RESEARCH ARTICLE

Post-fire recovery of ecosystem carbon pools in a tropical mixed pine-hardwood forest

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Abstract

Aim of the study: To analyze the recovery pattern of carbon pools in terms of size and the relative contribution of each pool to total ecosystem C along a fire chronosequence of tropical mixed pine-hardwood forest.

Area of study: Las Joyas Research Station (LJRS), core zone of Sierra de Manantlán Biosphere Reserve (SMBR) in the state of Jalisco, central western Mexico.

Materials and methods: Carbon stored in aboveground plant biomass, standing dead trees, downed woody debris, forest floor, fine roots and mineral soil, was compared with a nested analysis of variance (ANOVA) in post-fire stands of eight-year-old, 28- and 60-year-old stands of mixed *Pinus douglasiana*-hardwood forest.

Main results: The total ecosystem carbon in eight-year-old stands was 50% lower than that of 60-year-old stands. Carbon content in the biomass and mineral soil increased with stand age. The carbon in the biomass recovered to the undisturbed forest in the 28 years of succession. The main C storage in the eight-year-old stands were the mineral soil (64%) and downed woody debris (18%), while in the 28- and 60-year-old stands, live tree biomass and mineral soil were the two largest components of the total C pool (43% and 46%, respectively).

Research highlights: We found a significant effect of high-severity fire events on ecosystem C storage and a shift in carbon distribution. The relatively fast recovery of C in ecosystem biomass suggests that mixed *Pinus douglasiana* hardwood forest possess functional traits that confer resilience to severe fire events.

Key words: chronosequence; carbon dynamics; mineral soil; *Pinus douglasiana*; fire effects.

Abbreviations used: LJRS, Las Joyas Research Station; DBH, diameter at breast height; DL, duff layer; LL, litter layer; DWD, downed woody debris; ANOVA, analysis of variance; CO_2, carbon dioxide; SMBR, Sierra de Manantlán Biosphere Reserve; C, carbon. AGV, above ground vegetation.

Introduction

Wildfires influence the earth´s climate via the release of carbon and greenhouse gases, atmospheric aerosols, and by the alteration of surface albedo (Bowman *et al.*, 2013). Therefore, has been a common perception that fire suppression decrease the rate of release of CO_2 caused by burning and maximize C storage in ecosystem pools (Tilman *et al.*, 2000; Hurteau & Brooks, 2011). However, there is enough evidence about how

a changing climate and policies that encourage fire suppression has contributed to modify forest structure, fuel loads, and fire behavior, causing a shift from low- to high-severity fires (Agee & Skiner, 2005; Schoennagel *et al.*, 2017). In this sense, managers of fire-prone forests must trade off the promotion of C storage against the reduction of fire hazard (Hurteau *et al.*, 2008; Bowman *et al.*, 2013).

Understanding the role of fire regimes on ecosystem carbon dynamics is critical for the implementation of climate change mitigation strategies in forested landscapes (Hurteau & Brooks, 2011; Williams *et al.*, 2012; Bowman *et al.*, 2013). The effects of wildfires are strongly influenced by variability in vegetation types, site conditions, fire behavior, and the diversity of fire regimes at the landscape level, which are characterized by the range of variation in frequency, seasonality, intensity, severity, size, and spatial pattern of the fire events (Agee, 1993; Scott *et al.*, 2014). For this reason, there is a need to study fire effects in different forest ecosystems and environmental conditions, particularly in mountain forest ecosystems in tropical regions of the world (Pregitzer & Euskirchen, 2004), where the effects of wildfires on the forest C balance and post-fire response of C pools have been little studied (Pompa-García & Sigala-Rodríguez, 2017). This is crucial in the context of increasing wildfire activity and severity as a consequence of fire suppression policies and human-induced climate change that has been reported for other regions like the western United States (Westerling *et al.*, 2006; Schoennagel *et al.*, 2017).

Worldwide, the majority of pine forests are under a frequent low-severity fire regime (which means a temporal frequency lower than 35 years). Under this wildfire regime, the majority of fires have low severity, and wildfire events with moderate or high severity occur in a smaller proportion (Agee, 1993). The low-severity fires reduce the tree basal area by less than 30% (Boerner, 1981; Keyser *et al.*, 2008), mainly affecting the C storage in shrubs, herbs, and the forest floor layer (Boerner, 1981), while high-severity fires induce high tree mortality (> 70%) and elevated carbon emissions, alter the distribution of carbon pools on forest ecosystems, and may have long-term effects on post-fire forest structure and function (Kashian *et al.*, 2006; Alexander *et al.*, 2012; Mitchell, 2015).

Carbon recovery patterns have been widely documented from boreal and temperate forests, which are dominated by stand-replacing fire regime (mean return interval 50 to >250 years) (Wang *et al.*, 2001; Litton *et al.*, 2004; Gough *et al.*, 2007; Dore *et al.*, 2008; Alexander *et al.*, 2012; Kashian *et al.*, 2013). Using data from chronosequences, C recovery in aboveground

biomass has been described as a relatively slow C accumulation during stand regeneration, followed by a fast accumulation during stand development, then reaching a maximum and remaining relatively constant or declining in old-growth forest stands (Bormann & Likens, 1979). Site productivity, stand density and composition play a key role as a source of variation in forest C storage after fires (Litton *et al.*, 2004; Kashian *et al.*, 2006; Alexander *et al.*, 2012; Spies *et al.*, 1988). C stored in belowground components varies less than that in aboveground pools (Kashian *et al.*, 2006; Gough *et al.*, 2007). However, a significant increase in post-fire mineral soil C has been observed, associated with rapid root turnover and potential incorporation of fire-created debris into the mineral soil C pool over time (Seedre *et al.*, 2014).

