Carbon Cycling in Southwestern Forests: Reservoirs, Fluxes, and the Effects of Fire and Management

September 2015
Intermountain West Frequent-Fire Forest Restoration

Ecological restoration is a practice that seeks to heal degraded ecosystems by reestablishing native species, structural characteristics, and ecological processes. The Society for Ecological Restoration International defines ecological restoration as “an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability….Restoration attempts to return an ecosystem to its historic trajectory” (Society for Ecological Restoration International Science and Policy Working Group 2004).

Most frequent-fire forests throughout the Intermountain West have been degraded during the last 150 years. Many of these forests are now dominated by unnaturally dense thickets of small trees, and lack their once diverse understory of grasses, sedges, and forbs. Forests in this condition are highly susceptible to damaging, stand-replacing fires and increased insect and disease epidemics. Restoration of these forests centers on reintroducing frequent, low-severity surface fires—often after thinning dense stands—and reestablishing productive understory plant communities.

The Ecological Restoration Institute at Northern Arizona University is a pioneer in researching, implementing, and monitoring ecological restoration of frequent-fire forests of the Intermountain West. By allowing natural processes, such as low-severity fire, to resume self-sustaining patterns, we hope to reestablish healthy forests that provide ecosystem services, wildlife habitat, and recreational opportunities.

The Southwest Fire Science Consortium (SWFSC) is a way for managers, scientists, and policy makers to interact and share science. SWFSC’s goal is to see the best available science used to make management decisions and scientists working on the questions managers need answered. The SWFSC tries to bring together localized efforts to develop scientific information and to disseminate that to practitioners on the ground through an inclusive and open process.

ERI working papers are intended to deliver applicable science to land managers and practitioners in a concise, clear, non-technical format. These papers provide guidance on management decisions surrounding ecological restoration topics. This publication would not have been possible without funding from the USDA Forest Service and the Southwest Fire Science Consortium. The views and conclusions contained in this document are those of the author(s) and should not be interpreted as representing the opinions or policies of the United States Government. Mention of trade names or commercial products does not constitute their endorsement by the United States Government or the ERI.

Author: Tyson L. Swetnam and Donald A. Falk
Reviewers: David W. Huffman, Matthew D. Hurteau, Thomas E. Kolb, and Amy E.M. Waltz
Series Editor: Tayloe Dubay
Cover Photo: New research shows that bigger and older trees, like this large ponderosa pine in the Valles Caldera National Preserve, NM, do not slow their carbon intake over time but instead increase the magnitude of carbon they take up. Photo by T.L. Swetnam

Please use the following citation when referring to this Working Paper:
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### Key Points about Carbon in Southwestern Forests

- Drought and wildfires are increasing in area, frequency and severity, based on current trends.
- A reorganization of almost all southwestern forest ecosystems is predicted to occur in the next 50 to 100 years because of global warming.
- Ecosystems sequester less carbon following a catastrophic fire.
- Carbon reservoirs for all forest types are expected to decline in the future as climate change reduces annual precipitation and increases temperatures.
- New research has shown bigger and older trees do not slow their carbon uptake rate over time. In fact, they increase the magnitude of carbon they take up.
- A single large tree can sequester more carbon per year than is contained in all sapling size trees growing in the same footprint area. A single old growth southwestern USA conifer can hold as much as 16 tons of C.
- Carbon reservoirs vary widely across elevations, aspects, and topographic positions: valley bottoms contain a vast majority of carbon in (1) larger and taller trees and (2) in deeper soils, relative to those of ridges and hillslopes.
Introduction

Forests play a key role in regulating the carbon cycle of the Earth system. Understanding carbon storage in forest ecosystems has become increasingly important as human activities release more carbon dioxide (CO$_2$) into the Earth’s atmosphere. The intent of this working paper is to explain the basics of the carbon cycle detailing how much carbon moves through vegetation, water, and soils over time. The paper also summarizes where current science suggests that carbon cycling patterns are most likely to change in the coming years to decades, and how management can influence these changes.

Water (H$_2$O) and atmospheric gases, particularly carbon dioxide, interact with living things, soils and rock to regulate natural habitats and sustain ecosystems (NRC 2001). The capacity of landscapes to transfer (“flux”) and store (“sequester”) elemental carbon has a direct effect on atmospheric concentrations of CO$_2$ with further feedbacks on the water and nitrogen cycles. In the literature, carbon contained in vegetation and soils is typically referred to as “reservoirs” or “pools” (Post et al. 1990, Schimel 1995, Cole et al. 2007).

Flux – A Measure of Carbon Gain and Loss

Gross Primary Production (GPP) includes the total carbon sequestered by the process of photosynthesis. Net Primary Production (NPP, Woodwell and Whittaker 1968) is the GPP minus autotrophic respiration (i.e. the breathing that plants do to sustain their own metabolism). Net Ecosystem Production (NEP, Randerson et al. 2002, Lovett et al. 2006) is NPP minus heterotrophic respiration (i.e. the breathing microorganisms, animals and fungi do to sustain their metabolism by consuming plant-derived materials) (Kirschbaum et al. 2001, Dore et al. 2010).

