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Continuous Monitoring of Soil Respiration After a Prescribed Fire: Seasonal Variations in CO_2 Efflux

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Abstract: Prescribed burns have recently become a widespread environmental management practice for biodiversity restoration to reduce fuel load, to provide forest fire suppression operational opportunities, to favor plant recruitment or to manage wild species. Prescribed fires were again applied in Doñana National Park (southern Spain) after decades of non-intervention regarding fire use. Here, we assessed their impacts on the soil CO_2 effluxes over two years after burning to test the hypothesis that if the ecosystem is resilient, soil respiration will have a rapid recovery to the conditions previous to the fire. Using soil automated CO_2 flux chambers to continuously measure respiration in burned and unburned sites, we showed that soil respiration varies among seasons but only showed significant differences between burned and unburned plots in the fall season one year after fire, which corresponded with the end of the dry season. Comparing soil respiration values from the burned plots in the three fall seasons studied, soil respiration increased significantly in the fall one year after fire, but decreased in the following fall to the values of the control plots. This study highlights the resilience of soil respiration after prescribed fire, showing the potential benefits of prescribed fire to reduce catastrophic wildfires, especially in protected areas subjected to non-intervention.

Keywords: low-intensity burn; prescribed fire; soil pore degasification; automated LI-COR 8100 chambers; Mediterranean ecosystem; Donaña National Park

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1. Introduction

Fires are a natural or human-induced disturbance of forest ecosystems, affecting the landscape and the dynamics and structure of plant and animal communities [1–3]. Since the 1970s, a considerable increase in the fire regime and fire intensity in Mediterranean areas has been detected [4], partly due to rural depopulation and changes in forest management, which have led to an increase in abundant coarse woody fuel. On the other hand, climate change is causing an increase in the frequency and duration of dry periods, leading to large fires [5,6]. For example, in 2022, Spain suffered its worst fire year since 2000: 450 forest fires of more than 30 hectares were recorded, with a total exceeding 310,000 burned hectares. This figure corresponds to 1.6% of the Spanish forest area [7] and is equivalent to 39% of the total of 786,049 hectares that burned in the European Union in the same year, according to data from the European Forest Fire Information System (EFFIS).

The main direct effects of forest fires are obviously the massive reductions in vegetation, but their indirect effects are diverse and complex to study. An extensive literature indicates that, in environments prone to fires such as a large part of the Iberian Peninsula, native plant communities are relatively resilient to fires, recovering progressively afterwards, although with considerable variability depending on the type of forest cover affected [8]. On the other hand, the richness and abundance of animal communities are significantly reduced in the first years after the last fire event [9,10]. The fire history is an important modulator of animal diversity [11], because frequently animals can survive the effects of direct fire [12], particularly during low severity fires [13]. However, fire is always a biodiversity threat worldwide: it has been shown that across nine taxonomic groups which have been assessed systematically that at least 1071 species were threatened by an increase in fire frequency or intensity, while only 55 species were threatened by exclusion of fire [14].

Although fire is usually perceived as a very negative element for the ecosystem, some authors consider it as one more factor affecting ecosystem processes, even as an ecosystem service [15]. Sten [16] states that fire is a keystone process which promotes biodiversity by maintaining a patchwork of habitats, supporting plants and animals; when natural areas do not burn following their historical pattern, they may be vulnerable to highly destructive fires, causing a biodiversity decline [16]. Wildfires, earlier perceived as destructive disturbances, can be understood as a natural, inherent and fundamental process, which promotes and maintains biodiversity in ecosystems [15,17]. Habitats such as forests, natural grasslands, meadows and rivers have benefited from fires for millennia, with fires supporting, provisioning and regulating ecosystem services, such as pest populations, catastrophic fires, pollination enhancement, or water regulation [15,16].

Prescribed fires can be used as an alternative that mimics the original role of wildfire to meet specific objectives [15,18]. Prescribed burning has long been used by Australian Aborigines to encourage hunting [19–21] and more recently has been applied for reducing fire risk [17,22], for biodiversity restoration [23] (Legge et al., 2011) or biodiversity conservation [24,25] and to reduce greenhouse gas emissions [26]. It is also used in the Brazilian savannah with no net loss of species diversity [27], in the USA to increase plant diversity [28], and in the Iberian Peninsula to reduce fuel load and favor plant recruitment [29–32].

Another example of fire benefits is its use in Doñana National Park (southern Spain) as a habitat management tool to favor wild rabbit populations, the main prey of the endangered Iberian lynx, *Lynx pardinus*, and the Spanish imperial eagle, *Aquila adalberti* [33,34]. Before the creation of the Doñana National Park, the scrubland was periodically cleared and burned for sowing wheat. This practice favored rabbits, which tended to be more abundant in areas with grass and low or medium vegetation cover [35]. But the traditional management system was abandoned after the creation of the National Park, whose conservation strategy regarding fire has been based on non-intervention. This strategy has led to the aging of the scrubland and its tremendous high density, which is very unfavorable for predators specialized in hunting rabbits, such as the Iberian lynx [36] or Spanish Imperial eagle [37]. In 1989, some experimental plots were burned in Doñana, and after a few years, the abundance of rabbits had multiplied more than four times compared to the control plots [38]. But burning was never applied again, and was replaced by clearing the scrubland, very likely because of the negative perception and the costs of prescribed fire management [33,34,39]. In 2020, given the extremely low level of the rabbit population [40], prescribed fire was applied to new experimental plots, and fauna, vegetation and soil have been monitored to study local effects of prescribed fires at the ecosystem level and to assess their viability.

