880 and C in the same plot in 1990. An alpha level of 0.05 was used for all tests, and square root transformations enabled all data to meet normality and equal variance ANOVA assumptions. While statistical analyses were conducted on transformed data, all data presented here are untransformed. We also visually compared our sites to average values from all Forest Inventory Analysis data (FIA) plots from Arizona (O'Brien 2002). The FIA data summary we used included the average number of ponderosa pine trees per unit area in 15 DBH classes (approximately 5-cm increments per class up to 75 cm DBH). We applied the allometric equations and element concentrations described above to estimate live tree biomass C, N, and P in FIA plots.

To assess relationships between 1880s stand structure and contemporary C storage from infilling, we used simple linear regression of 1880s tree density (number of trees/ha) in each plot vs. 1990s tree C (Mg C/ha) for infilling trees. We also examined whether the maximum 1990s C in infilling trees in a plot was a function of 1880s tree density in the same plot. For this analysis, we parsed the data into bins that included all plots encompassed by 25 units of 1880s tree density (all plots with 0–25 trees/ha, 26–50 trees/ha, 51–75 trees/ha, etc.). Then, for each bin of plots, we selected the plot with the highest (which we term maximum) 1990s C storage in infilling trees. This resulted in 15 values of maximum tree C, which we regressed against the midpoint of the 15 corresponding bin values for tree density.

Results

As expected, tree density increased 9–10 fold between the 1880s and the 1990s at all sites (Fig. 1). Pre-fire exclusion density ranged from 87 to 133 trees/ha among sites, while contemporary forests ranged from 612 to 955 trees/ha. The locations we sampled have stem densities comparable to the average Arizona ponderosa forest (741 trees/ha) as represented by FIA data (Fig. 1). There was a significant site × time interaction ($P = 0.049$) and

one-way ANOVAs revealed some differences among sites in both the 1880s and 1990s tree densities (Fig. 1). However, differences in tree density among sites were small relative to differences between the 1880s and 1990s.

All sites except one (a heavily harvested site with complete fire exclusion, Kaibab National Forest) had greater tree C storage in the 1990s than in the 1880s (Fig. 1), so there was a significant site × time interaction ($P < 0.001$). Tree C storage in the 1880s ranged from 22 to 46 Mg/ha across sites compared to 28 to 85 Mg/ha in the 1990s. Trees that established after the 1880s (i.e., infilling) contained 16–70% of the total tree C present in the 1990s. Averaging across all sites, mean C accumulation in all trees (both infilling trees and those established prior to 1880) during the period of fire exclusion was 0.27 ± 0.09 $Mg·ha^{-1}·yr^{-1}$ (mean ± 1 SE), ranging from -0.08 $Mg·ha^{-1}·yr^{-1}$ (Kaibab National Forest) to 0.44 $Mg·ha^{-1}·yr^{-1}$ (Camp Navajo). Considering only trees that established during the post-1880 fire exclusion period, the mean rate of C accumulation due to infilling was 0.22 ± 0.06 $Mg·ha^{-1}·yr^{-1}$.

The rate of C accumulation in trees that were already established by the 1880s varied substantially among sites ($P < 0.001$). At three sites, trees established before the 1880s accumulated C at rates ranging from 0.08 to 0.22 $Mg·ha^{-1}·yr^{-1}$, but two harvested sites had lower C in this pool in the 1990s than in the 1880s (Kaibab National Forest and Mt. Trumbull). There were only weak ($R^2 < 0.07$) correlations between tree density in the 1880s and C storage in the 1990s due to infilling (Fig. 2). However, maximum C storage in the 1990s from infilling was negatively correlated with 1880s stand density, and the slope was especially steep for harvested sites (Fig. 2).

Most of the trees that established after fire exclusion were ponderosa pines, except at the site that lacked 20th century fire exclusion and harvesting (North Rim). At this site, Gambel oak accounted for up to ∼50% of stems (Appendix S1: Fig. S1), although proportionally much less biomass due its smaller stature. Other species always accounted for <13% of the infilling trees. Ponderosa pine was also the most important species for C storage in all of the sites we sampled (Appendix S1: Fig. S1). Even when Gambel oak accounted for a large fraction of 1990s stems, it accounted for <25% of 1990s live tree C (Appendix S1: Fig. S1).

