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Effects of Fire Frequency and Soil Temperature on Soil CO_2 Efflux Rates in Old-Field Pine-Grassland Forests

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Abstract: Soil CO_2 efflux (R_s) is a significant source of carbon dioxide from soils to the atmosphere and is a critical component of total ecosystem carbon budgets. Prescribed fire is one of the most prevalent forest management tools employed in the southeastern USA. This study investigated the influence of prescribed fire on R_s rates in old-field pine-grassland forests in north Florida, USA, that had been managed with prescribed fire annually and biennially for over 40 years, or left unburned for approximately the same period. Monthly measurements were taken of R_s, soil temperature (T_s), and soil moisture from August 2009 to May 2011. Results showed that sites managed with annual and biennial dormant season prescribed fire had significantly lower monthly mean R_s rates and estimated annual soil carbon fluxes than sites where fire had been excluded. While T_s explained a significant amount of the temporal variations in R_s, it did not explain the differences in R_s among prescribed fire treatments. Our results provide new insight into the effects of prescribed fire and fire exclusion on soil carbon fluxes, and suggest that future methods to model ecosystem carbon budgets should incorporate not only current vegetative conditions, but also prescribed fire management activities.

Keywords: soil respiration; prescribed fire; soil CO_2 efflux; soil temperature; forests

1. Introduction

The influence of long-term forest management practices on soil CO_2 efflux (R_s) rates plays a key role in determining total ecosystem carbon budgets [1–3]. It has been estimated that soil CO_2 efflux represents one of the largest global terrestrial fluxes of carbon to the atmosphere, with the total annual R_s flux (75 Pg C year^{-1}) an order of magnitude greater than current annual anthropogenic carbon (C) emissions from fossil fuel combustion (6 Pg C year^{-1}) [4]. Soil CO_2 efflux is a function of various interrelated biogeochemical factors that govern the production of autotrophic soil CO_2 efflux by plant roots and associated mycorrhizal fungi (R_a) and heterotrophic soil CO_2 efflux by soil micro and macro biota(R_h) [3–6].

Fire can influence R_s rates by differentially impacting the R_h and R_a sources of CO_2 [4,7]. For example, short-term autotrophic production of CO_2 can be reduced by fire due to both aboveground and belowground plant mortality and injury. While the long-term impacts of fire on R_a are variable, R_a has been shown in some cases to increase with time since fire as vegetation recovers following disturbance [8]. In many cases, the burning of vegetation and surface fuels reallocates nutrient resources via incomplete combustion and subsequent deposition of ash, char, and other residues [8,9]. In the short-term period following the deposition of those residues, both plants and soil microbes may respond positively to the availability of such resources, subsequently increasing R_s rates. Long-term prescribed fire management regimes may also impact R_h sources of CO_2, by influencing vegetation composition, structure and associated litter and duff quality, production, and accumulation rates [10] which in turn have been shown to influence soil microbial populations and metabolic activity [11]. Fire can also reduce R_h by killing soil microbes through heating of litter and duff layers and upper soil horizons [4]. Previous studies in multiple ecosystems have shown that both fire and forest management can influence R_s rates, soil carbon pools, and various coupled biogeochemical processes [12–16]. For example, in a study of a mixed conifer forest in California, USA, Ryu et al. [17] found that prescribed fire reduced R_s rates while simultaneously altering soil conditions that would otherwise be associated with increased R_s rates. However, two studies that investigated the influence of prescribed fire in a different mixed conifer forest in California and an upload oak (*Quercus* spp. L) forest in Missouri, USA, found that while prescribed burning significantly altered forest floor conditions, there was no clear effect on R_s rates [18]. The contrasting results reported by these studies demonstrate the complex nature of predicting the influence of prescribed fire on R_s. While many factors influencing R_s rates have been identified, much remains to be determined regarding the effects of specific forest and land management practices on overall R_s rates [2–4], especially where management has been long-term rather than experimental.

Frequent prescribed fire is one of the dominant tools for forest management in the pine-grassland forests of the southeastern USA [19,20]. Many of the current pine-grassland forests in the region are old-field forest assemblages that exist on former agricultural lands estimated to cover up to 21 million ha across the southeastern USA [21]. Across many of these forests, frequent (1–3 year return interval) prescribed fire is used to perpetuate native species assemblages, reduce the risk of destructive wildfires, and promote and restore wildlife habitat [22]. Although less frequently cited, the impacts of prescribed fire regimes on soil carbon sequestration are likely to increase in importance as important commodity trade partners adopt carbon credit exchanges (e.g., Canada). The long term consequences of varying fire return intervals for carbon cycling in pine grasslands can inform fire management decisions and projections of carbon sequestration capacity.

This study sought to investigate the impacts of fire regime, specifically annual burning, biennial burning, and prolonged fire exclusion, on R_s rates in old-field pine-grassland forests. In addition, this study sought to interpret the potential response of R_s to biotic and abiotic factors, including soil temperature, soil moisture, forest stand characteristics, and soil physical properties and chemistry. The intent of this research is to build upon our understanding of the effects of frequent fire on carbon dynamics and sequestration in pine-grasslands and similar woodland and savanna communities worldwide. Studies such as this also provide insight into the response of ecosystem carbon dynamics to forecasted changes in temperature and moisture regimes due to global climate change.

2. Materials and Methods

2.1. Study Site

The study was conducted on Tall Timbers Research Station (TTRS) in Leon County, FL, USA, approximately 30 km from the cities of Tallahassee, Florida (to the south) and Thomasville, Georgia (to the north) (30°39′ N, 84°12′ W; Figure 1). The study utilized research plots established on old field land for long-term study of fire regimes. The Stoddard Fire Plots, which are 0.2 ha plots established in 1960, have each been managed with a constant fire return interval until the present [10,23,24]. The study also utilized a 9.2 ha plot named NB66 that had been fire-excluded since 1966 [24]. Prior to establishment of the plots, the areas had been burned at 1–2 year intervals since agricultural abandonment which occurred from the late 1800s to the 1920s. Soils within the sites were heavily cultivated for growing corn and cotton from the 1820s until abandonment with subsequent understory and overstory vegetation assemblages highly influenced by past agricultural practices [23] but largely representing a subset of species occurring in native pine communities of the region [10,25]. Soils were classified as fine-loamy, kaolinitic, thermic Typic Kandiudults of the Orangeburg and Faceville series (Natural Resource Conservation Service (NRC) Soil Survey Geographic Database (SSURGO)).

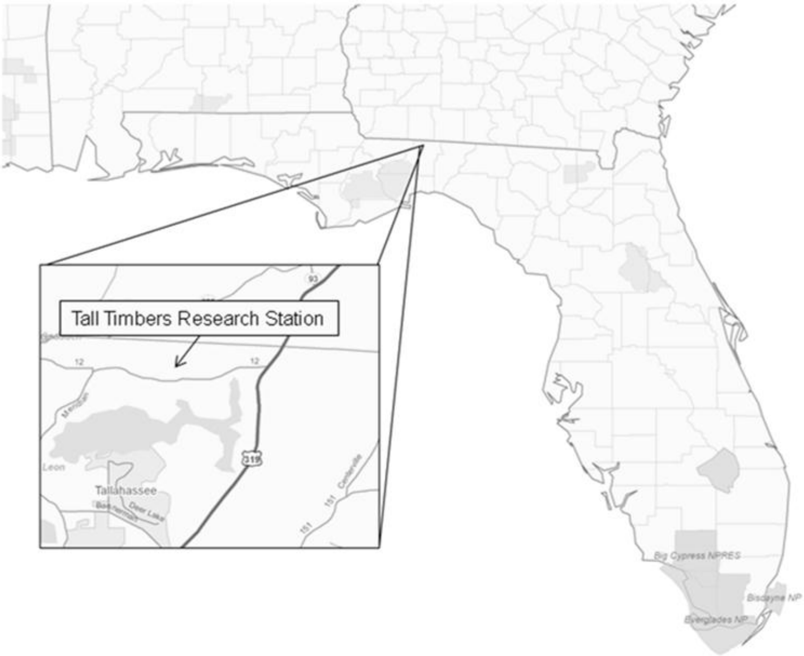

Figure 1. The research site, Tall Timbers Research Station, was located in Leon County, FL, USA. The site is approximately 30 km north of the city of Tallahassee, FL, USA.