In this work, we assessed the impacts of fire on soils through continuous monitoring of soil respiration to evaluate the potential use of prescribed fire in Doñana National Park. Soil respiration is the result of the activity of root and rhizosphere organisms (autotrophic respiration) and the microbial decomposition of organic matter (heterotrophic respiration) [41]. Therefore, it is closely related to ecosystem productivity and soil fertility, being considered as a key indicator of soil health and quality to support plant growth [42]. The effects of fire on soil respiration are still under investigation, as many factors influence soil carbon fluxes. Among the most studied factors so far are rainfall regime, soil moisture and temperature (e.g., [43,44]), forest management practices (e.g., [45,46]), vegetation patches (e.g., [45,47]) or fertilization (e.g., [48,49]). There is agreement on the influence of some of these factors on soil respiration. For example, many studies show that soil respiration is exponentially correlated with soil temperature when water is not limited [50], and both soil saturation and drought suppress soil respiration [51]. However, there is no consistency in the literature on the effect of fire on soil respiration. Some authors show increased respiration rates soon after burning, likely a result of high nutrient availability coming from the removal of vegetation, decomposition of organic matter and ashes, which leads to large microbial activity [52–54]. In other cases, decreased respiration rates were found, likely due to lower soil organic carbon availability, or because the high soil temperatures and low moisture caused a reduction in microbial biomass [55–57]. Finally, in some cases, soil respiration seems to be resilient to fire, showing no net changes after fire, either because fire did not have a significant impact on soil organic matter or soil microorganisms, or because quick plant resprouting limited the extent to which the fire affected root respiration [57,58]. Contrasting results of fire on soil respiration are the result of context dependencies, such as the characteristics of the fire (including its nature or intensity), the type of habitat and soil, the plant and microorganism communities belowground, as well as soil temperatures and moisture after fire [59]. Soil respiration in arid and semi-arid environments, which have a low productivity, have received little attention (but see [54]); moreover, measurements in these environments are challenging because of the high spatial and temporal variability in soil temperatures and moisture [44,57].

CO_2 chamber systems have been widely used to assess the impacts of fire in soils, particularly on the gas exchange and CO_2 fixation by soils (e.g., [46,56–58,60–62]). Most of these studies used discrete data acquisition over time due to the technical complexity of the maintenance of these chambers. Only a few studies (e.g., [63]) have used continuous data acquisition; however, they did not focus on prescribed fire effects. Here, we were interested in the variation in the effects of fire on soil respiration over the different seasons in a semi-arid environment at Doñana National Park. Thus, we continuously monitored soil respiration during two years after burning and compared seasonal variations in CO_2 flux in burned and unburned soils. Monitoring of fungus communities and soil parameters during the first year after the prescribed fire in Doñana provided some cues to predict the impacts in soil respiration: the richness of fungus communities, such as wood saprotrophs or mycoparasites, although significantly altered during the first six months following fire, had recovered after 12 months [64]. Alterations in the soil variables, such as organic carbon and moisture, had recovered three months after fire [65], and only soil nitrogen and potassium had higher values one year after fire [64]. Thus, it is expected that one year after fire, the heterotrophic respiration coming from fungus or from other microbial activity depending on organic carbon would show no differences with control areas. Alternatively, we could expect that prescribed fire could potentially increase soil CO_2 fluxes in Doñana National Park, such as those seen in semi-arid ecosystems [42], or that there are daily or seasonal CO_2 flux variations in response to fire, as it has been reported in arid and semi-arid ecosystems [42,57].

2. Materials and Methods

2.1. Study Area

The study was conducted on the Atlantic coast of southwestern Spain, in the Doñana Biological Reserve, a restricted area of the Doñana National Park (37°10′ N, 6°23′ W; 54,252 ha, Figure 1). The climate is Mediterranean, with very hot and dry summers, and mild and wet winters. The annual average temperature is around 17 °C, and rainfall is generally concentrated from October to April. The three main biotopes present in the national park are marshland, sand dunes and scrubland. The marshland is usually flooded from October–November to May–June, and occupies about 55% of the Doñana National Park area. Around 30% of its area is Mediterranean scrubland, and the rest, 15%, is sand dunes with scattered pine forest (*Pinus pinea*) and isolated cork oak trees (*Quercus suber*). A detailed description of the Doñana National Park can be found in [66].