Net Ecosystem Exchange (NEE) is the term scientists use for measured NEP. NEE is the amount of carbon that enters and leaves an ecosystem over some period of time measured from eddy flux towers, i.e. the AmeriFlux network (http://amerifluxornl.gov/). A negative NEE (positive NEP) value indicates that an ecosystem is acting as a carbon sink. Carbon storage occurs when NEP exceeds the amount of carbon respired from heterotrophs and soils or oxidized during wildfire. Gradients in elevation, slope and aspect, and topographic position modify local temperature and wetness values affecting the NPP of southwestern ecosystems (Whittaker and Niering 1975, Anderson-Teixeira et al. 2011). For example, desert grasslands (on average) sequester ~240 pounds (lbs) or 0.12 tons (t) of carbon per acre per year (t C ac$^{-1}$ yr$^{-1}$)(Sims and Singh 1978) while mixed-conifer forests can sequester upwards of 1.5 t C ac$^{-1}$ yr$^{-1}$ (Anderson-Teixeira et al. 2011, Perdrial et al. unpublished data).

In fire-adapted ecosystems, episodic wildfires break up the spatial continuity of vegetation and lower the risk of catastrophic impacts on watersheds and carbon pools (Bond and Keeley 2005, Hurteau and Brooks 2011, Moody et al. 2013, Sidman et al. 2015). Importantly, wildfires do not release all of the carbon in vegetation through combustion. Typically, only 30–40% of the carbon is oxidized at the time of the fire, mostly by flaming and smoldering combustion (Loehman et al. 2014). The majority of carbon (>60%) remains in unburned material, ash and black charcoal from incomplete combustion and heating without oxygen (Johnson et al. 2004, Meigs et al. 2009, Loehman et al. 2014). Litter and downed woody debris losses by combustion can reach 100% during a high intensity fire (Campbell et al. 2007, Figure 1).

Dissolved organic and inorganic carbon (DOC/DIC) in soil and stream water make up a small but measurable percentage of the carbon reservoir (Cole et al. 2007, Stielstra 2012, Perdrial et al. 2014). Under normal conditions the release of gaseous carbon from soils is generally <50 lbs C ac$^{-1}$ yr$^{-1}$ or 0.025 t C ac$^{-1}$ yr$^{-1}$, and dissolved carbon from ground water and stream run-off is <13 lbs C ac$^{-1}$ yr$^{-1}$ (Stielstra 2012, Condon 2013, Perdrial et al. 2014). Following a wildfire the quantity of carbon leaving in stream run-off can increase over a thousand fold as black carbon and ash are flushed across burned surfaces with no vegetation or detritus to slow down the flow (DeBano et al. 1998, 2000, Ice et al. 2004). Carbon can also be deposited into soils by erosion and deposition, e.g. alluvial debris fans. Condon (2013) measured ~3.8–4.1 t C ac$^{-1}$ in a debris fan produced after a fire in a mixed-conifer forest in New Mexico. Deposition of carbon into sediments by fluvial transport is a potentially significant long-term sink removing atmospheric carbon (Chaopricha and Marin-Spiotta 2014). For example, DOC/DIC and particulate carbon flushed into rivers as run-off can be deposited in delta sediments (Jaffé et al. 2013, Masiello and Louchouarn 2013).

Reservoirs – The Stores of Carbon in Organisms and Inorganic Material

Aboveground biomass (e.g. vegetation and surface fuels) makes up varying percentages of the total carbon reservoir depending on forest type and topographic location. Remaining carbon reservoirs are located belowground in (1) soils, (2) regolith, and (3) ground water. Belowground biomass is made up of fine and coarse woody roots, while SOC includes detritus, mycorrhizae, fungi, and soil biota (microorganisms and bacteria) (Lal 2005, McKinley et al. 2011). In wet forests total SOC can exceed the aboveground carbon. Aboveground carbon stocks have been reported in southwestern forests to range from <1 to 159.85 t C ac$^{-1}$ (Whittaker and Niering 1975, Finkral and Evans 2008, McKinley et al. 2011, Anderson-Teixeira et al. 2011, Sorensen et al. 2011). A recent study (O’Connor 2013) estimated the aboveground carbon in one 1/8th acre mixed-conifer plot to be equivalent to ~356.0 t
Such a large value rivals wet temperate coastal conifer forests (Smith et al. 2006) and suggests some old growth southwestern forest stands may hold more carbon than has been previously reported. The largest trees in southwestern forests tend to grow on lower topographic positions, e.g. drainage bottoms near an available groundwater subsidy, and in locations free of high-severity fire and logging during the modern era. Historically, frequent surface fires kept surface debris volume low in dry forest ecosystems. In less frequent fire regimes and more productive vegetation types, e.g. mixed-conifer and spruce fir forests, surface fuels contribute significantly to total carbon both in the soil and at the surface. Fire suppression has resulted in the accumulation of surface fuels in many forests in the Southwest over the 20th century (Allen et al. 2002).

Topographic position modifies the potential size of carbon reservoirs at local scales. Ridges tend to have shallower soils with rocky parent material close to the surface. Rain and snowmelt water accumulate as run-off and ground water toward valley bottoms. Consequently, ridges and steep slopes have shorter trees and less SOC/SIC relative to valley bottoms where precipitation and eroded soil accumulate with shallower water tables. Perdrial et al. (unpublished data) found wet mixed-conifer stands in the Jemez River Basin had on average 36.7 t SOC $\text{ac}^{-1}$ on ridges and slopes compared to 55.75 t SOC $\text{ac}^{-1}$ in riparian areas.