Results for N and P were qualitatively similar to C (Fig. 3). Sites that we sampled in the 1990s contained 121– 330 kg N/ha in trees, which is comparable to the average of 167 kg N/ha in Arizona forests sampled for the FIA. Reconstructed tree N for the 1880s ranged from 87 to 152 kg/ha across sites and all sites except one (site × time interaction $P < 0.001$; again due to the Kaibab National Forest site) had greater tree N storage in the 1990s than in the 1880s. Across all sites, the rate of N accumulation in tree biomass during the period of fire exclusion ranged from -0.1 $kg·ha^{-1}·yr^{-1}$ (Kaibab National Forest) to 1.7 $kg·ha^{-1}·yr^{-1}$ (Camp Navajo),
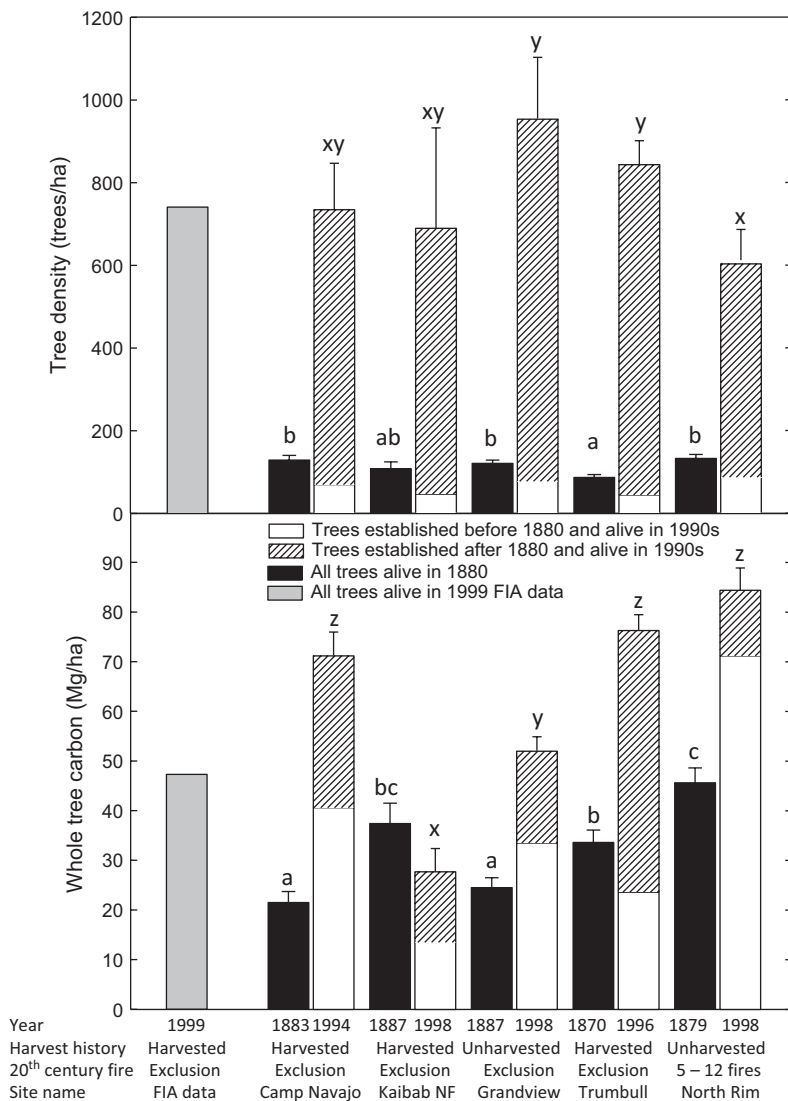
FIG. 1. Tree density and carbon storage prior to fire exclusion (1880s data) and after approximately 120 yr of fire exclusion (1990s data) at five sites northern Arizona sites. For comparison, mean values calculated using 1999 Forestry Inventory Analysis (FIA) data for Arizona (O'Brien 2002) are also shown (gray bar). There were significant site by time interactions for both density and tree carbon ($P < 0.001$). Statistical differences ($P < 0.05$) among sites in the 1880s data are denoted with a, b, and c, while x, y, and z denote differences among sites in the 1990s data. At every site for both density and carbon, 1880s values differed significantly from 1990s values by paired t tests ($P < 0.05$). Vertical bars denote mean + 1 SE.