Here we present the results of a study on the recovery of carbon pools after wildfire events that opened up gaps, reinitiating succession in mixed pine-hardwood forests of central-western Mexico. Lower-montane moist pine forest in Mexico covers 6.1 million hectares (3.2% of the country's area). These forests thrive in warm temperate humid climates (mean annual temperature of 11–19 ºC with a potential evapotranspiration: annual precipitation ratio less than 1), with a dry spring season and a summer rain regime (Cuevas-Guzmán & Jardel, 2004). *Pinus* species are the dominant component (>50% basal area), mixed with broad-leaved tree species of genera like *Quercus*, *Carpinus*, *Clethra*, *Cornus*, *Magnolia*, and *Styrax*, among others (Cuevas-Guzmán & Jardel, 2004). Mixed pine-hardwood stands develop in advanced successional stages in mesic sites, and the dominance of pines is maintained by recurrent wildfires (Jardel, 2008). The specific objective of the study was to analyze the recovery of carbon pools, in terms of size and the relative contribution of each pool to total ecosystem C along a fire chronosequence of tropical mixed pine-hardwood forest. Carbon content was quantified in stands of 8- and 28-year-old that originated from fire and a > 60-year-old that typifies mature mixed pine-hardwood forests in the study area. We hypothesize that after wildfire ecosystem C storage will increase with stand age.

Material and methods

Study Area

The study was conducted in Las Joyas Research Station (LJRS), in the zone core of Sierra de Manantlán Biosphere Reserve (SMBR) in the state of Jalisco, central western Mexico (19° 14' 49"–19° 37' 30" N

and 104° 14' 49"–104° 18' 16" W). LJRS has an extension of 1245 ha in a mountainous landscape with complex relief, with an elevation range of 1500 m to 2242 m. The climate is warm temperate with a mean annual temperature of 15 ± 2 °C, ranging from 12.8 °C in January to 20 °C in May. Mean annual rainfall is 1826 ± 94 mm, and the potential evapotranspiration:annual rainfall ratio is 0.5–0.6. According to the Holdridge Life Zone System, the bioclimatic conditions correspond to a lower montane moist forest (Cuevas-Guzmán & Jardel, 2004).

The soil parent materials are Tertiary extrusive igneous rocks, like basaltic porphyries, basalts, andesitic basalts, and volcanic tuffs. A typical soil catena in the area is a gradient from Inceptisols in ridges and upper slopes, Alfisols in middle to lower slopes, and Ultisols in hollows and stream banks. The vegetation is a mosaic of pine-oak forests associated with convex landforms (mountaintops and upper slopes), mixed hardwood forests (cloud forest) in concave landforms (ravines and hollows), mixed pine-hardwood forest in intermediate conditions, and secondary scrub in abandoned agriculture fields (Cuevas-Guzmán & Jardel, 2004). The dominant species in pine-oak and mixed pine-hardwood forests is *Pinus douglasiana* Martínez.

Most fires in the SMBR occur between April and early June, at the end of the dry season. Fires are relatively small in area (mean: 189 ha, mode: 50 ha) and the most common ignition factors are human-related activities (Balcázar, 2011). Frequent low-severity surface fires characterize the historical fire regime in the pine-oak forest, with a fire return interval ranging from three to12 years (Cerano-Paredes *et al.*, 2015).

Fire suppression in LJRS used to encourage the recovery of mixed hardwood forests and mixed pine-hardwood forests cover through natural regeneration, has led to decreased fire frequencies and accumulation of fuel. Forest floor and woody debris loads for stands

without fires in 20 years have been estimated, respectively, at 37 to 58 Mg ha^{-1}, and 31 to 38 Mg ha^{-1} (Alvarado-Celestino *et al*., 2008). Under these conditions, mixed-severity fire events occurred in 1983 and 2003, causing larger fires; while there is no estimate of the burned area in 1983, the total area burned in the 2003 fire was 390 ha. The result was a heterogeneous spatial pattern formed of low-, moderate-, and high-severity patches, and others did not burn. High-severity fire patches were considered those where intense surface fire with smoldering combustion and torching caused high tree mortality (> 70%), consumption of the entire organic soil layer, and the restarting of succession (Jardel, 2008). The size of patches ranged from 1 to 40 ha and there was not post-fire management, vegetation recovered through natural regeneration. The sites burned at high-severity were selected for the present study (Table 1).

Sampling design

To analyze the recovery of ecosystem carbon pools along a post-fire chronosequence, we compared stands eight and 28 years following a fire, and mature stands (>60 years). The 60-year-old stands have not had low-severity fires for at least 30 years and represent late-successional condition in the absence of fire (Jardel, 1991; Cuevas-Guzmán & Jardel, 2004). It was assumed that the mature forests are representative forests in this region.

The use of the chronosequence method relies on the assumption that all variation among sites is due to differences in time since the disturbance (Walker *et al*., 2010). Therefore, a nested sampling design was used to help prove that assumption. Each stand age class was replicated three times. To minimize the impact of spatial autocorrelation, the stands were not samples in close proximity to one another. This was achieved by

Table 1. Stand characteristics in a fire chronosequence of tropical mixed pine-hardwood forest.

Stand age (years)	Stand replicate	Geographic coordinates		Extension affected by fire (ha)	Basal area (m² ha⁻¹)	DBH range (cm)	Height range (m)
		LN	LW				
8	1	19°36'04"	104°16'22"	2	10.9 ± 3.3	2.5-45	2.3-30
	2	19°36'20"	104°16'05"	1	8.5 ± 2.7	2.5-48	1.7-22
	3	19°35'43"	104°15'01"	1	10.5 ± 4.6	2.5-36	2.0-23
28	1	19°35'07"	104°15'33"	9	43.2 ± 3.4	2.5-61	2.5-30
	2	19°35'00"	104°15'39"	8	39.9 ± 2.4	2.5-64	1.5-29
	3	19°35'20"	104°15'30"	12	50.7 ± 4.9	5.0-63	2.8-27
60	1	19°35'14"	104°16'06"	--	47.7 ± 6.5	2.5-71	2.8-45
	2	19°35'53"	104°17'52"	--	47.8 ± 8.9	2.5-66	1.0-33
	3	19°35'19"	104°16'44"	--	56.3 ± 7.1	2.5-78	2.0-44

selecting replicate stands with distances between them in the range of 0.5 to 2.4 km. Within each stand we randomly established three 500 m^2 circular plots (12.62 m radius), giving a total of 27 plots.