Large soil inorganic carbon (SIC) reservoirs also exist in the deeper profiles of the soil, regolith (i.e. aggregate rocks and fractured bedrock), and crystalline bedrock (Schlesinger 1982, Raich and Schlesinger 1992, Jobbágy and Jackson 2000) where $\text{CO}_2$ reacts with water to form carbonic acid ($\text{H}_2\text{CO}_3$) which then percolates deep into the lithic zone. SIC precipitate compounds, such as calcium carbonate ($\text{CaCO}_3$), essentially remove carbon from the active carbon cycle (deB. Richter and Billings 2013). Schlesinger (1982) reported that in arid environments (i.e. desert scrub and grassland Aridisol soils) SIC carbonates (caliche) outweigh the soil organic carbon (SOC) by a factor of 10:1.

Figure 1: Wind driven crown fires consume surface detritus, needles and fine branches but leave heavier woody fuels intact. Above, the Las Conchas Fire incinerated more than 30,000 acres of timber in a single burning period near Cochiti Mesa, Santa Fe National Forest, in summer 2011. Photo by T.W. Swetnam

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Unprecedented Ecosystem Die-Off, Conversion, and Renewal

Globally, forests are already dying at an unprecedented rate related to drought and increased temperatures (Allen et al. 2015, Breshears et al. 2005). As air temperatures increase, relative humidity decreases resulting in larger vapor pressure deficits (VPD), which increases water stress on trees (Williams et al. 2013, Anderegg et al. 2015a). Increased atmospheric temperatures are predicted to be the dominant factor for tree mortality in the future (McDowell et al. 2011, 2013, Williams et al. 2013). Future average annual rainfall in the Southwest is predicted to decrease compared to historical averages (Jardine et al. 2013, Garfin et al. 2013). The frequency of extreme events, both dry and wet, are also predicted to rise with warming (Kendon et al. 2014). This increase in the “wildness” of the weather will result in negative impacts on much of the vegetation in the Southwest. Based on such scenarios, widespread forest death is predicted to occur within the next 50–100 years (McDowell 2013, Williams et al. 2013, Allen et al. 2015). Increased temperatures have led to a greater number of larger and more severe fires and longer fire seasons (Westerling et al. 2006, Moritz et al. 2012, Dennison et al. 2014). Anderegg et al. (2015b) found that conifers suffer carbon assimilation reductions for a longer period (1–4 years) than do deciduous trees due to recent high temperatures and drought.

In response to warming, some biomes may shift up-slope to stay within their favorable temperature and precipitation zones (Breshears et al. 2008). Trees are evolved to function near their physiological limits, an adaptation that maximizes their fitness in competition with other plants (Allen et al. 2010, Anderegg et al. 2015a,c). Unfortunately, living on the edge also results in the inability to adjust to large variations in climate. When this happens a species may become incapable of persisting under the new conditions or at least be unable to reproduce at its current location (Falk 2013).

Common Vegetation Types: Fire Regimes, Carbon Reservoirs, and Expected Changes

Forests cover ~20% of the surface area in the Southwest, and are the largest reservoirs of carbon (Smith et al. 2006, Ryan et al. 2010). The largest vegetation types by area are relatively lower in productivity (e.g. desert grassland, chaparral, and piñon-juniper woodlands). The highest productivity types (e.g. mixed-conifer, and subalpine spruce-fir) constitute only 5% of the forested area (Anderson-Teixeira et al. 2011). Table 1 summarizes published values of median and maximum (99% confidence interval) carbon reservoirs in common vegetation types as well as SOC and NPP estimates.

Reservoirs of carbon are distributed non-linearly amongst individual trees in a forested stand. Fluxes of

Frequently Used Terms

- **ac**: per acre
- **C**: Periodic table symbol for the element Carbon.
- **DIC**: dissolved inorganic carbon – e.g. carbonic acid (H$_2$CO$_3$) which forms when carbon dioxide (CO$_2$) reacts with stream or soil water (H$_2$O+CO$_2$ ↔ H$_2$CO$_3$).
- **DOC**: dissolved organic carbon – e.g. particulate plant cellular material in stream or soil water.
- **Flux**: the transfer of carbon or CO$_2$ between the atmosphere and plants (vertical flux) or between plants and animals (lateral flux).
- **GPP**: gross primary production – the total amount of carbon captured by a plant or ecosystem per year, measured as NPP plus plant respiration.
- **lbs C**: units in pounds of carbon.
- **NEE**: Net Ecosystem Exchange, the measurement of C entering and leaving an ecosystem, often measured using scientific equipment called “eddy-covariance” or “eddy flux” towers.
- **NEP**: NPP minus heterotrophic respiration per year.
- **NPP**: net primary production – the net amount of carbon per year captured by a plant or ecosystem minus respiration.
- **Reservoir**: an organism or place where carbon is stored over time.
- **SIC**: soil inorganic carbon – mineral compounds from parent rock or soil-water chemical reactions, e.g. calcite or calcium carbonate (CaCO$_3$).
- **SOC**: soil organic carbon – includes living roots, dead wood and plant material, bacteria, fungus, and other organisms.
- **Respiration**: the oxidation of carbon compounds as a result of metabolism.
- **t C**: tons of carbon, equal to 2,000 lbs.
- **yr**: per year
carbon are related directly to tree size and age, while climate has an important but indirect effect (Enquist et al. 1998, Michaletz et al. 2014). In some cases an individual large diameter tree can contain the majority (>50%) of carbon in a forest stand (Lutz et al. 2012). Stephenson et al. (2014) found the rate of carbon accumulation in older trees increases continuously with tree size. This finding alters the conventional thinking that older forests are “senescent” and sequester less carbon than do younger trees. In fact, larger trees, sequester an exponentially larger amount of carbon per unit area than do smaller seedlings. Incredibly, a large diameter tree can sequester as much carbon in a single year as the carbon in an entire mid-sized tree. Al. (2014) found the rate of carbon accumulation in older forests during the arid fore-summer and late fall (Liu et al. 2011, Dewar 2011). Today grasslands utilized for grazing may not be capable of spreading fire. The loss of fire in southwestern grasslands has led to an “infilling” of woody shrubs and trees (Brown and Archer 1989, 1999, Romme et al. 2009a).