with a mean rate (± 1 SE) of $1.1 ± 0.3$ kg·ha^{-1}·yr^{-1}. The rate of N accumulation in trees already established in 1880 ranged from -0.6 to 0.7 kg·ha^{-1}·yr^{-1} across sites, while the rate of N accumulation due to infilling ranged from 0.6 to 1.9 kg·ha^{-1}·yr^{-1}. In these ecosystems in the 1990s, ponderosa pine contained 52–87% of the N in trees, Gambel oak contained 9–42%, and other species accounted for 1–3% (*data not shown*).

Trees in the 1880s contained 10–15 kg P/ha across sites, while 1990s trees contained 10–29 kg P/ha (Fig. 3), resulting in a mean rate of accumulation of $0.10 ± 0.03$ kg P·ha^{-1}·yr^{-1} between the 1880s and 1990s. Differences among sites and species and the relative importance of

infilling, followed the same patterns as those described above for N.

DISCUSSION

Tree densities in the southwestern USA increased following fire exclusion (Fig. 1), leading to changes in fire and pest regimes (Parker et al. 2006). Our data build on existing knowledge by synthesizing tree-ring reconstructions to calculate live tree C and nutrient history across a broad spatial scale. One hundred twenty years ago, the ponderosa pine-dominated ecosystems of northern Arizona, on average, contained less C, N, and P in trees
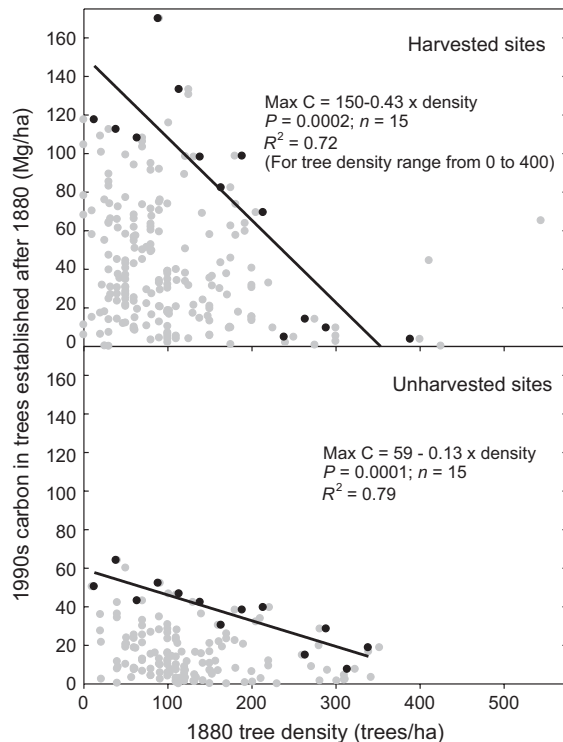
Fig. 2. The relationship between tree density in the 1880s and the amount of 1990s carbon stored in trees that established after the 1880s (i.e., infilling) for both harvested and unharvested sites (see Table 1). For both harvested and unharvested sites, direct correlations between density and carbon storage for individual plots (gray circles) were significant ($P < 0.002$) but weak ($R^2 < 0.07$), and best-fit lines are not plotted. Maximum C (black circles) was correlated with 1880s tree density as shown in solid regression lines. We determined maximum tree C in 15 bins, with each bin including all plots encompassed by 25 units of tree density. We regressed these 15 values of maximum tree C against the midpoint of the 15 corresponding bin values for tree density (solid best-fit lines and associated regression statistics).

than they do today. However, changes in tree element storage are much less dramatic (and more variable among sites) than changes in tree density. While the number of trees per hectare increased 9–10 fold since the 1880s, element storage in trees has, at most, tripled. These results have important implications for linking fire exclusion with long-term biogeochemical change, and they suggest that the role of forest infilling may have been over-estimated in previous regional C budgets.

Implications for understanding long-term ecosystem dynamics

Despite dramatic increases in tree density following fire exclusion, a large fraction (28–66%) of the C, N, and P in the 1990s was in trees that were already established by 1880 but not subsequently harvested. Thus, an important conclusion from our analysis is that the 1880s forest was on a trajectory to accumulate C, N, and P in tree biomass even without the infilling that accompanied fire exclusion.