To minimize the effect of variation in site conditions, stands were located in the same elevational range (1950 to 2150 m), within the same soil type (Alfisols), in the mid-portion of N-facing slopes dominated by *Pinus douglasiana* (> 70% basal area). Mean slope inclinations showed no significant difference (from 22 to 38%). Mean stem density did not differ among stands, but tree basal area in the eight-year-old stands was four times lower than in the 28- and 60-year-old stands (Table 1).

Field sampling

The ecosystem carbon pools sampled within each 500-m^2 circular plot were: live and standing dead trees (>2.5 cm of diameter at breast height, DBH), understory (trees < 2.5 cm of DBH, shrubs <1.3 m in height and herbaceous plants), forest floor layer (litter and duff layer), downed woody debris, fine roots and mineral soil. The vegetation and soil samples were taken in the dry season, between January and June 2011.

DBH (cm) was measured at 1.30 m height of all live and standing dead trees (>2.5 cm of DBH) using standard diameter tape graduated into 0.1-cm. The total height (m) of all live and standing dead trees within the plot was measured using a Suunto clinometer. All live trees were identified to species level. Understory was clipped at the base in four 1-m^2 subplots located 13 m from the center of each plot following the direction of the main four cardinal points. Components were stored in paper bags, labeled, and transported 3-4 days after sampling to the laboratory to determine dry weigh.

Downed woody debris (DWD), defined as all dead wood lying or standing (with a zenith angle 45°) was sampled using the planar intercept method (Van Wagner, 1982). Starting from the center of each plot, three 20-m transects were established. The direction of the first transect was chosen randomly; the second transect was placed 120 degrees from the first and so on. The criteria used for decide which DWD was intersected by transect were the proposed by Brown (1974). According to its size, the DWD was classified into fine (< 0.6 cm), regular (0.6–2.5 cm), medium (2.5–7.6 cm), and coarse (>7.6 cm). DWD pieces < 2.5 cm in diameter intersected by transect were counted in the last 5-m section. While, DWD pieces 2.6–7.5 cm were counted along the 20-m transect. DWD >7.6 cm were measured in diameter (cm) at the point of intersection and the decay was classified in

five categories following the classification of Waddell, (2002). DWD pieces of all size were randomly collected, stored in paper bags, labeled, and transported 3-4 days after sampling to the laboratory to assess the carbon concentration (%).

The forest floor was divided into two layers: the litter layer (LL) and the duff layer (DL). The LL is composed of fresh plant residues (excluding woody debris) that keep their structure and have an identifiable origin; the DL includes decomposed organic matter that has lost its original structure. The depth (cm) of the LL and DL was measured using a graduated needle, every 3-m starting from the center of each plot and along four transects (12.6 m) following the direction of the main four cardinal points (16 points per plot). LL and DL bulk density samples were collected in three random points per plot following the method proposed by Ottmar & Andreu, (2007) modified by Morfín *et al.*, (2012). At each sampling point, 30-cm sharpened steel square was positioned on top of the LL and DL and inserted until the bottom of the square was embedded in mineral soil. Thirteen iron markers were positioned in a systematic pattern within the square and inserted until flush with the top of the litter layer. The litter was carefully removed from the square and placed within a labeled paper bag. The distance between the top of each marker and the top of the DL was measured and recorded. To measure the DL, each marker was inserted further until flush with the top of the duff layer. The duff layer was carefully removed from the square and placed within a labeled paper bag. The distance between the top of each marker and the top of the mineral soil was measured and recorded. These thirteen depth measurements were averaged to represent the LL and DL depth for the sample. LL and DL samples were transported every 3-4 days after sampling to the laboratory to determine dry weigh. A total of 81 litter and 81duff bulk density samples were collected.

The fine roots (< 5 mm of diameter) were sampled at eight points systematically selected from the 16 points used for forest floor depth measurements. Soil samples were taken from the top 40 cm of mineral soil with a cylindrical soil corer (5-cm diameter, 15-cm height), placed in plastic bags, labeled, and transported every 3-4 days after sampling to the laboratory to determine dry weight. Fine roots in the forest floor were not considered in this study.

Mineral soil samples were taken with a cylindrical soil corer (5-cm diameter, 15-cm height) at four depth intervals (0–10, 10–30, 30–50, and 50–70 cm) in eight points systematically selected from the 16 points used for forest floor depth measurements. For each soil depth, four of the eight samples were used to determine

soil bulk density by the core method. Soil was placed in plastic bags, labeled, and transported every 3-4 days after sampling to the laboratory.

Laboratory analyses

The fine roots were separated from soil manually with tweezers and placed in a petri dish with water to eliminate soil particles. The live and dead roots were not separated. To biomass determination, the samples of understory, DWD, LL, DL and fine roots were oven-dried to constant weight at 60 °C and weighed. Sub-samples (0.5 g) were ashed in a muffle furnace at 500 °C for 4 h to determine inorganic content to report the data on a dry ash-free basis. The samples were ground and passed through a 40-mesh sieve (0.420 mm) and then pooled into one composite sample per plot for total carbon concentration analyses. Mineral soil samples were oven-dried at 50 °C for 48 h. Bulk samples were weighed and the volume of coarse fragments (> 2 mm) were determined and used to correct bulk density for each plot; the eight soil subsamples were pooled into one composite sample for each depth per plot, which was then passed through a 100-mesh sieve (0.149 mm) for total carbon concentration analyses.

Understory, DWD, LL, DL, fine roots, and mineral soil samples were analyzed for total carbon concentration (mg g^{-1}) by combustion and coulometric detection using an automated CO_2 analyzer (UIC model CM5012, Joliet, IL, USA).