Sims and Singh (1978) reported aboveground NPP to be 0.12 – 0.84 t C ac⁻¹ yr⁻¹ for desert grasslands with total NPP between 1.02–1.72 t C ac⁻¹ yr⁻¹. The majority of the organic carbon in grasslands is belowground. In western montane grasslands, root-to-shoot ratios as high as 3.7:1 are reported (Schenk and Jackson 2002, Jackson et al. 1996). Schlesinger (1982) reported SOC in soil profiles for Arizona desert grassland to be 33.09 t C ac⁻¹. In the Valles Caldera National Preserve, a 10-year monitoring program found aboveground carbon production varied with climate and grazing over time from 1.5 to 3.44 t C ac⁻¹ yr⁻¹ (Van Horn et al. 2012).

Standing aboveground biomass in grassland varies greatly year-to-year based on prior rainfall and the remaining standing dead biomass from the previous season. Grasslands can rapidly sequester carbon during summer rain events, having a linear correlation with precipitation (Sims and Singh 1978). Grasslands are more efficient than trees at instantaneously sequestering carbon following a growing season precipitation event. However, increased winter precipitation tends to favor woody species over grasslands as the soil moisture moves deeper into the soil profile (Brown et al. 1997).

### Implications of Climate Change

Grasses will be an important component of carbon...
storage and flux in many Southwest ecosystems into the foreseeable future. Encroachment by woody plants into grasslands across all elevations should be expected to continue in the absence of active fire management programs (Bond and Keeley 2005). A predicted net decline in summer precipitation relative to winter precipitation may also lead to woody plants being favored over grasses in certain locations. Alternately, capture of previously forested areas by grasses and other herbaceous species following high-severity fire is one potential outcome of continued wildfire activity (Savage and Mast 2005, Savage et al. 2013).

Most trees and woody plants use so-called “C3” photosynthesis, while most (but not all) grasses use “C4” photosynthesis. As temperatures within plants increase typically beyond 10 degrees Celsius or 50 degrees Fahrenheit (F) the carbon fixing efficiency of C3 plants decreases due to increased “photorespiration,” in which the enzyme RuBisCO wastefully oxidizes the carbon fixed during the initial reactions of photosynthesis (Monson and Baldocchi 2014). This loss in efficiency results in less growth and a decrease in fitness. C4 plants do not suffer as much photorespiration due to their unique strategy of building up CO₂ inside bundle sheath tissues in the leaves. As temperatures increase, C3 trees and shrubs become less efficient, and C4 grasses will have a competitive advantage (Collatz et al. 1998). Paleocological records from central New Mexico support this prediction of shifts in dominance of C3 and C4 plants with data from the Holocene over 12,500 years covering cool/wet to hot/dry periods (Hall and Penner 2013).

**Interior Chaparral and Encinal**

Interior chaparral and encinal are common at lower elevations (4,000–7,500 ft msl) in the southern parts of Arizona and New Mexico (Shreve 1915, Whittaker and Niering 1975, Brown 1978). In southeastern Arizona encinal, “oak” in Spanish, is typified as a savannah grassland with Madrean oaks, e.g. Mexican blue oak (Quercus oblongifolia), Emory oak, (Q. emoryi), and Arizona white oak (Q. arizonica), that fills the ecotone between desert grassland and Madrean pine-oak woodland. Interior chaparral is more dense and shrub-dominated than encinal. Common interior chaparral species include shrub live oak (Q. turbinella), manzanita (Arctostaphylos pungens) and rosewood (Vauquelinia californica).

Historically, interior chaparral fires are thought to have been infrequent and high intensity, typically top-killing the aboveground biomass (Schussman et al. 2006) similar to coastal chaparral systems in California. Chaparral species tend to be fire-adapted obligate resprouters or seeders with fire enhancing germination. The actual fire interval of interior chaparral is understudied in the Southwest. Reconstructions of a chaparral fire regime using Big-cone Douglas fir in southern California found a historical interval between 6 and 60 years with an average of 30 years (Lombardo et al. 2009). Similar fire regimes are likely in interior chaparral across the Southwest with dominant climatic patterns being comparable and reconstructions of fire regimes in pine-oak stands adjacent to interior chaparral tending to support similar intervals (Barton 1999, 2002, Kaib et al. 1996). The fire regime of encinal is
further related to desert grassland and the higher elevation Madrean pine-oak.