Additional evidence for this assertion comes from the unharvested site where 5–12 fires during the past century diminished infilling (North Rim). Surprisingly, this site has pine C accumulation rates similar to sites with full fire exclusion (Appendix S1: Fig. S1). Further corroboratory evidence comes from ecological restoration sites where thinning of small conifers has a modest impact on contemporary live tree C, N, and P storage (e.g., ~30% reduction; Kaye et al. 2005, North et al. 2009, Dore et al. 2010). Infilling also replaces, rather than augments, storage in bunchgrasses biomass (e.g., 2–8 kg N/ha), so the net change in C, N, and P in live plants due to infilling is even slightly smaller than the effect shown here for trees.

The modest role for infilling trees in the C, N, and P cycles was unexpected because of the striking observations (both visual and measured) of new tree establishment. This result has implications for restoration management that has become an important alternative to fire exclusion. The 1880s forest structure is commonly used as the "reference condition" for ecological restoration in the southwestern USA because it is the last and best date for which we can quantify forests structure prior to fire exclusion (Moore et al. 1999, Fulé et al. 2002b). Our data refine our understanding of the 1880s forest, and in particular, our estimates of the range of variability for changes in storage of C, N, and P in trees. To put our results into context, consider as a hypothetical starting point that the 1880s forests were in a biogeochemical steady state. In a steady state forest, the amount of new C, N, or P accumulating in tree biomass (from recruitment of new trees plus growth of existing trees) is roughly balanced by biomass loss from tree mortality during the same time period. Thus, if we consider only trees established prior to 1880 (as we did in our calculations) and assume that growth rates of trees did not change dramatically after the 1880s, then the quantity of C, N, or P in trees established prior to 1880 should have declined over time. This is precisely what Fellows and Goulden (2008) found for C in wilderness areas in California. Yet, this pattern did not occur in our unharvested sites (nor in one harvested site), suggesting that (1) live tree C, N, and P in the 1880s were not in a biogeochemical steady state, (2) growth rates of trees after 1880 were higher than growth rates of trees prior to the 1880s, or (3) a combination of the two.