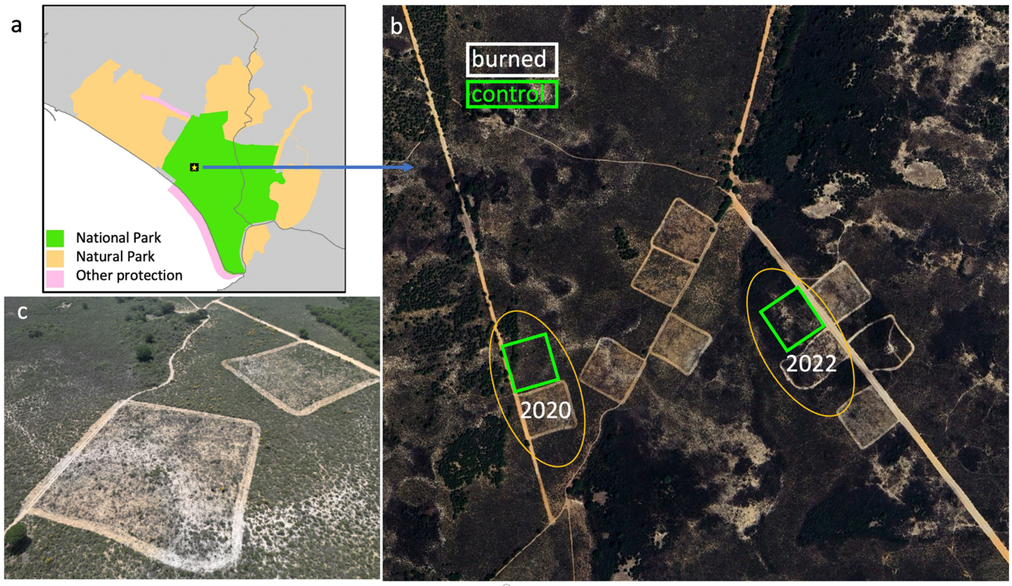

Figure 1. Location of the study area. (**a**) The Doñana National Park, (**b**) burned and control plots, and (**c**) aerial photograph of burned plots from different years.

The parent soil materials in the park are eolian sandy sediments (Holocene) overlying gravels and other sandy sediments (Pliocene–Pleistocene). Soil types such as Typic Xeropsamment, Aquic Xeropsamment and Humaqueptic Psammaquent are found in dune tops, slopes and interdune depressions, respectively [67]. In particular, the scrubland in which we carried out this study is located on alfisols (subtype Palexeralf), which usually contain clay minerals such as kaolinite and smectites (hectorite, vermiculite and montmorillonite). Geomorphology, through water availability, controls the vegetation pattern at different scales with a sequence of xerophytic scrub (drier ridges of the dunes), mixed scrub (mid-slope scrub) and heather (in floodable depressions) [68].

Considering the morphological and physicochemical properties of the soils in the research area of the Doñana Natural Park, the soils consist of fine sands with small amounts of clay minerals (illite, kaolinite, and chlorite) and organic matter. Given their purely siliceous nature and the absence of carbonates, the soils have a slightly acidic pH (pH~5.3). The salinity is very low (<35 µS/cm), as indicated by the chloride and sulphate content. The cation exchange capacity (CEC) is very low, at 1.8 ± 0.6 cmol/kg [65].

2.2. Prescribed Fire Plots

Prescribed burns were carried out in 100 × 100 m plots in 2020 and 2022 in the scrubland (37°1′9″ N, 6°29′5″ W, Figure 1). The shrub layer was the main fire-spread vector, and the main constituting species were *Halimium halimifolium*, *Ulex australis*, *Stauracanthus genistoides*, *Cistus salvifolius*, *Cistus libanotis*, *H. commutatum*, *Salvia Rosmarinus*, and *Lavandula stoechas* (Figure 2). We considered the first prescribed fire the one that was applied between the 7 and 10 November 2022 because soil respiration was measured during one year immediately following this fire. The prescribed burns in 2020 were carried out between the 24 and 26 October 2020, and soil respiration was measured between March 2022 and November 2022, thus constituting the second year after burning.