The aboveground carbon reservoir in chaparral ranges from 1 to 8 t C ac\(^{-1}\) (Whittaker and Niering 1975). Schlesinger (1982) reported ~23.57 t C ac\(^{-1}\) of SOC in chaparral soils. The NPP of interior chaparral in the Sky Islands was estimated to be ~0.78 t C ac\(^{-1}\) yr\(^{-1}\) by Whittaker and Niering (1975).

**Implications of Climate Change**

As unprecedented landscape-scale wildfires continue to burn, interior chaparral will likely recover in its current locations and expand into higher elevation forest types, excluding tree species such as pine (Savage and Mast 2005). Evidence of type conversion from pine-oak, pine and mixed-conifer forest to chaparral following historical wildfires have persisted for more than one hundred years in the Rincon Mountains of Arizona (Iniguez et al. 2009). More recent conversion from pine forest to chaparral has been noted at sites across the Mogollon Rim (Savage and Mast 2005, Savage et al. 2013) and Sky Islands (Barton 2002, Iniguez 2006).

Existing chaparral types will likely decrease in productivity as global warming progresses and their ideal eco-physiological climate zone moves upward in elevation. Conversions of other forested types to chaparral decrease the long term carbon sink capacity of former forested areas.

**Pine-Oak Woodland**

Multiple species of oak (Quercus arizonica, Q. emoryi, Q. grisea, Q. hypoleucoides, Q. oblongifolia) and pine (Pinus arizonica, P. cembroides, P. discolor, P. ponderosa) are typical of pine-oak woodland the Madrean Sky Islands (Shreve 1915, Whittaker and Niering 1975, Niering and Lowe 1984). Gambel's oak (Q. gambelii) is the most common oak species, with ponderosa pine at higher elevations around the Mogollon Rim.

Pine-oak woodlands historically experienced spreading fires on short to medium intervals (3–40 years) and had a frequent mean fire interval (MFI, ~4 years) similar to higher elevation ponderosa forests (Swetnam et al. 1992, Kaib et al. 1996). Such a fire regime would typically have involved low-intensity burns with favored survival of larger fire resistant thick barked trees.

The carbon reservoir of pine-oak is similar to higher elevation assemblages of ponderosa pine with average values between 16 and 27 t C ac\(^{-1}\) in mature stands (Whittaker and Niering 1975). Schlesinger (1982) found ~34.45 t C ac\(^{-1}\) of SOC in pine-oak woodland soils. Measured values of NPP were 0.82 t C ac\(^{-1}\) yr\(^{-1}\) in the Santa Catalina Mountains (Whittaker and Niering 1975).

**Implications of Climate Change**

Some modern fires in pine-oak have burned with higher intensity than in the past as evidenced by the loss of large forested pine-oak stands following recent fires in the Madrean Sky Islands (Dillon et al. 2011). Contributing factors to these higher intensity fires are likely related to fire suppression and an increase in density and continuity of fuels.

Madrean pine-oak forests have been observed to convert to oak-scrub (interior chaparral type) woodlands after modern wildfires (Barton 2002, Iniguez 2006, Iniguez et al. 2009). Retreat of pine-oak ecosystems to higher elevations is likely to occur as global warming alters their typical precipitation and temperature regimes (Allen and Breshears 1998).

Carbon storage initially decreases from stands burned in high intensity fires but should recover more quickly for species that resprout from the root crown than those from seed. Long term declines in productivity related to warming and drying conditions will however lead to less overall carbon storage (Williams et al. 2013, Anderleeg et al. 2015b).

**Piñon-Juniper Woodland**

By area, piñon pines and juniper (P-J) woodlands and savannas are the largest forest type in the western U.S., covering ~100 million acres (Miller and Tausch 2000, Romme et al. 2009a, Anderson-Teixeira et al. 2011). P-J stands are dominated by several species of piñon (or pinyon) pine including P. cembroides, P. edulis, and P. monophylla. Several juniper species co-occur in varying frequency, including Juniperus deppeana, J. monosperma, J. osteosperma, and J. scopulorum. Romme et al. (2009a) describe three different types of P-J in the western U.S. based on structure, understory, and disturbance regime: woodlands, savannas, and shrublands. Woodlands and shrublands tend to be winter precipitation dominated, while savannas tend to have more summer precipitation (Romme et al. 2009a).

Fire return intervals in central New Mexican P-J were frequent (10–25 years) before the 20th century (Margolis 2014). Conversely, P-J in Nevada, Colorado, and Utah are reported to tend toward an infrequent fire interval of up to 400 years (Brown et al. 2008, Romme et al. 2009a, Swetnam and Brown 2010). In either case, many P-J stands have undergone an increase in density following European settlement related to grazing, changes in climate and disturbance regimes. Margolis (2014) found up to a 600% increase in tree density of mixed P-J and ponderosa dominated stands in New Mexico following the collapse of the frequent grass fire regime in the early 20th century.