Our sites may not have been at steady state in the 1880s if pre-1880 tree recruitment was pulsed in a way that stands in the 1880s were young relative to the age when a biogeochemical steady state is reached. Forests in this region are composed of age cohorts resulting from temporal and spatial variability in climate and disturbance that caused pulses of establishment (Savage et al. 1996, Mast et al. 1999, Brown and Wu 2005). Over time, the C, N, and P stored in a particular cohort first increase and then eventually decline, analogous to development of biomass in even-aged stands (Ryan et al. 1997). Typically, large, dominant trees accumulate C at the fastest rate
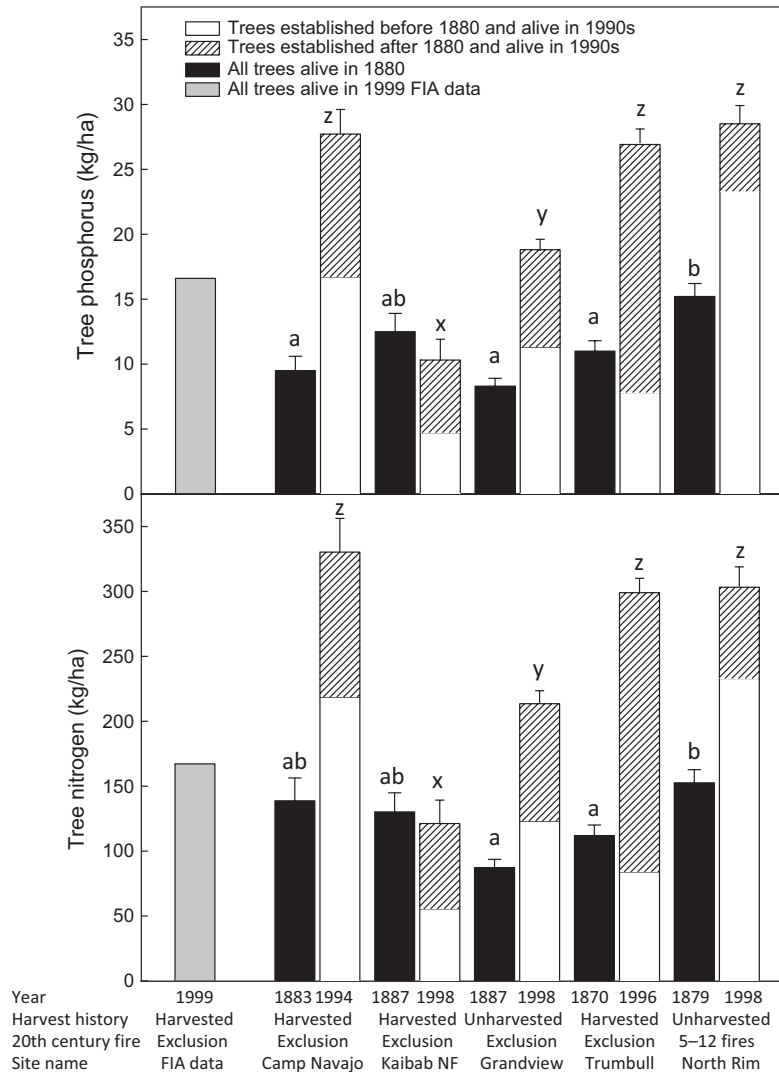
FIG. 3.   Tree nitrogen and phosphorus storage prior to fire exclusion (1880s data) and after approximately 120 yr of fire exclusion (1990s data) at five sites. For comparison, mean values calculated using 1999 Forestry Inventory Analysis (FIA) data for Arizona (O'Brien 2002) are also shown (gray bar). There were significant site × time interactions for both nitrogen and phosphorus ($P < 0.001$). Statistical differences ($P < 0.05$) among sites in the 1880s data are denoted with a, b, and c, while x, y, and z denote differences among sites in 1990s data. At the Kaibab National Forest site, 1880s values did not differ significantly from 1990s values ($P > 0.05$), but at all other sites, paired t tests showed significant differences between the 1880s and 1990s for both N and P ($P < 0.05$). Vertical bars denote mean + 1 SE.

(Binkley et al. 2006, Stephenson et al. 2014). Thus, it is possible that in 1880, which we count as the starting year, the sites we sampled were composed of cohorts of trees that due to their age and size were still increasing in growth rate. In stands with fast-growing cohorts and low mortality, C, N, and P would naturally accumulate in live biomass.

Which cohorts grew fast in our stands? We cannot reconstruct age structure data for the 1880s with our dataset, but we did estimate the size of each tree in the 1880s. Focusing on ponderosa pine trees that were alive in both the 1880s and 1990s, we calculated the change in C storage for individual trees during this time period. As expected, there was

a correlation between 1880s diameter of a tree and the amount of C that trees accumulated between the 1880s and 1990s; large trees added more C (Appendix S1: Fig. S2). But the largest trees were also rare, so intermediate size classes (between 10 and 60 cm DBH in the 1880s) contributed the most to total C accumulation between the 1880s and 1990s (Appendix S1: Fig. S3). The 30–40 cm size cohort accounted for the greatest percentage of C accumulating in all trees alive in both the 1880s and 1990s for the harvested (17%) and unharvested (24%) datasets. We cannot determine whether these fast-growing size cohorts were anomalously abundant in the 1880s forest relative to the size distribution of a forest in a biogeochemical steady state.

If 1880s ecosystems were not at biogeochemical steady state because they were composed of fast-growing cohorts (e.g., many 30–40 cm DBH trees), then the ecosystems of the 1880s were poised for C, N, and P accumulation by a mechanism that is independent of fire exclusion. Eventually, mortality rates in the stand will increase and diminish the net biomass accumulation rate in live trees. While tree mortality rates are increasing throughout the western USA, they are accelerating more slowly in Arizona than in other regions (Van Mantgem et al. 2009), which may explain why Fellows and Goulden (2008) found C declines in California forests while we observed increases.