For this study, sampling took place within three annually burned (1YR), three biennially burned (2YR), and two fire-excluded (UB) Stoddard Fire Plots, and an additional 0.2 ha fire-excluded study area (UB) was established within the Tall Timbers NB66 study site, making three replicates of each fire regime [10,23]. Replicate sets of plots each containing the three fire regimes were grouped within soil units, such that two sets were within Faceville (Fine, kaolinitic, thermic Typic Kandiudult) soil units and one was in an Orangeburg (Fine-loamy, kaolinitic, thermic Typic Kandiudult) soil unit. The study sites were located approximately 60 m a.s.l. Average annual precipitation was 137 cm with the majority falling during the summer months of June, July and August (National Climate Data Center 2009, Thomasville, GA, USA). Mean maximum and minimum temperatures for January and July for the area from long-term records (1971–2000) are 16.8 °C and 4.6 °C for January and 33 °C and 21.8 °C for July (National Climate Data Center 2009, Thomasville, GA, USA).

The overstory of the 1YR and 2YR burned plots consisted of a mixture of naturally regenerated shortleaf pine (*Pinus echinata* P. Mill), loblolly pine (*P. taeda* L.), and, to a lesser extent, longleaf pine (*P. palustris* P. Mill). The understory was composed of a mixture of grasses, forbs, and broadleaf woody plants which are typically topkilled by prescribed fire and then resprout [10,19,23,26]. The unburned plots, due to the prolonged fire exclusion, contained a closed midstory and overstory canopy of broadleaf deciduous trees of species including but not limited to: water oak (*Q. nigra* L.), laurel oak (*Q. laurifolia* Mich.), sweetgum (*Liquidambar styraciflua* L.), black cherry (*Prunus serotina* Ehrh.), and flowering dogwood (*Cornus florida* L.), in addition to mature pine trees.

2.2. Sampling

The Stoddard Fire Plots combined with NB66 representing each of three prescribed fire regimes (1YR, 2YR, UB) were grouped into blocks replicated three times for a total of nine plots. Sampling for this study took place within subplots randomly located within each of the Stoddard Fire Plots and NB66. To account for spatial variability within the subplots, measurements were taken at nine locations within in a square grid arrangement with 5 m separation, following Kobziar [16].

R_s (µmol CO_2 $m^{-2} \cdot s^{-1}$) was sampled at each subplot using a LI-COR Biosciences LI-8100 automated soil CO_2 sampling instrument with a 20 cm diameter survey chamber (LI-COR Biosciences Inc., Lincoln, NE, USA). The survey chamber fit onto 20 cm diameter × 10 cm height PVC collars inserted 8 cm into the ground. Sampling of R_s for all plots occurred monthly. During each monthly visit, all measurements were taken within two days. Over the course of study, any vegetative growth within the sample collars was clipped and removed prior to R_s measurement. The PVC collars were installed in June and July 2009 and sampling began in August. The PVC collars and soil surfaces contained within them were protected from fire during burns in March 2010 (1YR plots) and March 2011 (1YR and 2YR plots) by placing slightly larger diameter sheet-metal cylinders around them. As such, the measurements were not expected to respond to direct impacts of prescribed fire, e.g., changes to soil chemistry or injury of microorganisms near the soil surface, but rather general environmental conditions corresponding to the respective fire regime. Sampling consisted of a 120 s measurement initiated by a 15 s "dead-band" during which gases were allowed time to mix within the chamber. During R_s measurements, adjacent to each PVC collar, soil temperature (T_s) (°C) was measured at 10 cm depth using an Omega 8831 type E T-Handle temperature probe, and soil moisture content (M_s) (m^3/m^3) was measured at 5 cm depth using a Decagon Systems EC-5 soil moisture probe mounted on the LI-8100 (Omega Inc., Stamford, CT, USA; Decagon Systems Inc., Pullman, WA, USA). From August of 2009 until February 2010, each monthly sampling period involved measurement of R_s, T_s, and M_s eight times per day in order to assess for diurnal variability. An analysis of the preliminary results found that fewer daily measurements would be sufficient to capture the variability, so daily measurements were scaled back to three times per day (morning, mid-day and late afternoon-early evening) from March 2010 until the end of the study in May 2011. Equipment problems resulted in no field measurements being taken during the month of October 2010, but otherwise there were only few interruptions due to equipment problems or severe thunderstorms. The resulting dataset for the entire twenty-one-month study totaled 7566 R_s measurements. Some strong outliers in R_s, T_s, and M_s were attributed to measurement or equipment error and were isolated and excluded from the analyses.

Within a 15 m radius circular plot (0.07 ha) centered on the middle PVC collar in each subplot, basal area (BA) ($m^2 \cdot ha^{-1}$), pine basal area (PBA) ($m^2 \cdot ha^{-1}$), hardwood (broadleaf) tree basal area (HW BA) ($m^2 \cdot ha^{-1}$), and stand density (TPH) (trees ha^{-1}) were measured (only counting trees diameter at breast height > 10 cm). Forest stand characteristics were assessed once per subplot in the winter or spring of 2011. Soil total carbon and total nitrogen were measured in January 2013 (Table 1). Subplot level mean litter depth (Litter) (cm), duff depth (Duff) (cm) and total litter and duff depth (DL) (cm) were recorded as the average of three measurements taken from random locations with 30 cm of each PVC collar. Soil was sampled using a 2 cm diameter soil corer to 10 cm depth at 30 locations spread throughout each plot then combined, homogenized, and split to obtain subsamples for analysis. Samples were analyzed at Auburn University to determine percent total carbon and nitrogen with a TruSpec CN analyzer (Leco Corp., St. Joseph, MI, USA) using the dry combustion method, and $mg^{-1} \cdot kg^{-1}$ of phosphorus, calcium, magnesium, and potassium were determined with an iCAP analyzer (Thermo Fisher Scientific Inc., Waltham, MA, USA) using Mehlich 3 extraction. Bulk density to 10 cm depth was sampled at five locations within each plot using a 4.5 cm diameter soil sampler (Eijkelkamp Corp., Giesbeek, The Netherlands). Bulk density measurements were used to convert soil chemistry measurements to mass per unit area (kg^{-1} or Mg^{-1} per$\cdot ha^{-1}$).

Table 1. Environmental variables measured in each research plot, with abbreviation, unit of measurement, and measurement regime provided. Monthly measurements were made from August 2009 to April 2011.