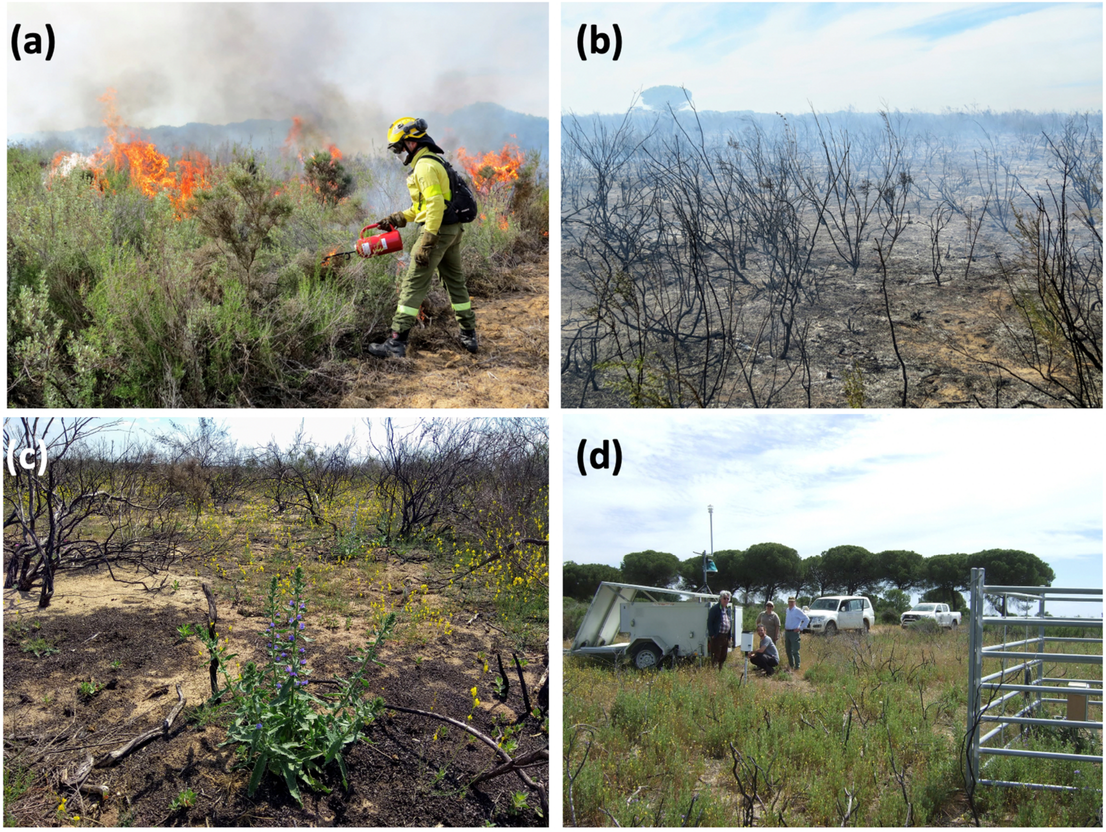

Figure 2. Series of photos during the study period: (**a**) while burning the plots, (**b**) one day later, (**c**) the first spring after the fire, and (**d**) the second spring after the fire.

Prescribed burns were conducted by the Andalusian Forest Fire Service (INFOCA) who monitored the main environmental parameters (temperature, relative humidity and wind speed), as well as the main characteristics of the fire (fire rate of spread and flame length) [64]. The goal of the prescribed burning was to have a fire with a low severity, and its characteristics were as follows. The evaluation of visual indicators of soil burn severity [69] showed low severity values (level 1–2 and exceptionally value 3) corresponding to the consumption of the litter layer, partial or total consumption of the humus layer but no signal of consuming organic carbon in the soil, or the presence of high levels of white ashes [69]. The temperatures recorded in the soil by the thermocouples (type K, 1 mm diameter, datalogger DT500, Campbell Scientific Inc., Logan, UT, USA, https://www.campbellsci.com (accessed on 15 October 2024)) located at different depths (leaf litter layer, humus layer and mineral soil; 2, 5 and 10 cm depth) at 5 points (center and corners of a 33 × 33 m central plot avoiding border effect) showed that high values that would be expected to affect the characteristic properties of the Doñana shrubland soil were not reached. Maximum temperatures of between 95 °C and 434 °C were recorded between the leaf litter and humus layers. However, low temperatures (<50 °C) were recorded in the mineral soil (at depths of 2–5 cm below the humus layer) at all measured sites (n = 15) except one, at which the temperature reached 176 °C. In all cases, the maximum temperatures were maintained for less than one minute. Thus, these temperature values (<100 °C in the mineral soil) fall into the "low" category of fire severity in the burned plots, which is typical of prescribed fires [64]. For comparison, soil temperatures (above the humus layers) of up to 55 °C were recorded during the central hours of the day in a similar scrubland in Doñana during the hottest days of summer [70].

2.3. Field Measurements of CO_2 Concentration

The CO_2 concentration measurements were recorded consecutively in two of the 100 × 100 m burned plots, as well as in the nearest unburned areas, which were used as controls (Figure 1). First, starting on 11 November 2022, we measured CO_2 concentrations, beginning just after burning the 2022 plot and continuing for one year (fall, winter, spring, summer and fall, until the end of September 2023); second, we measured the CO_2 concentrations in the burned plot in October 2020, during the spring, summer and fall one year after it was burnt (from March 2022 to 6 November 2022). In the first case, we set up four automated soil CO_2 flux chambers (LI-COR 8100, LI-COR Inc. Lincoln, NE, USA), two in the burned plots and two in the unburned plots; in the second case, only three flux chambers were available, two in the burned plot and one in the control plot. Because the location of the burned areas is in the middle of the National Park, all the devices depended on a solar panel generator and a remote control system (Figure 3). The chambers in the same treatment were around 3 m apart, and the distance between the chambers in the burned and unburned areas was around 20 m. A 20.3 cm diameter collar for each chamber was inserted deep in the soil, protruding from the soil by between 2 and 5 cm.