An alternative hypothesis is that the ecosystems of the past were at steady state for 1880s environmental conditions, but that conditions after the 1880s became more favorable for growth, such that trees established prior to 1880 grew faster after 1880. There is strong evidence in contemporary forests that reducing competition (e.g., by thinning) can increase the growth of remaining trees (Kaye et al. 2005, Kolb et al. 2007, Bailey 2008), and this may have been a factor affecting C storage changes in our harvested sites. For pine trees that were alive in both the 1880s and 1990s, the slope of the regression between individual tree C accumulation (y-axis) and 1880s tree diameter was greater in harvested stands than unharvested stands (Appendix S1: Fig. S2). In terms of competition, this means that after accounting for diameter effects (that is, comparing two trees of the same diameter in harvested and unharvested stands) trees in harvested sites grew more between the 1880s and 1990s than trees in unharvested sites, supporting the prediction that harvesting increased growth of remaining trees by reducing competition. Thus, at our harvested sites, reduced competition is likely one factor contributing to high C, N, and P storage in trees that established prior to 1880. However, we also observed high C, N, and P accumulation in pre-1880s trees in two unharvested sites, suggesting that factors other than thinning are affecting growth of trees that established prior to 1880.

Even if pre-existing trees and infilling trees compete, it is possible that growth was faster during the fire exclusion period if water, CO_2, or nutrient availability were higher in the fire exclusion period than prior to that period. Water availability in our study region varied over the 20th century, with an extended drought in the 1950s (Woodhouse et al. 2010) and pluvial periods at the start of the century and the 1980s (Salzer and Kipfmueller 2005). Temperatures in the second half of the century, specifically 1946–1994, were the warmest observed in a 2000-year reconstruction of climate in the study region (Salzer and Kipfmueller 2005). With multiple periods of drought stress evident in the climate record, it is not likely that a favorable climate promoted increased tree growth in the 20th century. Negative effects of drought may be alleviated by increased water use efficiency from elevated atmospheric CO_2 concentrations in the second half of the 20th century (Soulé and Knapp 2006), but the CO_2 fertilization effect can be constrained by low nutrient availability (Finzi et al. 2007).

We think it is unlikely that nutrient availability increased substantially during the fire exclusion period, indeed, we hypothesized the opposite; speculating that nutrient accumulation in trees might decrease nutrient supply by transferring N from the soil to tree biomass. Our estimated rate of N storage in trees ($1.1\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$) was about an order of magnitude smaller than annual net N mineralization (10 and $60\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$), annual plant uptake ($20\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$), or aboveground litterfall N fluxes of $\sim 10\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$ (Kaye and Hart 1998a, Kaye et al. 2005, Grady and Hart 2006, Hart et al. 2006, Kurth et al. 2014). Likewise, litterfall P fluxes ($\sim 1.2\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$) and annual plant P uptake ($\sim 4\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$; Kaye et al. 2005) are about an order of magnitude larger than the accumulation of P in tree biomass ($0.1\ \mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$) during fire exclusion. While we cannot say whether these small increases in tree N and P storage significantly decreased soil N and P availability, the data certainly do not support the hypothesis that soil N or P availability increased during fire exclusion and promoted growth of trees that established prior to 1880. One important caveat for interpreting our nutrient data is that we assumed constant C:N:P stoichiometry in plant tissues over time and space. Variability in plant N and P concentrations among sites could exist due to variation in soil properties, but spatial variability wouldn't change our main interpretation regarding 1880s vs. 1990s forests. Increasing atmospheric CO_2 over the past century likely decreased plant tissue nutrient concentrations but for pines foliar and wood N reductions are usually <5% (Grulke et al. 1993, Tissue et al. 1999, Finzi et al. 2007). The greatest variability in N and P concentrations is among plant tissues (orders of magnitude between wood and foliage) and our hypotheses were based on how infilling could change the abundance of different plant tissues. With the exception of fine roots, our data account for variation in N and P concentrations among plant tissues.

At this point, there appears to be strong evidence (both from contemporary thinning studies and our data; Appendix S1: Fig. S2), for the favorable conditions after 1880 hypothesis in stands where harvesting reduced competition for limiting soil resources. In unharvested stands (and with implications for all forests), further research is warranted to determine whether the fast-growing cohort hypothesis or favorable conditions after 1880 are driving 20th century accumulation of C, N, and P in trees that had established prior to the 1880s. While our results suggest that the mass of N and P transferred to growing plant canopies alone was likely too small to constrain nutrient supply or CO_2 fertilization of tree growth, existing data are inadequate for conclusively ruling out changes in nutrient supply over time. Regardless, the alarming increase in density of post 1880 trees seems to belie the importance of C, N, and P accumulation during the fire exclusion period in trees that had established prior to the 1880s.