Plot Variable	Abbreviation/Units	Measured
Soil temperature	T_s (°C)	Monthly
Soil moisture content	M_s (m^3/m^3)	Monthly
Basal area	BA ($m^2 \cdot ha^{-1}$)	Winter 2011
Pine basal area	PBA ($m^2 \cdot ha^{-1}$)	Winter 2011
Hardwood basal area	HWBA ($m^2 \cdot ha^{-1}$)	Winter 2011
Stand density	TPH (trees ha^{-1})	Winter 2011
Duff depth	Duff (cm)	Spring 2011
Litter depth	Litter (cm)	Spring 2011
Soil bulk density 0–10 cm	BD ($g \cdot cm^{-3}$)	Winter 2013
Soil total carbon 0–10 cm	C ($Mg \cdot ha^{-1}$)	Winter 2013
Soil total nitrogen 0–10 cm	N ($Mg \cdot ha^{-1}$)	Winter 2013
Soil phosphorus 0–10 cm	P ($kg \cdot ha^{-1}$)	Winter 2013
Soil calcium 0–10 cm	Ca ($kg \cdot ha^{-1}$)	Winter 2013
Soil magnesium 0–10 cm	Mg ($kg \cdot ha^{-1}$)	Winter 2013
Soil potassium 0–10 cm	K ($kg \cdot ha^{-1}$)	Winter 2013
Soil pH 0–10 cm	pH	Winter 2013

2.3. Analysis

Analyses sought to test for significant differences among the three fire regimes with regard to R_s, T_s, M_s and forest environmental conditions measured in the field. For each month, daily measurements per PVC collar were averaged, and the nine PVC collar means were averaged to produce a subplot-level mean value for each month. Repeated measures analysis of variance (ANOVA) was used to test for differences in these monthly means among the three fire regimes (n = 3 per fire regime) for R_s, T_s, and M_s over the twenty-one monthly sampling periods between August 2009 and May 2011. Significant treatment effects were identified at p-value < 0.05. To assess for differences in forest environmental conditions among the three fire regimes, one-way ANOVA tests were applied to each variable separately. Where significant differences were identified, differences were further investigated using Tukey's HSD test. Additionally, linear and nonlinear regression models (Equations (1) and (2)) were developed to predict the monthly response of R_s to T_s as well as R_s to M_s in separate equations within each fire regime and within each season. Non-linear models of the relationships between R_s rates and T_s per fire regime were explored using an exponential equation (Equation (2)) frequently used to describe the response of R_s rates to soil temperature [15,18,27,28]. The β_1 estimates developed using Equation (2) were used to estimate Q_{10} (Equation (3)), which describes the response of R_s to a 10° C change in soil temperature [4,15,27]. All statistical analyses were performed using JMP 9.0 (SAS Institute, Cary, NC, USA).

$$R_s = \beta_0 + \beta_1(\text{parameter}) \tag{1}$$

$$R_s = \beta_0 e^{\beta_1(T_s)} \text{ or } R_s = \beta_0 e^{\beta_1(\text{MTemp})} \tag{2}$$

$$Q_{10} = e^{10\beta_1} \tag{3}$$

where MTemp was air temperature, β_0, and β_1 were coefficients estimated through regression analysis.

Total monthly and annual soil carbon emissions per fire regime were estimated using the nonlinear regression models of R_s responses (Equation (2)) to changes in ambient temperature (MTemp) following Samuelson et al. [28]. Twenty-four hour 2 m elevation ambient temperature measurements recorded hourly from 1 August 2009–31 July 2010 at the Quincy, FL Automated Weather Network site located approximately 30 km from the study sites were used as the MTemp input to estimate hourly R_s rates. The estimated R_s rates ($\mu mol\ CO_2\ m^{-2} \cdot s^{-1}$) were then converted to hourly soil carbon fluxes ($g\ C\ m^{-2} \cdot h^{-1}$) which were then summed to estimate monthly and annual soil carbon fluxes ($Mg\ C\ ha^{-1} \cdot year^{-1}$).

3. Results

3.1. Differences in R_s, M_s, T_s, and Vegetation among Fire Regimes

Mean R_s rates varied significantly between fire regimes (p = 0.0007), with the highest R_s rates typically in the UB treatment and the lowest typically in the 1YR treatment (Figure 2; Tables 2 and 3). The treatment effect of fire regime on R_s rates varied monthly (treatment × time $p < 0.0001$), with the greatest difference between fire regimes observed during the summer months and the least during the winter months (Table 3). Across all treatments, R_s ranged from 0–11.98 μmol CO_2 $m^{-2} \cdot s^{-1}$ during the study period, with the highest R_s rates during the warmer months and the lowest rates during the cooler months (Figure 2).

Table 2. Results of the repeated measures ANOVA showing effects of prescribed fire regime (FR); and time (monthly means of measurements) on soil CO_2 efflux (R_s), soil temperature (T_s) and soil moisture content (M_s) (n = 9 three replicates within three treatments).

Analysis Period	Source	R_s			T_s			M_s		
		df	*F*	*p-Value*	*df*	*F*	*p-Value*	*df*	*F*	*p-Value*
Entire Study	Month	20	105.19	<0.0001	18	306.76	<0.0001	19	97.51	<0.0001
	FR × Month	40	3.25	<0.0001	36	4.04	<0.0001	38	1.68	0.0190
	FR	2	20.72	0.0007	2	3.09	0.1007	2	2.95	0.1130
Fall	Month	5	114.16	<0.0001	5	241.78	<0.0001	5	66.73	<0.0001
	FR × Month	10	4.12	0.0012	10	1.31	0.2684	10	2.06	0.0611
	FR	2	17.65	0.0031	2	2.70	0.1457	2	4.26	0.0705
Winter	Month	5	25.16	<0.0001	3	61.75	<0.0001	5	25.45	<0.0001
	FR × Month	10	1.96	0.0761	6	0.40	0.8650	10	1.96	0.0753
	FR	2	13.40	0.0061	2	10.48	0.0036	2	6.30	0.0335
Spring	Month	5	25.61	<0.0001	5	243.07	<0.0001	5	75.96	<0.0001
	FR × Month	10	2.73	0.0168	10	5.50	0.0001	10	1.03	0.4454
	FR	2	11.24	0.0054	2	4.11	0.0646	2	1.41	0.3003
Summer	Month	2	16.70	0.0003	2	38.05	<0.0001	1	139.44	<0.0001
	FR × Month	4	3.78	0.0327	4	4.70	0.0163	2	3.02	0.1235
	FR	2	16.03	0.0039	2	9.91	0.0126	2	1.32	0.3340

p-Values were considered significant at α = 0.05, *df* = degrees of freedom.

Table 3. Mean seasonal and total study period soil CO_2 efflux rates (μmol CO_2 $m^{-2} \cdot s^{-1}$) (R_s) per prescribed fire regime.

FR	Fall R_s	Winter R_s	Spring R_s	Summer R_s	Study Mean R_s
1YR	3.36 (1.71) b	1.24 (0.87) b	2.56 (1.21) b	4.93 (1.95) b	2.67 (1.87) b
2YR	3.75 (2.02) b	1.60 (1.24) b	3.09 (1.39) b	5.49 (2.11) b	3.09 (2.12) b
UB	4.93 (2.36) a	2.61 (1.49) a	3.98 (1.94) a	7.59 (2.25) a	4.22 (2.52) a

Values are seasonal means with standard deviations in parentheses. Letters show significant differences between fire regimes (Tukey's HSD test). *p*-Values were considered significant at α = 0.05.