Biomass and carbon calculation

Plant biomass was considered as the dry weight of living and dead plant material contained above- and below-ground per a unit of surface area at a given point in time. Above- and below- ground plant biomass are expressed in units of Mg ha^{-1}. Live and dead tree biomass was calculated using allometric equations proposed by Vargas-Larreta *et al*., (2017) for *Pinus douglasiana*, *Pinus herrerae*, and *Pinus oocarpa* and Cruz-Martínez, (2007) for broad-leaved species. DWD biomass was calculated using equations proposed by Van Wagner, (1982). Decay classes registered in field were grouped in three classes: 1, 2, and 3 for sound, 4 for intermediate, and 5 for rotten (Waddell, 2002). The mean diameter quadratic and specific gravity values used are given in Table 2. The biomass of the forest floor was estimated as the product of depth (cm) of the LL and DL layers and bulk density (Mg ha^{-1} cm^{-1}). Bulk density values for the same plots were previously reported by Quintero-Gradilla *et al.* (2015).

Table 2. Parameters for estimating downed woody debris (DWD) biomass with equations proposed by Van Wagner, (1982). Source: Morfín-Rios *et al.* (2012) and Morfín-Rios JE, Universidad de Guadalajara, México, unpublished data.

DWDsize (cm)	Mean quadratic diameter (cm²)	Specific gravity (g cm^{-3})
< 0.6	0.21	0.49
0.6–2.5	1.64	0.46
2.5–7.6	18.91	0.44
> 7.6 Sound		0.41
> 7.6 Intermediate		0.21
> 7.6 Rotten		0.14

The C content in the different pools was estimated by multiplying the biomass (Mg ha^{-1}) with carbon concentration (% of dry weight). C content in the mineral soil was calculated as the product of bulk density (g cm^{-3}), depth (cm) and C concentration (%). All C pools were scaled up to Mg C ha^{-1}, and mean stand-level estimates for each C pool were calculated (n = 3, plots). For live and standing dead trees carbon concentration was assumed to be 50% of biomass (IPCC, 2003). Total ecosystem carbon storage was estimated by summing the individual carbon pools within each plot.

Statistical analyses

All variables were tested for normality and homoscedasticity assumptions using the Kolmogorov–Smirnov and Levene's test, respectively. Data were log-transformed to meet assumptions when required (Zar, 1999), although they are reported in the original scale of measure. A nested analysis of variance (ANOVA) was used to test the effect of stand age after a wildfire on carbon content pools. Stand age (eight, 28, or 60 years) was the main fixed effect, and stands (repetitions) within each age were the nested random effects. After nested ANOVA, the means was compared by Tukey test (p = 0.05). Pearson's correlation was used to analyze the correlations between tree basal area and aboveground tree biomass and total ecosystem biomass, and the correlation between stand age and total ecosystem C content. All these analyses were done with SPSS software version 16 (SPSS Inc. 1999, IBM, Armonk, NY, USA).

Results

Biomass distribution in ecosystem components

Total ecosystem biomass was lower in eight-year-old stands (152.1 Mg ha^{-1}) than in the 28- and the 60-year-old

stands (380.4 and 432.8 Mg ha^{-1}, respectively; Table 3). Aboveground live tree biomass increases significantly with stand age ($F_{2,6}$ = 33.41, p = 0.001). Both the aboveground pine biomass species and broad-leaved species biomass increase with stand age. However, pine biomass was similar between 28- and 60-year-old stands, while broad-leaved biomass was highest in the 60-year-old stands. The biomass of standing dead tree was not affected by stand age (Table 3). Understory biomass differed significantly with stand age, and peaked early in the chronosequence in the eight-year-old stands, which had 6- to 9-fold greater understory biomass than in the 28- and 60-year-old stands, respectively (Table 3).

Similarly, the DWD biomass in the eight-year-old stands was 5-fold greater than in the 28- and 60-year-old stands ($F_{2,6}$ = 11.99, p = 0.008), and made up 56% of the total aboveground biomass (Table 3). A nested stand effect within the stand age was significant ($F_{6,18}$ = 5.39, p = 0.002), which means that the site factor was also significant.

The forest floor mass increased with stand age ($F_{2,6}$ = 40.58 p ≤ 0.001). Both LL and DL mass were lower in the eight-year-old stands than in the older stands. LL mass peaked in the 28-year-old stands, while the DL mass was similar between the 28- and 60-year-old stands. In contrast, fine root biomass was not affected by stand age.

Tree basal area was positively related with aboveground tree biomass (R^2 = 0.94, p < 0.001) and total ecosystem biomass (R^2 = 0.92, p < 0.0001). The

dead:live biomass ratio decreased with stand age from 1.80 in the eight-year-old stands to 0.09 and 0.23 in the 28-and 60-year-old stands, respectively.

Ecosystem carbon content

C concentration

The C concentration in the above- and below-ground biomass components, litter, and DWD varied from 39% to 51%, and no one differed significantly among forest stand by age (Table 4). In the three successional ages, the mineral soil C concentration was higher in the first 10 cm of the soil and decreased significantly (to 50%) up to 30 cm depth, and even further to 28% at 70 cm soil depth (Fig. 1). Differences among ages were only significant in the top 0–10 cm (Fig. 1).

C content pools

The C content in biomass components across the age sequence followed a similar pattern compared to the biomass (Table 5, Fig. 2). The C stored in aboveground tree biomass increased 6-fold from the eight-year-old stands to the 60-year-old stands. Similarly, forest floor C content increased by approximately 21.6 Mg C ha^{-1} from the eight-year-old stands to the 28- and 60-year-old stands. In contrast, C stored in understory decreased by 85% between the eight-year-old and 60-year-old

Table 3. Total biomass (Mg ha^{-1}) in a fire chronosequence of tropical mixed pine-hardwood forest. Values are average with standard error in parentheses. Different letters indicate significant differences between means (p < 0.05) with the post hoc Tukey test.