Implications for regional C accounting

Accounting for forest infilling has been a challenging but critical component of the U.S. C budget. A series of papers (Houghton et al. 2000, Pacala et al. 2001) estimated that C accumulating due to fire exclusion and infilling in western pine forests could account for ~13% of U.S. C sinks in the 1980s (0.05 out of 0.37 Pg C/yr; Table 1 of Pacala et al. 2001). For ponderosa pine forests, Houghton et al. (2000) used published estimates of forest structure changes based on a simulation model (ECOSIM; Covington and Moore 1994) to calculate tree C accumulation rates. The model does not simulate tree C directly, so output of timber volume or basal area were converted to tree C. This step is made difficult by the fact that conversions of board feet of timber volume to tree biomass depend on the log rules, saw kerf width, and the size of the trees. Likewise, conversions of basal area to stand C require detailed information about tree diameter distributions. Nevertheless, the model provided the best information available at that time and suggested a C accumulation rate in trees of 2.0 Mg·ha^{-1}·yr^{-1} prior to 1926 (all trees, not just infilling). A more conservative rate (0.9 Mg·ha^{-1}·yr^{-1}) was used for western forests more generally (Houghton et al. 2000). These values are substantially higher than our estimates of −0.08 to 0.44 Mg·ha^{-1}·yr^{-1} for all trees and 0.08 to 0.22 Mg·ha^{-1}·yr^{-1} for infilling trees only.

Lower than expected C accumulation rates were documented in two other studies of decadal scale C accumulation in western forests. Fellows and Goulden (2008) compared field surveys of the number of live trees in different DBH size classes from the1930s and 1990s in wilderness areas (presumably not logged) throughout California. They found that C stored in aboveground live biomass of trees decreased during this time interval, which they hypothesized to result from mortality of old trees outpacing C accumulation in existing and infilling trees. Hicke et al. (2004), using methods similar to ours, examined ponderosa pine and mixed conifer stands in Colorado, where tree C storage was <8 Mg/ha in the 1880s because tree densities were very low prior to fire exclusion. In these stands, C accumulation rates (0.09, 0.46, and 0.70 Mg·ha^{-1}·yr^{-1} in three adjacent stands) were comparable to those we measured. Sites that included a substantial cohort of old (established pre-fire exclusion) trees had higher C accumulation rates overall, especially in the older age classes. Hicke et al. (2004) noted that accumulation rates were still increasing exponentially in these young stands, and they concluded that the date of infilling or tree invasion was a critical factor in predicting C accumulation rates. Our results support this conclusion, but additionally our data (and Fellows and Goulden 2008) show that the age and size distribution of the cohort of trees that preceded infilling is an equally important factor for assessing contemporary C accumulation rates.

Competition also limited potential C accumulation from infilling in some of the stands we studied. To analyze the impact of competition on C storage from infilling, we used 1880s tree density as a predictor of competitive pressure from previously established trees on infilling trees (the results are qualitatively similar if we used 1880s C as the predictor variable). If competition from previously established trees suppressed the growth of infilling trees, we would expect stands with low density in the 1880s to have higher C storage in trees established after the 1880s (infilling trees). While 1880s stem density was only a weak predictor of average 1990s C, it was a stronger predictor of potential (maximum) 1990s C (Fig. 2). Stands with low tree density in the 1880s had greater potential for 1990s storage in infilling trees, reflecting lower competition at low stand density. Furthermore, this effect was stronger for harvested stands (steeper slope and larger intercept than unharvested stands in Fig. 2), which indicates that harvesting, as expected, further diminished competition between infilling trees and trees that had established prior to the 1880s.