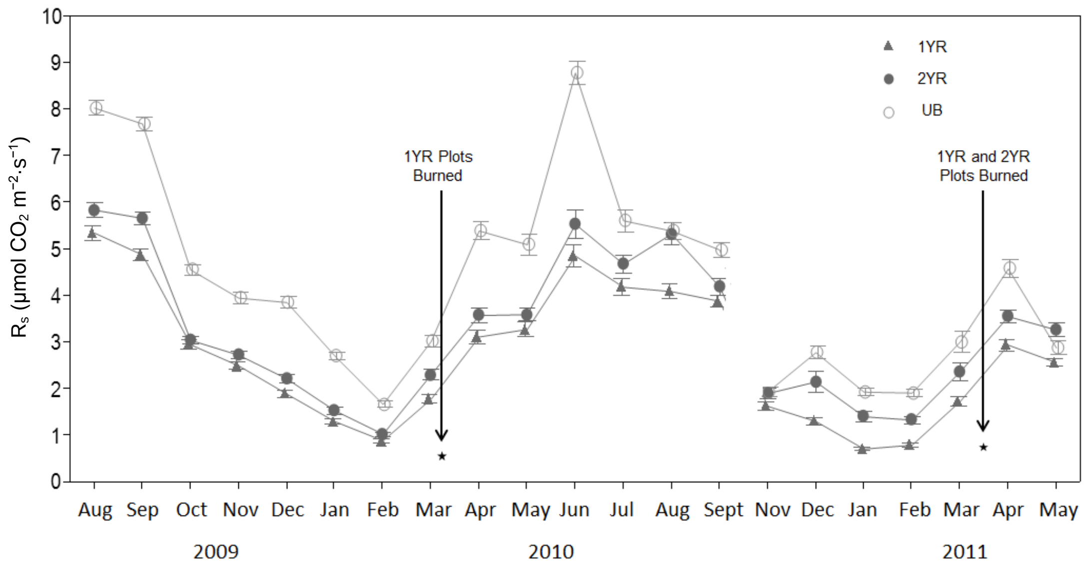

Figure 2. Monthly mean soil CO_2 efflux rates (R_s) (μmol CO_2 $m^{-2} \cdot s^{-1}$) for three prescribed fire regimes at the Tall Timbers Research Station near Tallahassee, FL, USA. Data were from 27 sample points per fire regime, measured three-times daily once per month. Measurements were not taken in October of 2010.

Although soil temperature did not differ significantly among the fire regimes (p = 0.1007), the lowest temperatures were in the UB sites and the highest in the 1YR sites (Figure 3). A distinct seasonal T_s trend among the fire regimes was observed, with the 1YR sites recording the highest mean T_s in the spring through fall seasons and the UB sites recording the highest mean T_s in the winter seasons. Soil moisture (M_s) did not differ significantly among the fire regimes (p = 0.11), although the lowest soil moisture contents were observed in the UB sites and the highest observed in the 1YR sites (Figure 4; Table 2).

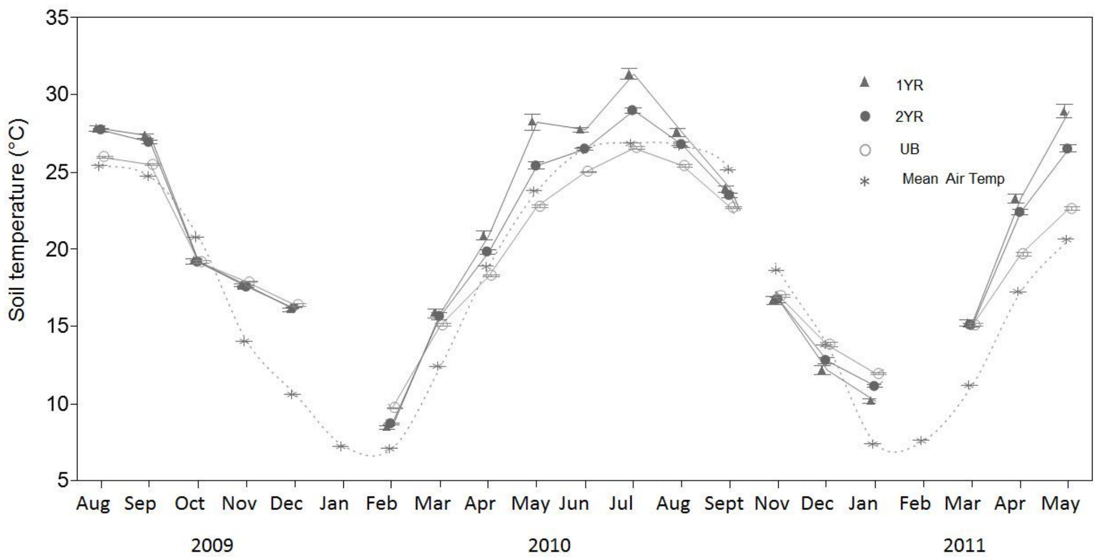

Figure 3. Monthly mean soil temperature (T_s) (°C) for three prescribed fire regimes at the Tall Timbers Research Station near Tallahassee, FL, USA. Mean monthly 2 m air temperature also shown for comparison. Data were from 27 sample points per fire regime, measured three-times daily once per month. Equipment problems eliminated measurements taken in January 2009 and February 2011. Measurements were not taken in October of 2010.

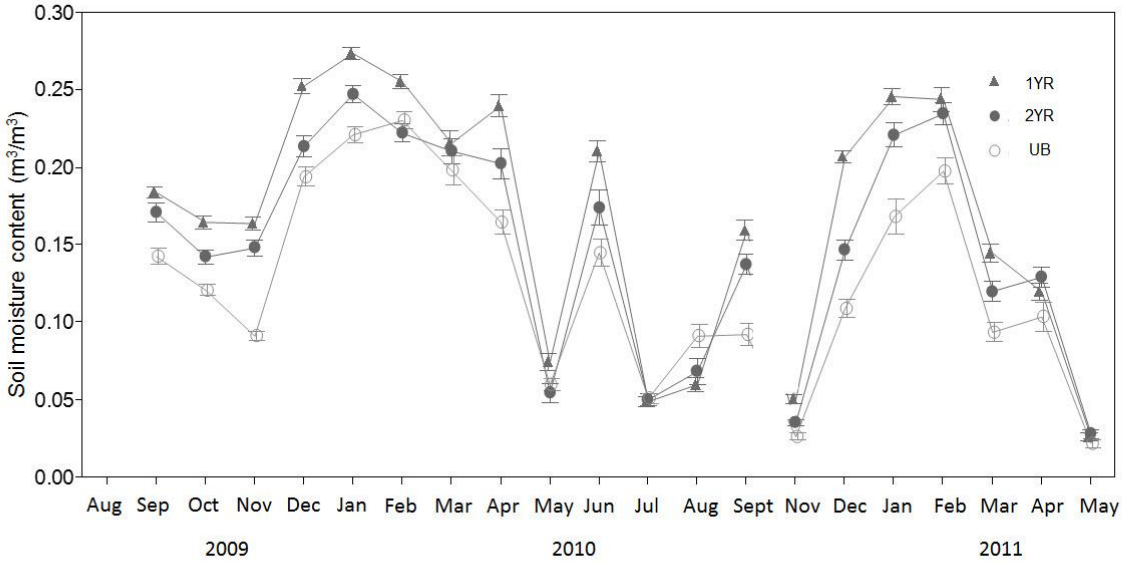

Figure 4. Monthly mean soil moisture content (M_s) (m^3/m^3) for three prescribed fire regimes at the Tall Timbers Research Station near Tallahassee, FL, USA. Mechanical difficulty resulted in erroneous data collected in August 2009. Measurements were not taken in October of 2010.