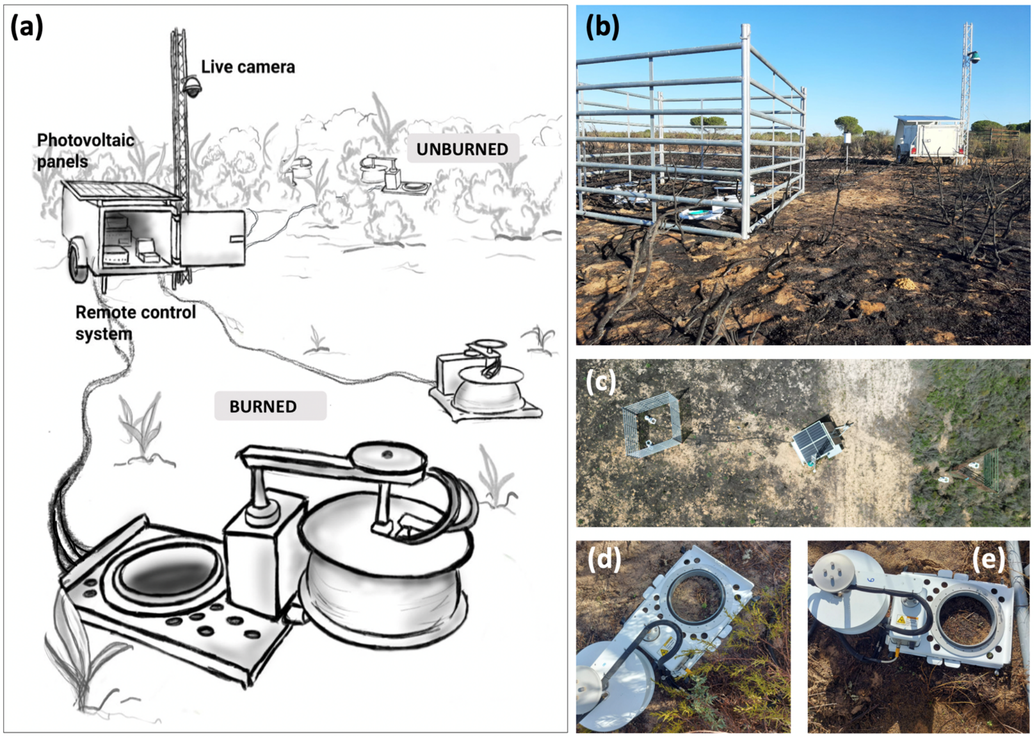

Figure 3. Schematic representation (**a**) and photos (**b**–**e**) of the continuous monitoring setup using automated soil CO_2 flux chambers (LI-COR 8100, LI-COR Inc. Lincoln, NE, USA), in the burned and the nearest unburned plots, connected to solar panels. The chambers alternatively measure CO_2 flux; in (**a**) the front chamber in the burned plot is open and not measuring, while the second chamber is closed and measuring. Photos show the front view (**b**) and bird's eye view (**c**) of the whole installation, and chambers in unburned (**d**) and burned (**e**) plots.

Prior to installation, the gas analyzer of the chambers was calibrated by LI-COR Inc. using precision gasses at controlled temperatures. The calibration function for CO_2 was adjusted by a rectangular hyperbola that also corrects for temperature and pressure, as well as band broadening and cross-sensitivity to water vapor. On the other hand, water vapor was calibrated using a third-order polynomial that also corrects for pressure and temperature. The infrared gas analyzer optical bench zero and span can drift over time with changes in temperature, cleanliness of the optical bench, and other factors. Setting of the zero and span was performed in the instrument measurements to ensure the analysis conformed to proper values, followed by monthly checking to ensure no deviations from the standard calibration.

The CO_2 concentration was recorded every second for each chamber, consecutively. The chamber temperature and pressure, water vapor mole fraction, relative humidity and other variables were simultaneously measured in the equipment to perform the water content correction of the CO_2 concentration values.

2.4. CO_2 Concentration and Soil Respitration Data Processing

Using SoilFluxPro software (version 5.2.0, LI-COR Inc. Lincoln, NE, USA), the CO_2 concentration values were water-corrected, and the dry CO_2 flux was obtained by linearly fitting the dry CO_2 concentration as a function of time. Thus, the linear fit of the increment of CO_2 in the volume of the chamber was positive (CO_2 efflux), and it was measured in μmol/m^2·s. Herein, CO_2 efflux will be called soil respiration. Therefore, we obtained one value of soil respiration every 12 min for each chamber, after allowing for a purge time of 10 to 15 min. The data were cleaned prior to analysis in order to remove inconsistent values or errors. This resulted in 16,782 adequate observation values, which constituted the robust dataset we analyzed (Supplementary Materials, Figure S1). The data were categorized according to the seasons as follows: spring (March to May), summer (June to August), fall (September to November), and winter (December to February). Because the prescribed fire occurred starting November 2022, the fall just after burning comprised the data of November following the fire (from 11 November to the end of November). The months were also categorized according to the growing season (the wet months: from November to May) and the non-growing season (the dry months, from June to October). The daily variation was represented by a variable that divided day hours (when plants are active) and night hours.

2.5. Statistical Analyses

First, we performed a preliminary analysis to know whether there were differences in the flux of the three control chambers. Because there were 2 chambers in the 2022 control plot and one chamber in the 2020 control plot, we carried out a pairwise comparison using *t* tests. The mean values of the 2022 flux control chamber were between the 2023 mean values (Figure 4).