Components	Stand age (years)		
	8	28	60
Aboveground biomass (Mg ha^{-1})			
Live biomass			
Pine trees	50.9 (7.5)[a]	287.2 (23.2)[b]	296.9 (30.1)[b]
Broad-leaved trees	2.8 (1.2)[a]	9.0 (2.2)[a]	50.7 (8.4)[b]
Total live trees (pines + broad-leaved)	53.7 (6.4)[a]	296.2 (21)[b]	347.5 (33.3)[c]
Tree saplings, shrubs and herbs	1.8 (0.6)[a]	0.2 (0.1)[b]	0.3 (0.1)[b]
Dead biomass			
Standing dead trees	3.6 (2.3)[a]	4.1 (1.8)[a]	7.5 (2.6)[a]
Litter layer (LL)	4.2 (0.6)[a]	18.3 (4.7)[b]	12.3 (0.5)[c]
Duff layer (DL)	6.2 (2.2)[a]	40.5 (2)[b]	42.5 (5)[b]
Total forest floor (LL + DL)	10.4 (1.8)[a]	58.8 (5.5)[b]	54.8 (4.4)[b]
Downed Woody Debris (DWD)	79.5 (16)[a]	17.2 (7)[b]	18.4 (3)[b]
Total aboveground biomass	**149 (3.5)[a]**	**376.5 (36.6)[b]**	**428.3 (31.4)[b]**
Belowground biomass			
Fine roots (< 5 mm)	3.1 (0.2)[a]	3.9 (0.3)[a]	4.5 (0.3)[a]
Total ecosystem biomass	**152.1 (5.4)[a]**	**380.4(36.5)[b]**	**432.8 (31)[b]**

Table 4. Carbon concentration (%) of ecosystem biomass components in a fire chronosequence of tropical mixed pine-hardwood forest. No significant differences were found ($p < 0.05$) with the ANOVA test for the same component between ages. Values are the average for the three ages (eight, 28, and 60 year) with the standard error in parentheses.

Ecosystem biomass components	Stand age (years)		
	8	28	60
Saplings	45.7 (0.5)	44.0 (0.8)	45.0 (0.4)
Shrubs	44.3 (0.5)	43.8 (0.9)	43.6 (0.6)
Herbs	42.7 (0.4)	40.8 (0.9)	39.2 (0.2)
Fine roots	41.8 (0.5)	43.2 (0.4)	43.5 (0.5)
Litter layer	47.2 (0.6)	47.9 (0.2)	47.2 (0.2)
Duff layer	44.4 (0.9)	45.9 (0.5)	45.4 (0.7)
Sound downed woody debris	47.5 (0.6)	46.1 (1.0)	48.5 (0.6)
Intermediate downed woody debris	48.9 (1.1)	49.8 (0.3)	50.4 (0.4)
Rotten downed woody debris	50.8 (1.0)	48.8 (1.2)	51.0 (0.9)

stands; likewise, C in DWD pool decreased with stand age, following an inverse J-shaped trajectory from 38 Mg C ha^{-1} in the eight-year-old stands to 9 Mg C ha^{-1} in the 60-year-old stands. The C content in fine root mass averaged 1.4 Mg C ha^{-1} and did not differ significantly among stand ages.

The soil bulk density showed no differences among stand ages at the same depth interval. The mean soil bulk density for each depth was 0.69 ± 0.03, 0.73 ± 0.02, 0.85 ± 0.02, and 0.88 ± 0.02 g cm^{-3} for 0–10, 10–30, 30–50, and 50–70 cm soil depth, respectively. Total mineral soil C (0-70 cm depth) increased significantly with stand age (Table 5, Fig. 2), from 147 Mg ha^{-1} in the eight-year-old stands to 161 and 203 Mg ha^{-1} in the 28- and 60-year-old stands, respectively (Fig. 3).

Total ecosystem C content increased with the stand age from 221 to 423 Mg C ha^{-1} ($F_{2,6} = 60.96$, $p < 0.000$, Table 5 and Fig. 4a). The correlation between stand age and total ecosystem C content was significant ($R^2 = 0.84$ $p < 0.001$). Eight years after a fire, C was mainly stored in the mineral soil (67%) and the dead
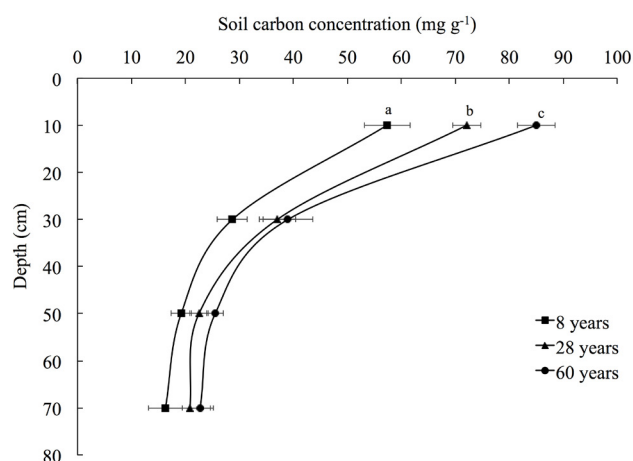

Figure 1. Distribution of carbon concentration (mg g^{-1}) in the mineral soil (at 10, 30, 50 and 70 cm depth) in a fire chronosequence of tropical mixed pine-hardwood forest. Each data point represents the average of C concentration by soil depth, horizontal bars are standard error, and lines are used to graphically visualize the trend in average C concentration with soil depth. Different letters indicate a significant difference at the same depth between ages ($p < 0.05$) with the post hoc Tukey test. The lack of letters indicates no significant differences.

Table 5. Nested analysis of variance (F and p) for carbon content (Mg ha^{-1}) in a fire chronosequence of tropical mixed pine-hardwood forest. Stand age is the fixed effects factor; stand is the nested effect within stand age as a random effect factor.