Forest stand characteristics and litter and duff depths varied significantly among fire regimes (Table 4A). Patterns were related to higher tree stocking and duff and litter accumulation with lower occurrence of fire. Duff depth was over an order of magnitude higher in the UB sites than the 1YR sites (Table 4A). Soil bulk density was significantly higher in the 1YR and 2YR return interval treatments and percent total carbon was higher in the 2YR treatment than in the unburned treatment (Table 4B). Values for nitrogen, phosphorus, calcium, magnesium, potassium, and pH all showed a decreasing trend from the 1YR to unburned treatments, although results were significant only for magnesium (Table 4B).

Table 4. Mean forest characteristics per prescribed fire treatment (FR). See Table 1 for abbreviations and units. Data in parentheses are standard deviation. Letters per column show significant differences between fire return intervals (Tukey's HSD test); *p*-Values were considered significant at $\alpha = 0.05$.

(A)

FR	TPH	HWBA	PBA	BA	Duff	Litter
1YR	282.9 (64.83) a	3.87 (6.28) a	7.92 (3.68) a	11.79 (7.22) a	0.08 (0.06) a	1.77 (0.91) a
2YR	400.81 (344.87) a	6.30 (4.28) ab	9.16 (6.14) a	15.45 (2.15) a	0.46 (0.41) b	2.17 (0.79) b
UB	1716.41 (681.42) b	15.73 (3.59) b	21.99 (11.22) a	37.72 (8.36) b	1.58 (0.55) c	2.81 (0.58) c

(B)

FR	BD	C	N	P	Ca	Mg	K	pH
1YR	1.24 (0.04) a	26.53 (2.49) ab	1.23 (0.18)	33.46 (25.18)	853.1 (506.4)	185.5 (69.8) a	38.08 (18.80)	5.48 (0.37)
2YR	1.26 (0.07) a	30.33 (4.16) a	1.18 (0.73)	11.69 (7.58)	737.8 (264.3)	141.5 (45.6) ab	27.54 (8.12)	5.29 (0.18)
UB	1.07 (0.04) b	21.56 (2.38) b	1.05 (0.16)	11.16 (4.78)	301.8 (185.4)	66.3 (23.4) b	25.21 (4.68)	4.86 (0.31)

3.2. Drivers of R_s within Treatment

Linear regressions indicated monthly mean T_s significantly predicted monthly mean R_s within each fire regime ($R^2 > 0.62$; Figure 5). In contrast, M_s did not predict R_s ($R^2 < 0.14$) [29]. Nonlinear exponential models also used to predict R_s from T_s and M_s by fire regime showed similar results as the linear models, in which case M_s was also not significant and not reported (Table 5). Model coefficients β_0 and β_1 from the nonlinear models were similar to those reported by Samuelson et al. [28] and Kobziar and Stephens [15]. Q_{10} values ranged from 1.65 to 2.16 and differed among fire regimes

(Table 5). The UB sites had the greatest R_s sensitivity to changes in soil temperature (Q_{10} = 2.16), while the 1YR sites were the least sensitive to soil temperature changes (Q_{10} = 1.65).

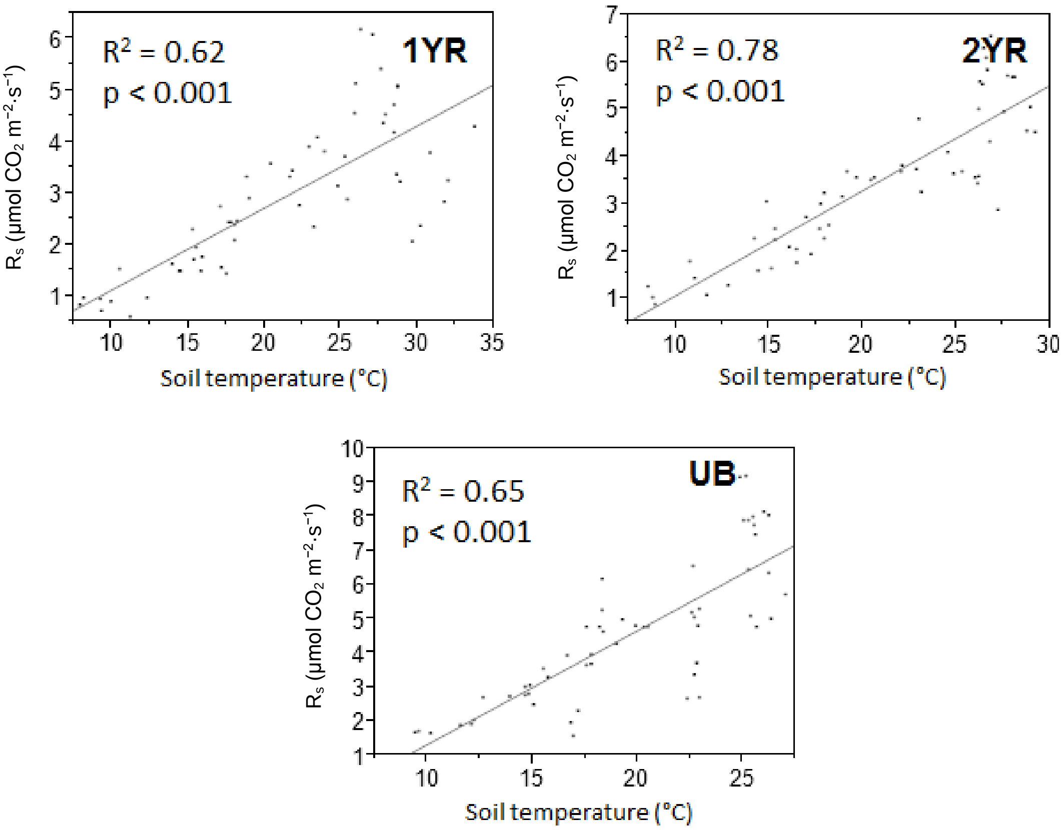

Figure 5. Linear regression of the relationships between monthly mean soil CO_2 efflux rates (R_s) (µmol CO_2 $m^{-2}\cdot s^{-1}$) and monthly mean soil temperature (T_s) (°C) for three prescribed fire intervals at the Tall Timbers Research Station near Tallahassee, FL, USA. Each point represents monthly mean values per sample plot. *p*-Values were considered significant at α = 0.05.

Table 5. Linear and nonlinear regression relationships between soil CO_2 efflux rates (R_s) and soil temperature (T_s) by fire return interval (FR).

FR	Model Type	Model and Estimates	Q_{10}	R^2	*p-Value*
1YR	Linear	$R_s = -0.5101 + 0.16029(T_s)$		0.62	<0.001
1YR	Nonlinear	$R_s = 0.9727\ e^{0.0502(T_s)}$	1.65	0.60	<0.001
2YR	Linear	$R_s = -1.1736 + 0.2218(T_s)$		0.78	<0.001
2YR	Nonlinear	$R_s = 0.7973\ e^{0.0673(T_s)}$	1.96	0.80	<0.001
UB	Linear	$R_s = -2.0303 + 0.3337(T_s)$		0.65	<0.001
UB	Nonlinear	$R_s = 0.9712\ e^{0.0770(T_s)}$	2.16	0.76	<0.001

Model data use mean monthly measurements of Rs and Ts.