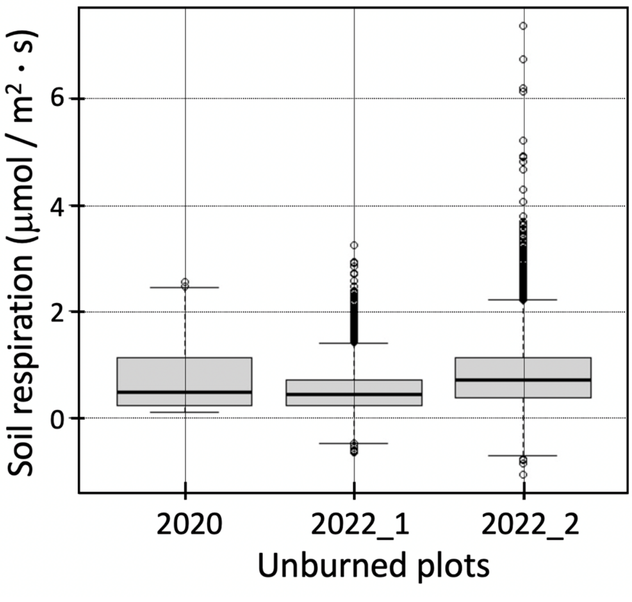

Figure 4. Box-plots showing soil respiration values from the three control chambers, the two in the unburned plots from the 2022 prescribed fire and the one in the unburned plot burned from the 2020 prescribed fire.

The effects of the fire and its interactions with the season, the growing season and the daily variations in soil respiration were explored using three similar independent linear mixed models. In all models, the soil respiration data (µmol/m^2·s) were the dependent variable. The fixed independent variables were the burning status of soils with two categories (burned and unburned), and in each model, a second variable was selected: either the seasonal variable with eight different categories (fall, winter, spring and summer of the first year after the burning; fall, spring, and summer of the second year and fall of the third year after the burning); the daily variation with two categories (day and night); or the growing season with two categories (growing or not-growing, as described before). Additionally, the interaction between the burning status and one of these three variables was included in each model. Finally, we used the chamber identity as a random effect variable in all models, in order to account for the covariance of different measures coming from the same chamber (temporal and spatial autocorrelation of continuous measurements). This analysis was performed with the *glmer* function of the lme4 package [71] in R v4.2.2 software.

Because the data did not follow normality assumptions (we used the Anderson–Darling test, Jarque–Bera and Kolmogorov–Smirnov with Lillieford correction tests, and Levene's tests for homoscedasticity), we tested which distributions and/or transformations and link functions of the models had the lowest AIC values. We finally selected a linear mixed-effects model with the gaussian distribution and identity link function, after the transformation of soil respiration data by centering and scaling it using the *center* and *scale* functions in R v4.2.2 [72]. Because we were interested in the effects of the prescribed fire, we further explored the significant differences of each model with a post hoc analysis using the function *emmeans* in R v4.2.2 [72], with Tukey pairwise comparisons. We explored the differences between burned and unburned treatments within seasons, growing seasons and daily times, and the differences among seasons or between growing seasons or daily times, in the control plots and in the burned plots.

Finally, we performed a specific linear mixed model to test the differences between the soil respiration values using only soil respiration values from only the three fall seasons (just after burning, and one and two years after burning). The model was similar to those described above except that the season had only these three categories.

3. Results

3.1. Effects of the Seasons

When we analyzed the differences between burned and unburned plots, we found that soil respiration showed significant differences between the burned and control soils (Table 1a). Similarly, soil respiration was significantly different between seasons (Table 1a). Finally, the interaction between the two factors, the fire treatment and the season, was also significant (Table 1a, Figure 5a). The soil respiration values varied between seasons, and the values in the burned plots closely followed the values in unburned plots.

The first variable in the model was the season, and in general, there was a trend along the study period, but not a seasonal pattern per se (Figure 5a). Post hoc analysis detected significant differences in the low values of soil respiration in the winter and spring just after fire compared to the higher and increasing values in the following summer, fall and spring (summer1, fall2 and spring 2 in Figure 5a); the soil respiration values decreased afterwards in the two last seasons: summer of the second year after fire and the fall three years after fire (Figure 5a).

In the model, the significant interaction term (between season and the burning treatments) means that the seasonal pattern in the burned areas is different than the one in the unburned areas. In this case, the variation among seasons in the burned plots follows a similar pattern to that in the unburned plots, but the peak of soil respiration values was in the second fall after fire (Figure 5a). In fact, with regards to the effect of fire within seasons, post hoc analysis detected higher values in burned plots with respect to unburned plots only in fall one year after fire ($p < 0.001$), and nearly significant differences for the values of the first summer after fire ($p = 0.060$, Figure 5a).

Table 1. Effects of the prescribed fire and its interactions with the seasons (**a**,**b**), the growing season (**c**), and the daily variations (**d**) on the soil respiration. The statistics χ2 and *p* correspond to the type II-ANOVA, Wald chi-square tests of the linear mixed models.