Pools	Variation source			
	Stand age		Stand nested within stand age	
	$F_{2,6}$	p	$F_{6,18}$	p
Live trees	33.400	0.001	1.780	0.058
Understory (saplings, shrubs and herbs)	6.100	0.035	1.380	0.273
Forest floor (litter + duff layer)	34.900	0.000	1.230	0.334
Dead wood (standing dead trees + DWD)	11.570	0.009	6.660	0.001
Fine roots	2.040	0.210	1.960	0.125
Mineral soil	15.960	0.004	0.554	0.760
Total ecosystem carbon pool	60.963	0.000	2.09	0.105

woody debris (18%), both making up 85% of the total ecosystem C content, while the live trees pool contributed 12% of the total ecosystem C content. In contrast, live trees and mineral soil were the two largest pools of the total ecosystem C pool in the 28-year-old (90%) and 60-year-old (89%) stands, C stored in dead wood accounted only for 3% of the total ecosystem C pool, in both 28-year-old and 60-year-oldstands and the forest floor represented 8% and 6%, respectively (Fig. 4b).

Discussion

The changes observed in aboveground plant biomass after stand-replacement fires reveal a fast recovery of C pools in the mixed pine-hardwood forests in LJRS. A significant reduction of total C ecosystem pools by plant mortality and forest floor layer consumption is a widely documented effect of high-severity fires in boreal and temperate forests (Litton *et al.*, 2004; Mac-Kenzie *et al.*, 2004; Kashian *et al.*, 2006; Alexander
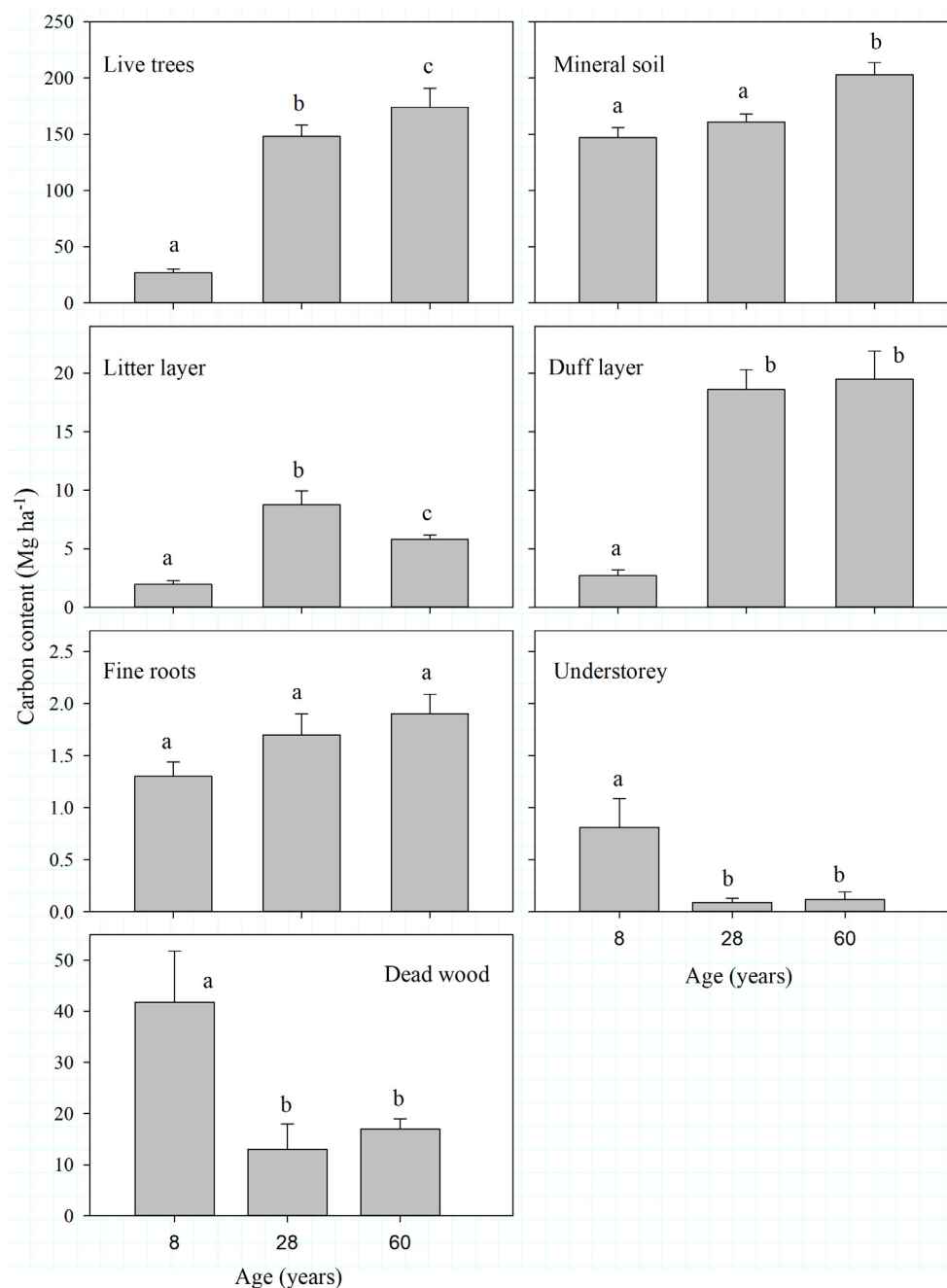
Figure 2. Carbon storage in ecosystem pools (Mg C ha^{-1}) in a fire chronosequence of tropical mixed pine-hardwood forest. Values are average with the standard error. Bars with different letters show significant differences between means ($p < 0.05$) with the post hoc Tukey test.

et al., 2012; Seedre *et al.*, 2014). In the study area, eight years after a fire the total ecosystem C stored was 48% of the C content in 60-year-old stands. Although the chronosequence is relatively short compared with other studies reported for temperate and boreal forests (Wang *et al.*, 2003; Litton *et al.*, 2004; Kashian *et al.*, 2006; Dore *et al.*, 2008; Alexander *et al.*, 2012; Carlson *et al.*, 2012; Kashian *et al.*, 2013), it suggests that the warm temperate and moist climate of montane forests at tropical latitudes facilitates a fast post-fire recovery of forest stands. C storage in ecosystem biomass increased with stand age, reaching in the first 28 years following fires a level similar to the 60-year-old stands. This rapid C recovery was mainly driven by accumulation of C in live trees and the forest floor recovery and followed the typical pattern of rapid C biomass accumulation in early stages of stand development (Seedre *et al.*, 2011; Alexander *et al.*, 2012; Kashian *et al.*, 2013).