3.3. Seasonal Variation in R_s and T_s Relationships

In the simple linear models and non-linear models predicting mean monthly R_s from T_s within each fire regime showed that the relationship was strongest during the fall and winter (R^2 = 0.69–0.90) and weakest during the spring and summer (R^2 = 0.11–0.63) in all fire regimes (Tables 6 and 7). Q_{10} also varied seasonally, with the lowest Q_{10} values observed during summer and the highest Q_{10} values observed during the winter in all fire regimes (Table 7).

Table 6. Linear regression relationship between soil CO_2 efflux rates (R_s) and soil temperature (T_s) by fire return interval (FR) and season. p-Values were considered significant at α = 0.05.

FR	Season [1]	Model and Estimates	R^2	*p-Value*
1YR	Spring	$R_s = 1.0261 + 0.0700(T_s)$	0.29	0.021
	Summer	$R_s = 12.8311 - 0.2799(T_s)$	0.40	0.068
	Fall	$R_s = -1.4494 + 0.2159(T_s)$	0.71	<0.001
	Winter	$R_s = -0.4895 + 0.1435(T_s)$	0.69	0.002
2YR	Spring	$R_s = 1.0808 + 0.0976(T_s)$	0.48	0.002
	Summer	$R_s = 15.7301 - 0.3751(T_s)$	0.28	0.144
	Fall	$R_s = -3.1609 + 0.3197(T_s)$	0.90	<0.001
	Winter	$R_s = -0.4894 + 0.1661(T_s)$	0.71	0.002
UB	Spring	$R_s = 1.5400 + 0.1302(T_s)$	0.11	0.170
	Summer	$R_s = 49.5720 - 1.6300(T_s)$	0.63	0.011
	Fall	$R_s = -4.3665 + 0.4270(T_s)$	0.71	<0.001
	Winter	$R_s = -2.0244 + 0.3544(T_s)$	0.90	<0.001

[1] Spring (March–May), summer (June–August), fall (September–November), and winter (December–February).

Table 7. Seasonal nonlinear models of soil CO_2 efflux (R_s) rates using soil temperature (T_s) as a predictor. Models are of monthly mean R_s responses to T_s. p-values were considered significant at α= 0.05.

FR	Season	Equation	Q_{10}	R^2	*p-Value*
1YR	Spring	$R_s = 1.5095\ e^{0.0238(T_s)}$	1.27	0.26	0.031
	Summer	$R_s = 37.6590\ e^{-0.0721(T_s)}$	0.49	0.45	0.049
	Fall	$R_s = 0.8564\ e^{0.0598(T_s)}$	1.82	0.66	<0.001
	Winter	$R_s = 0.2704\ e^{0.1200(T_s)}$	3.32	0.77	0.000
2YR	Spring	$R_s = 0.2778\ e^{0.1250(T_s)}$	3.49	0.33	0.012
	Summer	$R_s = 36.2629\ e^{-0.0692(T_s)}$	0.50	0.27	0.149
	Fall	$R_s = 0.5967\ e^{0.0823(T_s)}$	2.28	0.89	<0.001
	Winter	$R_s = 0.3701\ e^{0.1114(T_s)}$	3.05	0.78	0.001
UB	Spring	$R_s = 2.2967\ e^{0.0292(T_s)}$	1.34	0.10	0.195
	Summer	$R_s = 259.9167\ e^{-0.1388(T_s)}$	0.25	0.62	0.012
	Fall	$R_s = 0.6935\ e^{0.0883(T_s)}$	2.42	0.69	<0.001
	Winter	$R_s = 0.3990\ e^{0.1383(T_s)}$	3.99	0.96	<0.001

3.4. Total Carbon Emissions

Estimated total monthly soil carbon emissions were consistently higher in the unburned UB sites than the frequently burned 1YR and 2YR sites. Similarly, estimated total annual soil carbon emissions per fire regime showed the highest soil carbon efflux in the UB sites (16.88 Mg $ha^{-1}\cdot year^{-1}$) and the lowest in the 1YR (10.69 Mg $ha^{-1}\cdot year^{-1}$) and 2YR (12.68 Mg $ha^{-1}\cdot year^{-1}$) sites.

4. Discussion

Results of our study show that R_s was consistently higher in long fire-excluded pine-grasslands than in frequently burned pine-grasslands, while there was little difference between annually and biennially burned communities. Although determining specific mechanisms for the observed pattern was beyond the scope of this study, there is evidence that R_s responded to environmental conditions influenced by fire regime effects on forest structure.

In the UB sites, aboveground living tree biomass (≈150 Mg ha^{-1}) was much greater than in the 1YR and 2YR sites (≈50 Mg ha^{-1} and ≈80 Mg ha^{-1}, respectively), suggesting that the presumably corresponding higher tree root biomass in the unburned plots may have influenced R_s. Other studies investigating R_s rates across stand age and biomass gradients have found mean R_s rates to be higher in older stands with greater aboveground biomass [30,31]. In a trenching and exclusion experiment along a chronosequence of temperate forests in China, Luan et al. [32] found that R_s rates were significantly correlated with site basal area ($R^2 = 0.59$, $p < 0.05$).

Higher soil respiration rates in the unburned sites may have also been influenced by tree species composition and associated litter quality, specifically dominance by deciduous broadleaf trees which were essentially absent in the burned plots. Soil CO_2 efflux rates have been shown in other studies to be lower in coniferous forests than in broad-leafed forests of the same soil type [5]. In a study of R_s rates in a mixed conifer–deciduous forest in Belgium, Yuste et al. [33] found that mean R_s rates were lower under conifer tree canopies than under deciduous canopies, with total estimated annual carbon flux approximately 50% greater in the deciduous sites (8.8 $\pm$ 2.2 Mg C $ha^{-1}\cdot year^{-1}$) than in the coniferous sites (4.8 $\pm$ 0.7 Mg C $ha^{-1}\cdot year^{-1}$). In their review, Raich and Tufekciogul [5] suggested that the observed differences in R_s between coniferous and deciduous forests may have been driven by forest litter production and quality, carbon allocation, and autotrophic contributions to total R_s.

In our study, litter and duff depths were highest in the UB sites, reflecting higher tree stocking and lack of fire, in turn possibly contributing to higher R_s rates in the UB sites. Other studies have reported that frequent fire greatly reduces the accumulation of litter and duff [34]. The lower soil carbon levels and lowest R_s in the 1YR plots compared to the 2YR plots likely reflect limited inputs of organic matter because of annual burning. The 2YR plots in turn are assumed to have lower organic matter inputs to the soil than the UB plots because frequent fire, yet the total carbon was higher in the 2YR plots, suggesting lower rates of decomposition than the UB plots consistent with the lower R_s measured. It appears that some characteristic of the frequently burned environment suppressed soil respiration, whether through its effect on R_a or R_h. Increased bulk density associated with burning, found in this and other studies [35–37] has been attributed to infiltration of micropore space by ash and char, which might negatively influence microbial activity. Similar patterns of higher total carbon in the mineral soil of burned than unburned areas have been seen in many long-term fire experiments in the southeastern USA [36,38–41].