	Variables	χ2	*p*		χ2 [1]	*p* [1]
(**a**)	Fire	6.37	<0.001	(**b**)	6.89	0.009
	Season (8 and 3 categories)	5255.19	<0.001		377.03	<0.001
	Fire*Season	1492.03	<0.001		219.49	<0.001
(**c**)	Fire	4.85	0.028			
	Growing season	141.37	<0.001			
	Fire*Growing season	396.08	<0.001			
(**d**)	Fire	12.97	0.027			
	Daily variation	4.85	0.001			
	Fire*Daily variation	2.46	0.116			

[1] These statistics correspond to the model of the three fall seasons (the variable season with three categories). * indicates the interaction between the two variables.

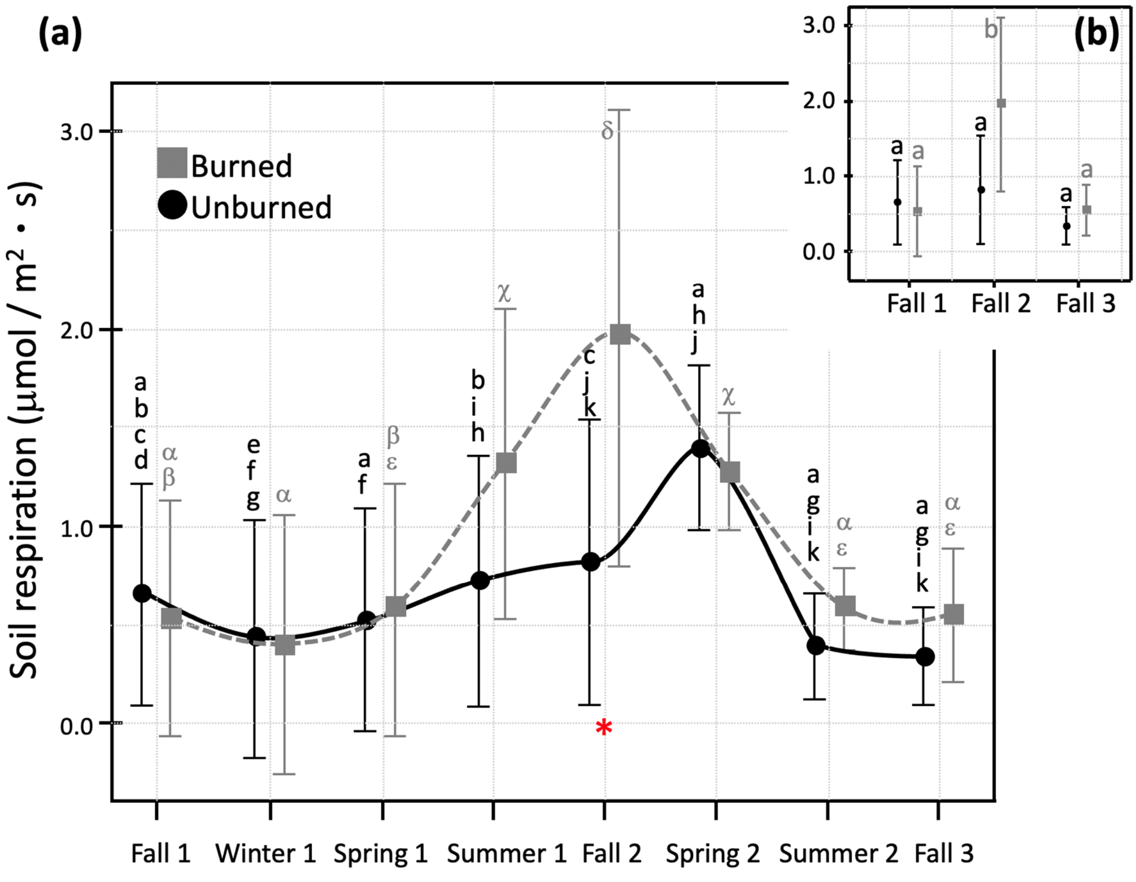

Figure 5. Differences in mean (and SD) soil respiration values between burned and unburned plots: (**a**) over the different seasons after the prescribed fires, and (**b**) among the three fall seasons after the prescribed fire (Fall 1: fall just before the prescribed fire, Fall 2: the fall one year after fire, Fall 3: the fall two years after fire). In (**a**), asterisks indicate a significant difference between burned and unburned plots within each season; means with the same letter did not show significant differences among seasons (Latin letters for control plots and Greek letters for burned plots). In (**b**), means with the same letters did not show significant differences among fall seasons.

When comparing the fall just after burning with the fall one year and two years later, we found that soil respiration showed significant differences between the burned and control soils (Table 1b). Similarly, soil respiration was significantly different between seasons (Table 1b). Finally, the interaction between the two factors, the fire treatment and the season, was also significant (Table 1b, Figure 5b). Post hoc analysis showed no differences in soil respiration values between the three control plots ($p > 0.110$), while in the burned plots, the second fall after fire showed the highest soil respiration values compared with the fall just after fire and the fall three years after fire. In fact, the soil respiration values of the burned plot from the second fall after fire were significantly higher than the values of the rest of the burned and also unburned plots ($p < 0.011$ in all these cases, Figure 5b).