The pattern of post-fire C pools recovery in the mixed *Pinus douglasiana*-hardwood forest can be described following the stand development stages of Oliver & Larson, (1990) and the results of previous studies about forest succession in these forests (Cuevas-Guzmán & Jardel, 2004):

(1) The eight-year-old stands correspond to the stand initiation stage, where *P. douglasiana* saplings are the most abundant species in the lower vegetation layer and pines represent 95% of live tree biomass (33.5% of total biomass). A high proportion of total biomass (50.5%) is concentrated in downed woody debris and forest floor biomass represents only 6.6%.

(2) Twenty-eight years after a fire, the developing stands are in the transition of the stem exclusion and
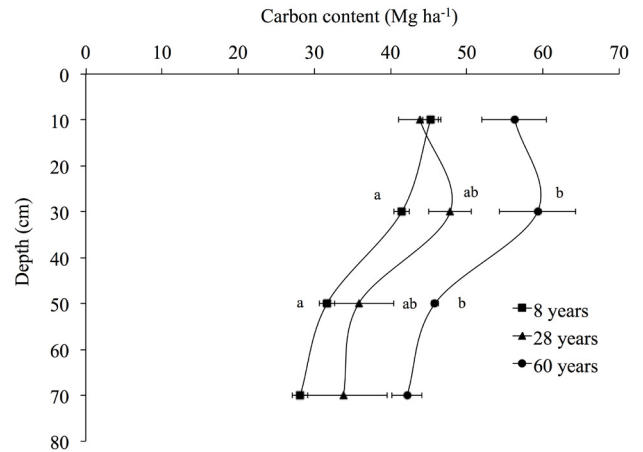
Figure 3. Distribution of soil carbon content in the mineral soil (at 10, 30, 50 and 70 cm depth) in a fire chronosequence of tropical mixed pine-hardwood forest. Each data point represents the average of C content by soil depth, horizontal bars are standard error, and lines are used to graphically visualize the trend in average C content with soil depth. Different letters indicate a significant difference between ages at the same depth ($p < 0.05$) with the post hoc Tukey test. The lack of letters indicates no significant differences.

understory reinitiation stage. Live tree biomass is now 71.3% of total biomass and pines represents 96.4% of this component, with an increase in understory of shade-tolerant broad-leaved species, dominated by *Clethra fragrans* L. M. González & R. Ramírez, *Fraxinus uhdei* (Wenz.) Lingelsh, *Viburnum hartwegii* Benth., *Ilex brandegeana* Loes. and *Myrsine juergensenii* (Mez) Ricketson & Pipoly (Quintero-Gradilla *et al.*, 2019). The forest floor shows a significant increase in biomass, reaching 19.1% of total biomass, and the proportion of downed woody debris is now reduced to 4.1%.
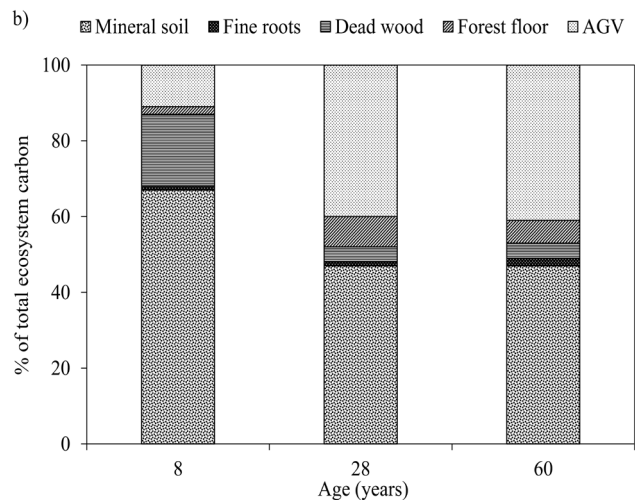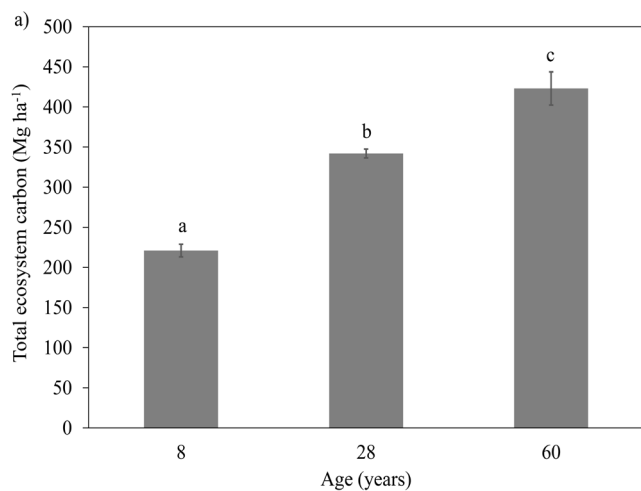
Figure 4. a) Total ecosystem carbon content, bars are average with standard error and different letters indicate a significant difference between ages ($p < 0.05$) with the post hoc Tukey test, and b) Relative contribution of each pool to the total ecosystem C in a fire chronosequence of tropical mixed pine-hardwood forest. Mineral soil (0-70 cm depth), fine roots (0-40 cm depth), dead wood (DWD + standing dead trees), forest floor (LL + DF), and AGV (live trees + understory).

(3) The 60-year-old stands are entering the maturation phase; live trees, downed woody debris, and forest floor represent 76.3%, 4.1%, and 12.1% of total biomass, respectively. The most significant change observed at this stage is the increase proportion of biomass (14.6%) of broad-leaved species under-canopy. The species with highest importance value index are *Cornus disciflora* DC., *Myrsine juergensenii* (Mez) Ricketson & Pipoly, *Carpinus tropicalis* Furlow*., Persea hintoni* C.K. Allen, and *Magnolia Iltisiana* A. Vázquez (Quintero-Gradilla *et al*., 2019).