The R_s rates observed in this study resulted in lower estimated total annual soil carbon emissions in the 1YR (37%) and 2YR (25%) sites relative to the UB sites. The estimated monthly carbon emissions for all sites were similar to those reported by Samuelson et al. [28] for an unburned loblolly pine plantation in southwestern Georgia, USA, while the estimated total annual soil carbon emissions reported in our study were similar to those (14.10 Mg $ha^{-1}\cdot year^{-1}$) reported by Maier and Kress [42] for an unburned loblolly pine plantation, but greater than those (7.78–9.66 Mg $ha^{-1}\cdot year^{-1}$) reported by the Samuelson et al. [28] study.

Temporal variability in R_s rates was explained more by soil temperature than any other recorded parameter. These results were consistent with other studies in southeastern USA forest systems in which R_s rates were found to have strong correlations with soil temperature [28,42,43]. The R_s correlation with T_s reported in this study (R^2 = 0.62–0.78 in linear models and R^2 = 0.60–0.80 in nonlinear models) were higher than those reported by Samuelson et al. [28] for a Georgia, USA loblolly pine plantation (R^2 = 0.38–0.56), much higher than those reported by Templeton et al. [43] across a range of loblolly pine plantations in 11 southeastern USA states (R^2 = 0.45), and similar to those reported for a loblolly pine plantation in North Carolina, USA (R^2 = 0.70) [42]. Caution must be used in comparing correlations among studies, as variations in the modeled R_s and T_s relationship may be influenced by statistical modeling techniques regardless of the biogeochemical couplings observed in the field. While T_s explained the majority of the temporal variability in R_s rates, a lack of significant differences in T_s among treatments suggests that temperature was not the key factor contributing to the differences in R_s rates among the treatments.

Over the course of this study's sampling period, relationships between R_s and T_s varied seasonally, with stronger relationships during the winter seasons. This pattern was evident in the R^2 values of the seasonal linear and nonlinear models as well as in the seasonal Q_{10} values. Distinct seasonal variations in Q_{10} values have been noted by others [44,45] and such variations have potential implications for modeling R_s values based on temperature measurements. Yuste et al. [45] suggested that while annual Q_{10} values may sufficiently model annual R_s rates, seasonal or shorter-term estimates of R_s should be based on season specific Q_{10} functions that capture the seasonal variation in R_s temperature response, as observed in our study.

The seasonal variation in the relationship between R_s and T_s may be the result of phenology-related shifts in the relative contributions of R_a and R_h to R_s. Previous research in partitioning the sources of R_s have shown that during periods of aboveground vegetative growth, R_a contributions to R_s can increase relative to R_h, as plants allocate recent C photosynthate belowground, driving higher root maintenance, root growth, and mycorrihizal fungal respiration rates [6,46]. In addition, other studies have shown that during periods of aboveground vegetative growth, the T_s and R_s relationship weakens as other variables such as soil moisture and available photosynthetically active radiation (PAR) become important in governing belowground C allocation by plants [47–49]. Similar to our findings, Fenn et al. [50] found that soil temperature explained less of the variation in R_s during the summer than during the spring in a multi-season study of R_s rates in a woodland in Oxfordshire, UK.

5. Conclusions

In this study comparing long-term fire disturbance intervals, soil temperature explained the majority of the temporal variation in R_s rates, but neither temperature nor moisture explained the differences in R_s observed among the fire frequencies. As such, we suggest that future efforts to model soil carbon fluxes in otherwise similar burned and unburned forests should account for the impacts of both seasonal variability and prescribed fire management regime on the relationships between R_s and T_s. Differences in CO_2 efflux rates, as well as soil chemistry and bulk density, reflect the long-term impact of contrasting fire disturbance regimes, as well as the biophysical consequences of those regimes. Lower total annual soil C emissions, combined with lower rates of soil C efflux and higher stored soil C, suggest that even biennially burned sites are effective at sequestering soil carbon.

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References

1. Raich, J.W.; Schlesinger, W.H. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* **1992**, *44*, 81–99. [CrossRef]
2. Schlesinger, W.; Andrews, J. Soil respiration and the global carbon cycle. *Biogeochemistry* **2000**, *48*, 7–20. [CrossRef]
3. Ryan, M.G.; Law, B.E. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* **2005**, *73*, 3–27. [CrossRef]
4. Luo, Y.; Zhou, X. *Soil Respiration and the Environment*; Academic Press: Burlington, MA, USA, 2006.
5. Raich, J.W.; Tufekciogul, A. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* **2000**, *48*, 71–90. [CrossRef]
6. Subke, J.; Inglima, I.; Cotrufo, M.F. Trends and methodological impacts in soil CO_2 efflux partitioning: A meta-analytical review. *Glob. Chang. Biol.* **2006**, *12*, 921–943. [CrossRef]

7. Neary, D.; Klopatek, C.; DeBano, L.; Folliott, P. Fire effects on belowground sustainability: A review and synthesis. *For. Ecol. Manag.* **1999**, *122*, 51–71. [CrossRef]
8. O'Neill, K.P.; Richter, D.; Kasischke, E. Succession-driven changes in soil respiration following fire in Black Spruce stands of interior. *Alsk. Biogeochem.* **2006**, *80*, 1–20. [CrossRef]
9. Medvedeff, C. The Effect of an Extreme Restoration Approach on Microbial Carbon Cycling in a Restored Subtropical Wetland. Ph.D. Thesis, University of Florida, Gainesville, FL, USA, 2012.
10. Glitzenstein, J.; Streng, D.; Masters, R.E.; Robertson, K.M.; Hermann, S.M. Fire-frequency effects on vegetation in north Florida pinelands: Another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. *For. Ecol. Manag.* **2012**, *264*, 197–209. [CrossRef]
11. Sulzman, E.W.; Brant, J.B.; Bowden, R.D.; Lajtha, K.S.; Mar, S.R.; Brant, B. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest. *Biogeochemistry* **2012**, *73*, 231–256. [CrossRef]
12. Johnson, D. Effects of forest management on soil C and N storage: Meta-analysis. *For. Ecol. Manag.* **2001**, *140*, 227–238. [CrossRef]
13. Johnson, D.W.; Knoepp, J.D.; Swank, W.T.; Shan, J.; Morris, L.; Van Lear, D.H.; Kapeluck, P.R. Effects of forest management on soil carbon: Results of some long-term resampling studies. *Eviron. Pollut.* **2002**, *116*, S201–S208. [CrossRef]
14. Certini, G. Effects of fire on properties of forest soils: A review. *Acta Oecol.* **2005**, *143*, 1–10. [CrossRef] [PubMed]
15. Kobziar, L.N.; Stephens, S.L. The effects of fuels treatments on soil carbon respiration in a Sierra Nevada pine plantation. *Agric. For. Meteorol.* **2006**, *141*, 161–178. [CrossRef]
16. Kobziar, L.N. The role of environmental factors and tree injuries in soil carbon respiration response to fire and fuels treatments in pine plantations. *Biogeochemistry* **2007**, *84*, 191–206. [CrossRef]
17. Ryu, S.; Concilio, A.; Chen, J.; North, M.; Ma, S. Prescribed burning and mechanical thinning effects on belowground conditions and soil respiration in a mixed-conifer forest, California. *For. Ecol. Manag.* **2009**, *257*, 1324–1332. [CrossRef]
18. Concilio, A.; Ma, S.; Li, Q.; LeMoine, J.; Chen, J.; North, M.; Moorhead, D.; Jensen, R. Soil respiration in response to prescribed burning and thinning in mixed-conifer and hardwood forests. *Can. J. For. Res.* **2005**, *35*, 1581–1591. [CrossRef]
19. Engstrom, R.T.; Palmer, W.E. Two species in one ecosystem: Management of Northern bobwhite and Red-cockaded woodpecker in the Red Hills. In *Bird Conservation Implementation and Integration in the Americas, Proceedings of the 3rd International Partners in Flight Conference, Asilomar, CL, USA, 20–24 March 2002*; Ralph, C.J., Rich, T.D., Eds.; USDA Forest Service Pacific Southwest Research Station: Albany, CL, USA, 2005; pp. 1151–1157.
20. Way, A.G. The Stoddard-Neel method: Forestry beyond one generation. *For. Hist. Today* **2006**, 16–23.
21. Frost, C. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In Proceedings of the 18th Tall Timbers Fire Ecology Conference: The Longleaf Pine Ecosystem: Ecology, Restoration and Management, Tallahassee, FL, USA, 30 May–2 June 1991; Hermann, S.M., Ed.; Tall Timbers Research, Inc.: Tallahassee, FL, USA, 1993; pp. 17–43.
22. Kobziar, L.N.; Watts, A.C.; Godwin, D.S.; Taylor, L. Perspectives on trends, effectiveness, and challenges to prescribed burning in the Southern US. *Forests* **2015**, *6*, 561–580. [CrossRef]
23. Clewell, A.; Komarek, R. NB66: The Initiation of a Long-Term Experiment in Forest Succession. Unpublished work, 1975.
24. Clewell, A. Forest development 44 years after fire exclusion in formerly annually burned old-field pine woodland, Florida. *Castanea* **2014**, *79*, 147–167. [CrossRef]
25. Robertson, K.M.; Ostertag, T.E. Effects of land use on fuel characteristics and fire behavior in pinelands of southwest Georgia. In Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems, Tall Timbers Research Station, Tallahassee, FL, USA, 17–19 October 2005; Masters, R.E., Galley, K.E., Eds.; Tall Timbers Research Station, Inc.: Tallahassee, FL, USA, 2007; pp. 181–191.
26. Myers, R.L.; Ewel, J.J. *Ecosystems of Florida*; University of Central Florida Press: Orlando, FL, USA, 1990.
27. Lundegardh, H. Carbon dioxide evolution of soil and crop growth. *Soil Sci.* **1927**, *23*, 417–453. [CrossRef]
28. Samuelson, L.J.; Johnson, K.; Stokes, T.; Lu, W. Intensive management modifies soil CO_2 efflux in 6-year-old *Pinus taeda* L. stands. *For. Ecol. Manag.* **2004**, *200*, 335–345. [CrossRef]