There are several components of the C budget missing from our data that must be considered for broader C accounting. We could not measure soil C change, and in some ecosystems, increased woody plant density can diminish soil C storage. For example, Jackson et al. (2002) found that long-term accumulation in trees was balanced by a relatively rapid C loss from soil during woody encroachment by mesquite. We do not expect this pattern in the ecosystems we studied because thick O horizons that develop after infilling are not present when intercanopy spaces are dominated by bunchgrasses (Kaye and Hart 1998b), A horizons under these O horizons have higher C concentrations than A horizons in adjacent grass patches, and adjacent grass and forest patches have similar C concentrations in the B horizon (Kerns et al. 2003). As a preliminary estimate of how infilling may have affected C accumulating in O horizons, we converted simulated changes forest floor fuels over the past century (using ECOSIM; Covington and Moore 1994) to C accumulation rates (by multiplying forest floor fuel mass by 0.48; Ross et al. 2012). Rates of C accumulation in forest floor fuels in forests with fire exclusion were ~0.25 Mg·ha^{-1}·yr^{-1} between the late 1800s and 2000s. Thus, it is likely that soil C increased, rather than decreased between the 1880s and 1990s, and furthermore, soil C accumulation rates may be of the same order of magnitude as the tree C accumulation rates that we measured.

Comparing two time points separated by over a century may have resulted in errors in our estimates of tree C accumulation rates. Most of the infilling at our sites likely occurred after 1919 (Savage et al. 1996, Sánchez Meador et al. 2009). If we assume that all of the C accumulation from infilling occurred after this time, then the rate of C infilling would increase to ~0.33 Mg·ha^{-1}·yr^{-1} (the same amount of C accumulating in 80 yr instead of 120). We may be missing some small trees in our reconstruction of the 1880s stand structure. Our stand reconstruction relies

on the long-term preservation of dead wood on the landscape. This method has been tested extensively (Moore et al. 2004), so we are confident that large stumps and downed trees are preserved, but we cannot rule out the possibility that some smaller trees died and decomposed prior to our field sampling. Missing small trees that established prior to 1880 would reinforce our conclusion that infilling after the 1880s is not a dominant C sink, while missing small trees that established after the 1880s (less likely due to short time between tree death and sampling) would lead to underestimates of the roll of infilling. In either case, our dataset shows conclusively that missing a few small trees represents a minor error in live tree C storage calculations.

Despite these caveats, our data from northern Arizona, combined with the results from California and Colorado, suggest that throughout the western U.S. tree C accumulation due to fire exclusion is substantially lower than previously thought (Houghton et al. 2000, Pacala et al. 2001). When Houghton et al. (2000) made preliminary calculations of C accumulation from fire exclusion, they considered them a starting point and an upper bound. Houghton (2003) subsequently halved those initial values to provide a more conservative estimate. Our data provide empirical evidence supporting this downward revision and suggest that future calculations of the U.S. C budget should be updated with even smaller sinks resulting from infilling of ponderosa pine forests. In addition, future analyses of ponderosa pine C budgets should take into account new research showing large C losses and very slow soil and plant C recovery following stand replacing fires (Ross et al. 2012) that are becoming more prevalent in this region.

Conclusions

Infilling of southwestern ponderosa pine ecosystems is visually striking and is known to cause dramatic changes in pest and fire behavior. Our results show that infilling also alters the C, N, and P cycles; in all but one of the sites we studied (and for the average among sites), tree element storage in the 1990s was greater than in the 1880s. Yet, in several ways the effect of infilling was substantially smaller than we expected. Tree C accumulation rates were smaller than those used in regional and national C budgets, and changes in tree N and P storage were not likely large enough to alter nutrient availability to contemporary forests. Surprisingly, even in one harvested site, infilling trees account for only about one-half of the C accumulation over the last century.

Conversely, the role of trees that had established prior to the 1880s was much more important than we expected. Even though they account for <10% of the stems, the older and larger trees that established prior to the 1880s contained about the same amount of C (at the stand level) as the trees that established after 1880, which accounted for >90% of the stems. The 1880s stand structure had an additional impact as high stem densities in the 1880s were

correlated with low maximum C storage in trees that established after the 1880s. A diverse array of harvested and unharvested sites, from large spatial extent with and without 20th century fires, supports these conclusions. The fact that C accumulation was roughly the same at sites with and without 20th century surface fires further emphasizes that long-term stand development, not just contemporary fire exclusion, is a major driver of tree C, N, and P dynamics in these ecosystems.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1407/full

Data Availability

Data associated with this paper are available in ScholarSphere: https://scholarsphere.psu.edu/files/s7526c50k.