The C stored in aboveground live tree biomass is higher in 60-year-old stands than in 28-year-old stands due to the biomass increase of the broad-leaved tree species growing under the canopy. The establishment of shade-tolerant species under the canopy of the first cohort of trees that regenerated after a stand-replacement disturbance is a common feature of the stand development process in dense forests (Oliver & Larson, 1990) and is favored by fire exclusion (Kane *et al*., 2013). Carbon storage in the understory layer was higher in the eight-year-old stands. The high C storage in herbaceous and shrub biomass reached in the early stages of forest succession have been associated with an open tree canopy that maintains favorable conditions for its establishment, such as light, moisture, and nutrients (Gilliam, 2007; Jules *et al*., 2008; Seedre *et al*., 2011). Favorable conditions that are decreased with forest succession after canopy closure (Gilliam, 2007).

Carbon content in fine roots did not show any correlation with stand age, consistent with previous studies (Howard *et al*., 2004; Gough *et al*., 2007). Carbon storage in standing dead trees did not change with stand age, suggesting that, eight years after the fire, C had already transferred from fire-killed trees to the downed woody debris pool. C content in DWD pool followed a pattern of high initial amounts of fire-killed fallen trees in the first years after a fire and then a reduction in C storage due to decomposition of dead wood in the intermediate stage, followed by an increase in the late stage of succession as a result of the natural mortality of trees (Spies *et al*., 1988; Brais *et al*., 2005; Kashian *et al*., 2013). The significant nested site effect on C storage in downed woody debris suggests that there was high variability that could not be explained only by stand age and that could be associated with microsite variation, decay heterogeneity, and management history (Harmon *et al*., 1986).

C stored in the forest floor layer was 80% lower in eight-year-old than in 28- or 60-year-old stands, an effect related to fire consumption of surface fine fuels. Forest floor starts to accumulate C with regeneration and increases throughout the life of a stand until it reaches the maximum accumulation, where there is a balance between production and decomposition (Gough *et al*., 2007; Seedre *et al*., 2011), as described by Quintero-Gradilla *et al*., (2015).

The carbon pool in the mineral soil is the long-term product of history, decomposition, and vegetation changes (Harden *et al*., 2000). The higher total soil C content at 70 cm of depth observed in 60-year-old stands may be associated with long-term processes strongly associated with clay particles and non-crystalline minerals that play an essential role in the protection and stabilization of organic matter in the soil (Six *et al*., 2002). Since soils in the study area are Alfisols with a characteristic subsurface argillic horizon (Martínez *et al*., 1993), they play a key role in C accumulation. On the other hand, the effects of wildfires have been observed in the first years after fire and mainly in the superficial horizons, as reported by Quintero-Gradilla *et al.,* (2015) and others (Wang *et al*., 2001; Litton *et al*., 2004; Kashian *et al*., 2013).

Total ecosystem carbon increased with stand age due to additional C content in the broadleaf trees' strata and the higher content in mineral soil in 60-year-old stands. The pattern of change of the total ecosystem carbon storage with stand age coincided with previous post-fire chronosequences that showed slow C accumulation during stand regeneration, followed by a fast accumulation during stand development, then reaching a maximum and remaining relatively constant or declining in old-growth forest stands, reported for tropical forests (Pregitzer & Euskirchen, 2004) and for temperate and boreal forests (Wang *et al*., 2003; Pregitzer & Euskirchen, 2004; Kashian *et al*., 2013; Seedre *et al*., 2014).

Regeneration of vegetation exerts strong control on post-fire C recovery, capturing carbon lost during or after burning (Litton *et al*., 2004; Kashian *et al*., 2006). Although tree mortality was high (> 70% reduction in basal area) in the sites examined in this study, mixed-severity fires created small gaps (< 40 ha) where the trees that survived the fire and the trees of surrounding stands functioned as seed sources, which, together with favorable climatic conditions, promoted the subsequent fast regeneration and then the recovery of C stocks. The relatively fast recovery of ecosystem C in biomass suggests that mixed *Pinus douglasiana*-hardwood forest possesses functional traits like small winged seeds dispersed at long distances, fast growth rate, and shade intolerance, which confer resilience to severe fire (Keeley & Zedler, 1998).

The management of fire-prone forest must considering a trade-offs between maximizing carbon storage by increasing carbon density through fire suppression and maintaining long-term carbon stability which

means minimizing loss of carbon from the system by reducing the risk of high-severity fires (Hurteau & Brooks, 2011), as well as other forest management goals such as biodiversity conservation, watershed protection, timber production, and other ecosystem services (Hurteau *et al.*, 2008; Bowman *et al.*, 2013; Syphard *et al.*, 2016). Fire-induced change in carbon distribution among ecosystem pools could have several implications for C storage at the landscape level (Kashian *et al.*, 2006). In the first years after a fire, when the majority of the carbon is stored in DWD and the mineral soil, a fire recurrence could expose the soil to erosion and loss of C (Neary & Overby, 2006; Gough *et al.*, 2007). Based on this assumption, it is recommended the protection of those sites to promote regeneration. Not protecting the stands from repeated fires could lead to a failing recovery, with consequent changes in the forest structure, soil carbon, and species composition (Kashian *et al.*, 2006). Some examples are the transition from forest to grassland or shrubland, with a diminished capacity for carbon storage, observed by Savage & Mast, (2005) in southwestern United States ponderosa pine forest and Alanís-Rodríguez *et al.*, (2012) in a forest of *Pinus pseudostrobus* forest in northern Mexico.

However, long periods of fire suppression in fire-prone ecosystems, has resulted in an increased fuel loads and a change in vegetation structure, that can contribute to intense wildfires that produce greater levels of CO_2 and other greenhouse gas emissions (Hurteau & North, 2009; Hurteau & Brooks, 2011). It is critical to understand the implications of fire management actions to carbon management and other goals as conservation and climate change mitigation.

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