Grier et al. (1992) reported the average carbon in P. edulis - J. monosperma stands to range from 4.8 t C ac\(^{-1}\) in a 90-year-old stand up to 12.1 t C ac\(^{-1}\) in a 350-year-old stand. NPP in these systems was estimated between 0.47 to 0.64 t C ac\(^{-1}\) yr\(^{-1}\) (Grier et al. 1992). Alligator juniper (J. deppeana) can grow to substantial size (>70 inches diameter), and survive multiple fires. Such large, old growth trees are the most significant local reservoir of carbon in some P-J landscapes.
Implications of Climate Change
Piñons were especially hard hit by the 1996 to early 2000s drought in Arizona and New Mexico. In a few cases, stands of piñon pine exceeded 97% mortality, while juniper in the same stands experienced <1% mortality (McDowell et al. 2008). Across the Southwest, average piñon pine mortality was 25% during the early 2000s drought (Meddens et al. 2014). Predicted climate patterns for the mid to late 21st century suggest similar drought conditions will persist and increase in intensity (Williams et al. 2013, McDowell et al. 2013). Drying and increased temperatures may lead to even larger and more widespread mortality events in P-J where even the junipers experience greater mortality. Although large stand-replacing fires in P-J appear to be increasing, the reportedly long fire return interval of P-J makes evaluating whether recent events are outside of a historical range of variability difficult.

Ponderosa Pine Forest
Ponderosa pine (P. ponderosa) are the archetypal forest tree of the Southwest. The Mogollon Rim is home to the largest contiguous belt of ponderosa in the U.S., with stands also occurring throughout the Sky Island bioregion. Ponderosa forests mix with lower elevation pine-oak species, as well as higher elevation mixed-conifer species along the boundaries of its preferred climate zone. In productive sites ponderosa pine can grow to very large size (Figure 3).

Fire regimes in ponderosa are very well studied (Dieterich and Swetnam 1984, Swetnam and Dieterich 1985, Savage and Swetnam 1990, Fulé et al. 1997, Mast et al. 1999, Friederici 2003, Van Horne and Fulé 2006, Falk et al. 2011). Historically, spreading low-intensity surface fires were largely entrained by both bottom-up fuels continuity and top-down periodic climate patterns, especially the El Niño Southern Oscillation (ENSO) (Swetnam and Betancourt 2010). Frequent low intensity fire in gentle topography resulted in stands of large, old-growth trees with high base height and wide canopy spacing (Merriam and Stejneger 1890, Woolsey 1911, Shreve 1915). Modern tree densities are much higher with smaller average size and are prone to high intensity and severity fires (Allen et al. 2002). Recent landscape-scale fires that burned through ponderosa forest include the Rodeo-Chediski Complex Fire (2002) and the Wallow (2011) in Arizona; Las Conchas (2011) and Whitewater-Baldy Complex Fire (2012) in New Mexico, with each setting and being surpassed for the record largest in state history.

Carbon stocks in ponderosa forest are reported to average 19.8 to 30.1 t C ac⁻¹ on the Mogollon Rim (Finkral and Evans 2008, Sorensen et al. 2011). Dore et al. (2010) measured ~55 t C ac⁻¹ for an undisturbed stand, and 39.4 t C ac⁻¹ in a recently thinned stand in central Arizona. Other studies in the Madrean Sky Islands found 57 t C ac⁻¹ (Whittaker and Niering 1975, Swetnam 2013). These values are little more than half those reported in ponderosa pine in the Pacific Northwest (93.56 t C ac⁻¹, Law et al. 2001, Smith et al. 2006). Kaye et al. (2005) reported NPP for a ponderosa pine stand in Arizona to be ~1.05 t C ac⁻¹ yr⁻¹. The NPP of a productive ponderosa pine stand in New Mexico was measured to be ~1.65 t C ac⁻¹ yr⁻¹ (Anderson-Teixeira et al. 2011).

Implications of Climate Change
Overall, decreases in the extent of ponderosa pine are expected as global warming proceeds and regional drying intensifies (Rehfeldt et al. 2006, Notaro et al. 2012, Williams et al. 2013). Stands burned in recent high-severity fires are in some areas being replaced by shrub species and oaks (Iniguez 2006, Falk 2013). When entire stands are killed, seed sources are lost and ponderosa is not be able to recover in an area (Haire and McGarigal 2010). Dore et al. (2012) report the greatest decline in GPP was observed for stands burned at high severity, while treated (thinned) stands recovered and increased GPP within a few years. Micro-site feedbacks...
related to tree shading likely increased soil moisture, which helped further increase carbon assimilation (Dore et al. 2012).

Hurteau and Brooks (2011) and North and Hurteau (2011) have shown that fuel treatments can mitigate the potential for a high-severity fire in ponderosa pine and mixed-conifer ecosystems. Small diameter trees, while making up the majority in number of trees in the stand typically constitute only ~18% of the total carbon (Hurteau et al. 2008). By removing ladder fuels that enable crown fire most of the carbon in the stand can be maintained (Hurteau et al. 2011). Initially fuels treatments remove carbon from the system, but over time the stands improve both their capacity to sequester carbon and store a greater amount of carbon (Dore et al. 2010, 2012).

**Mixed-Conifer Forest**

Although it covers only a small percentage (<3%) of the total forested area in the Southwest (Anderson-Teixeira et al. 2011), mixed-conifer forests are the most productive and contain the largest reservoirs of C. Mixed-conifer species typically include Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa and southwestern white pine (*P. strobiformis var. arizonica* or *P. flexilis*). Quaking aspen (*Populus tremuloides*) is a common post-fire species that can exist in large clonal stands amongst mixed-conifer (Romme et al. 2009b). Mixed-conifer is variously classified as wet or dry depending on its elevation and aspect of exposure (for more details see Ecological Restoration Institute Working Paper No. 28).