29. Godwin, D.R. The influence of prescribed fire and mechanical fuels mastication on soil CO2 efflux rates in two Southeastern U.S. pine ecosystems. Ph.D. Thesis, University of Florida, Gainesville, FL, USA, 2012.
30. Ewel, K.; Cropper, W.; Gholz, H. Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. *Can. J. For. Res.* **1987**, *17*, 325–329. [CrossRef]
31. Amiro, B.D.; Barr, A.G.; Barr, J.G.; Black, T.A.; Bracho, R.; Brown, M.; Chen, J.; Clark, K.L.; Davis, K.J.; Desai, A.R.; et al. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res.* **2010**, *115*, 2156–2202. [CrossRef]
32. Luan, J.; Liu, S.; Wang, J.; Zhu, X.; Shi, Z. Rhizospheric and heterotrophic respiration of a warm-temperate oak chronosequence in China. *Soil Biol. Biochem.* **2011**, *43*, 503–512. [CrossRef]
33. Yuste, J.C.; Nagy, M.; Janssens, I.A.; Carrara, A.; Cuelemans, R. Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration. *Tree Physiol.* **2005**, *25*, 609–619. [CrossRef]
34. Bizzari, L.E.; Collins, C.D.; Brudvig, L.A.; Damschen, E. Historical agriculture and contemporary fire frequency alter soil properties in longleaf pine woodlands. *For. Ecol. Manag.* **2015**, *349*, 45–54. [CrossRef]
35. Wahlenberg, W.G. Effect of fire and grazing on soil properties and the natural reproduction of longleaf pine. *J. For.* **1939**, *33*, 331–338.
36. Boyer, W.D.; Miller, J.H. Effect of burning and brush treatments on nutrient and soil physical properties in young longleaf pine stands. *For. Ecol. Manag.* **1994**, *70*, 311–318. [CrossRef]
37. Williams, R.J.; Hallgren, S.W.; Wilson, G.W. Frequency of prescribed burning in an upland oak forest determines soil and litter properties and alters the soil microbial community. *For. Eco. Manag.* **2012**, *265*, 241–247. [CrossRef]
38. Heyward, F.; Barnette, R.M. *Effect of Frequent Fires on Chemical Composition of Forest Soils in the Longleaf Pine Region*; Technical Bulletin 265; University of Florida Agricultural Experiment Station: Gainesville, FL, USA, 1934.
39. Greene, S.W. Effect of annual grass fires on organic matter and other constituents of virgin longleaf pine soils. *J. Agric. Res.* **1935**, *50*, 809–822.
40. Wells, C.G. Effects of prescribed burning on soil chemical properties and nutrient availability. In *Proceedings of the Prescribed Burning Symposium*; USDA Forest Service Southeastern Forest Experiment Station: Asheville, NC, USA, 14–16 April 1970; pp. 86–99.
41. McKee, W.H. *Changes in Soil Fertility Following Prescribed Burning on Coastal Plain Pine Sites*; Research Paper SE-234; USDA Forest Service Southeastern Experimental Forest Research Station: Charleston, SC, USA, 1982.
42. Maier, C.A.; Kress, L.W. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. *Can. J. For. Res.* **2000**, *30*, 347–359. [CrossRef]
43. Templeton, B.S.; Seiler, J.R.; Peterson, J.A.; Tyree, M.C. Environmental and stand management influences on soil CO_2 efflux across the range of loblolly pine. *For. Ecol. Manag.* **2015**, *355*, 15–23. [CrossRef]
44. Janssens, I.A.; Pilegaard, K. Large seasonal changes in Q_{10} of soil respiration in a beech forest. *Glob. Chang. Biol.* **2003**, *9*, 911–918. [CrossRef]
45. Yuste, J.C.; Janssens, I.A.; Carrara, A.; Cuelemans, R. Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Glob. Chang. Biol.* **2004**, *10*, 161–169. [CrossRef]
46. Kuzyakov, Y. Sources of CO_2 efflux from soil and review of partitioning methods. *Soil Biol. Biochem.* **2006**, *38*, 425–448. [CrossRef]
47. Ekblad, A.; Högberg, P. Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Acta Oecol.* **2001**, *127*, 305–308. [CrossRef] [PubMed]
48. Davidson, E.; Richardson, A.; Savage, K.; Hollinger, D.A. distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. *Glob. Chang. Biol.* **2006**, *12*, 230–239. [CrossRef]
49. Wertin, T.M.; Teskey, R.O. Close coupling of whole-plant respiration to net photosynthesis and carbohydrates. *Tree Physiol.* **2008**, *28*, 1831–1840. [CrossRef] [PubMed]
50. Fenn, K.M.; Malhi, Y.; Morecroft, M.D. Soil CO_2 efflux in a temperate deciduous forest: Environmental drivers and component contributions. *Soil Biol. Biochem.* **2010**, *42*, 1685–1693. [CrossRef]