Mixed-conifer fire regimes tend to be low to mixed severity with fire return intervals of 4–15 years in dry mixed-conifer and 8–26 years in wet mixed-conifer (Baisan and Swetnam 1990, O’Connor et al. 2014, Huffman et al. 2015). North aspects and shaded drainage bottoms tend to hold more moisture (including snow) and have higher fuel moistures during fire seasons reducing the overall probability of fire in moderate years. There is some evidence of high-severity fire driven by topography on steep hillslopes in this forest type (Margolis and Balmat 2009, Margolis et al. 2011).

**NEE** in mixed-conifer can exceed 1.5 t C ac⁻¹ yr⁻¹ in wet years but declines to ~1.05 t C ac⁻¹ yr⁻¹ in dry years (Anderson-Teixeira et al. 2011, Perdrial et al. unpublished data). Old growth stands in white-fir and Douglas-fir dominated drainage bottoms have been measured to hold up to 159.85 t C ac⁻¹ in aboveground biomass (Whittaker and Niering 1975, Anderson-Teixeira et al. 2011). Woody debris can also be a significant contributor to local carbon stocks in mixed-conifer forests, for example in a New Mexican mixed-conifer forest down woody debris loads ranged from <1 to 9.04 t C ac⁻¹ (Valles Caldera Trust, common stand exam data).

Not considering riparian trees like Fremont cottonwood (*Populus fremontii*), which can grow to enormous size, the largest trees in southwestern forests are located in the mixed-conifer type. For example, an old growth Douglas-fir standing 135 ft in height and 5.25 ft in bole diameter contains ~16 t carbon in its aboveground biomass alone (Swetnam 2013), based on published wood-specific gravity and carbon density (Lamlom and Savidge 2003, Chojnacky et al. 2014).

**Implications of Climate Change**

Mixed-conifer forest has an increased likelihood of wildfire as temperatures continue to increase and precipitation patterns decline. Fires in mixed-conifer are likely to become more severe, leading to greater releases of C (O’Connor et al. 2014). Reduced productivity from declines in precipitation should also be expected (Anderegg et al. 2015c). Conversion to aspen or scrub oak and lower elevation pine species in areas of high severity are also likely. Some common mixed-conifer species are likely to invade higher elevations sites previously occupied by only sub-alpine spruce and fir species (O’Connor et al. 2014).

**Aspen Disclimax Forest**

The presence of large clones of quaking aspen across the Southwest appear to follow from stand-replacing fires in the 18th and 19th century (Patton and Avant 1970, DeByle et al. 1987, Margolis et al. 2011). Extant aspen clones are relatively fire resistant, maintaining high fuel and soil moisture throughout the fire season.

Most aspen stands occur at elevations equivalent to mixed-conifer and spruce-fir, making it the most productive forest type, estimates for maturing aspen clone NPP have been reported to be as high as ~2.37 t C ac⁻¹ yr⁻¹ (Whittaker and Niering 1975, Gosz 1980). Gosz (1980) measured NPP from an aspen clone in New Mexico which had ~37.14 t C ac⁻¹ of aboveground C. An aspen stand with biomass C of 62.8 t C ac⁻¹ was measured in the Pinaleño Mountains in Arizona (Swetnam 2013). Reported SOC from mature aspen stands in northern Utah were 41.79–67.0 t C ac⁻¹ and were greater than in adjacent mixed-conifer stands (Woldeselassie et al. 2012).

**Implications of Climate Change**

Aspen recruitment after fire may result in an increase in their distribution, mainly at higher elevation, based on observational records of aspen recruiting into burned areas in the 19th and 20th centuries (Margolis et al. 2011). However, 20th century fire suppression and drought have resulted in a reduction of area and vigor of many aspen clones (DeByle et al. 1987, Allen et al. 2010, Anderegg et al. 2015a), allowing other early successional species (such as *Q. gambelii* and *Robinia neomexicana*) to establish post-fire dominance. Conifers eventually over-top aspen stands in areas without fire (DeByle et al. 1987). Existing aspen clones at lower elevations will be
more susceptible to drought and potential conversion to oak or chaparral following disturbance in a hotter and dryer future climate. Anderegg et al. (2015a) have suggested by the 2050s hotter drought stresses may be frequent enough to kill large areas of aspen forest across the Southwest.

**Spruce-Fir Forest**

The smallest extant forest type in the Southwest, Engelmann spruce (*Picea engelmannii*) and sub-alpine fir (*Abies lasiocarpa*) make up less than 3% of the forested landscape by area.

These forests burned historically on multi-century or longer intervals (Margolis et al. 2011), allowing for biomass to accumulate in trees and in the soils. In the Pinaleño Mountains, spruce were shown to have increased in area following a mountain-scale fire in the late 1600s (O’Connor et al. 2014).

Spruce-fir forests are less productive than lower elevation mixed-conifer stands because of shorter growing seasons. NPP in spruce-fir reaches 1.41 t C ac⁻¹ yr⁻¹ (Whittaker and Niering 1975, Anderson-Teixeira et al. 2011). Measured biomass of spruce-fir varies from 61.9 to 110.16 t C ac⁻¹ (Whittaker and Niering 1975, Anderson-Teixeira et al. 2011, Swetnam 2013). SOC varies from 27.07–46.54 t C ac⁻¹ by topographic position with riparian positions having greater C than hillslopes (Perdrial et al. unpublished data, Woldeselassie et al. 2012).

**Future Implications of Climate Change**

Expected global warming scenarios will result in increased temperatures and more growing days in these stands, possibly making them more productive, but also more likely to experience wildfires. As these systems are burned they will likely be replaced by lower elevation species including white fir and Douglas-fir. Spruce-fir forests are also subject to episodic native insect outbreaks, as well as newly arrived invasive species (e.g. spruce aphid, Lynch 2009), which can kill large numbers of trees (O’Connor et al. 2015).

The small extant area in which spruce-fir forests exist is likely to change as global warming continues. These forests have the greatest risk of running out of habitable area as new trees only germinate up-slope at higher elevation seeking more favorable climatic conditions. They are also at greater risk of high severity fire when they do burn, leaving their former habitat space to be recolonized by other species such as aspen or pine.

**Future of the Carbon Cycle in Southwestern Ecosystems**

The concentration of atmospheric CO₂ for at least the last 200,000 years was consistently ~280 parts per million (ppm) (IPCC 2013). Atmospheric CO₂ began to increase in the late 19th century due to anthropogenic land use and expanded fossil fuel combustion (Barnola et al. 2003, Neftel et al. 1994). As of 2015, atmospheric concentrations now exceed 400 ppm and are increasing annually by +2 ppm (Solomon 2007, Stocker et al. 2013). In the Southwest, mean annual temperatures are projected to increase by 2–9 degrees F by the end of the current century (Garfin et al. 2013).

Forests can act as both carbon sinks and sources depending on age, stand density, and disturbance regime. Increases in the size and severity of fires (Westerling et al. 2006, Dennison et al. 2014), droughts (van Mantgem et al. 2009, Allen et al. 2010, Williams et al. 2013), and insect outbreaks (Raffa et al. 2008, Negron et al. 2009, O’Connor et al. 2015) all negatively impact carbon flux and reservoirs of forests. Forest fires contribute to a positive feedback loop (Ramanathan and Carmichael 2008), further increasing the mean annual temperature of the atmosphere (Stocks et al. 1998, Cox et al. 2000, Friedlingstein et al. 2006).

Recent carbon sinks in southwestern forests have turned into sources following wildfires with large amounts of CO₂ released initially through combustion and later by decomposition. Dore et al. (2010, 2012) found that severely burned ponderosa pine forests can act as continuous carbon sources for up to five years after fire. Many other forests in the Southwest that were logged early in the 20th century (see Woolsey 1911) are reentering a phase of significant carbon assimilation as stands mature with trees that are now 50 to 90 years of age. In the Valles Caldera, which was logged intensively in the mid-20th century Anderson-Teixeira et al. (2011) and Perdrial et al. (unpublished data) found the maturing mixed-conifer forests to be significant net carbon sinks (up to 1.5 t C ac⁻¹ yr⁻¹) prior to the 2011 Las Conchas and 2013 Thompson Ridge fires.

Taken collectively, forest dieback from drought and fire are having serious effects on carbon sequestration in the Southwest (Breshears and Allen 2002, Allen et al. 2015). Loss of forested areas from persistent drought and wildfires further reduce regional carbon reservoirs and increase watershed vulnerability to extreme events (McDowell et al. 2013, Jardine et al. 2013, Moody et al. 2013, Anderegg et al. 2015c). Major restoration efforts, such as the Four Forest Restoration Initiative (4FRI) in northern Arizona, Southwest Jemez Landscape Restoration Program in New Mexico, and FireScape in the Sky Islands of southern Arizona, are directly confronting the issue of restoring natural wildfire in southwestern forest ecosystems. Although these initiatives are a step in the right direction there are millions of additional acres in southwestern forests that will require future treatment to better cope with climate change impacts.

Mitigating negative impacts on the carbon cycle should vary by forest biome and by management unit. Prioritization efforts to increase existing carbon reservoirs generally run parallel to other traditional management objectives that involve continued access.
to clean water, protecting threatened and endangered species, ensuring sustainable yields for timbering, improvement of grazing forage and wildlife habitat, and reducing fire risk (Garfin et al. 2013). Improving ecosystem resistance to catastrophic fire includes creating greater heterogeneity amongst densely packed low-frequency, high-intensity fire regime vegetation types and opening up the canopy cover of high-frequency, low-severity fire regime vegetation types. Increasing resilience to disturbances beside fire (e.g. insects, drought, disease) also include reducing inter-tree competition by thinning existing stand density.

The complete collapse of all mature forests that took centuries to develop due to high-severity fire and extreme drought represents the starkest outcome for southwestern forests in the future. Entire watersheds burned at high severity, as seen in the 2011 Las Conchas Fire (Figure 1), are a parable of such a worst-case scenario where nearly all of the extant forest is lost and extreme post-fire impacts on water quality and wildlife are observed.

Restoration toward historical conditions has the benefit of both increasing carbon storage and decreasing the probability of severe fire with increased resilience and ecosystem function (Hurteau and Brooks 2011). Reinitiating low-severity fires in areas where it traditionally did the job of clearing detritus and small trees favoring the survival of large diameter individuals is one ideal objective for large areas of the Southwest, particularly in ponderosa pine, pine-oak, and other low-severity fire systems (Allen et al. 2002, Friederici 2003). Protection of large diameter trees is also an important aspect of carbon banking. Within old growth stands, enough mid-development trees should also be kept to replace trees as they die-off due to natural factors (windthrow, root rot, lightning, individual tree torching, etc.). In this way the largest amount of forest carbon can be retained in perpetuity.
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