3.2. Effects of the Growing Season: Dry and Wet Periods

In this model, we corroborated previous results regarding the effect of fire on soil respiration values: soil respiration values showed significant differences between burned and control plots; and values were higher in burned areas than in unburned areas (Table 1c, Figure 6a). Soil respiration values were significantly different between growing seasons (Table 1c); in the control plots, values were significantly higher in the wet season than in the dry season (post hoc analysis, $p < 0.001$, Figure 6a). Finally, the interaction between the two factors, the fire treatment and the growing season, was also significant (Table 1c, Figure 6a). Soil respiration values varied between the two growing seasons, but the values differed between burned and unburned plots. Using the post hoc analysis, we detected that in the wet season, there were no differences between soil respiration values in the burned and unburned plots ($p = 0.954$), while in the dry season, there were differences between the burned and unburned plots ($p = 0.019$): soil respiration values were higher in the burned plots than in the unburned plots (Figure 6a). Moreover, values in the burned plots were significantly higher in the dry season than in the wet season ($p < 0.001$, Figure 6a).

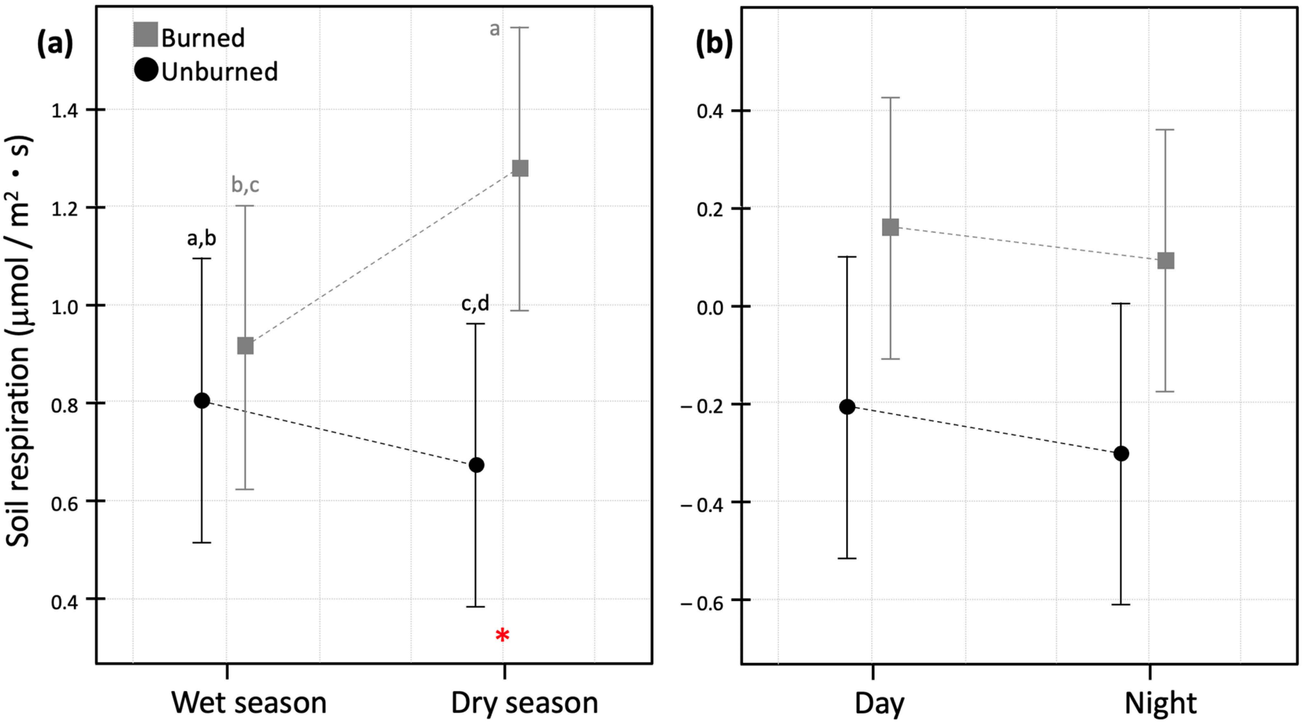

Figure 6. Differences in mean (and SD) soil respiration values between burned and unburned plots: (**a**) in the growing season (wet) and non-growing season (dry), and (**b**) during the day and at night. Asterisks indicate significant differences between burned and unburned plots within each category; means with the same letters did not show significant differences.

3.3. Effects of the Daily Variations: Day and Night

The model of the daily variation in values of soil respiration showed again that the soil respiration values were significantly different between the burned and control plots (Table 1d), and that the soil respiration values were significantly different during the day and at night (Table 1c). However, in this case, there were no significant differences in the interaction between the two factors, showing that the same trend was found in the burned and unburned plots (Table 1c, Figure 6b). First, soil respiration values were higher in the burned than in unburned plots, both at night and during the day; and second, the values were higher during the day than during the night in both the burned and unburned plots (Figure 6b).

4. Discussion

We wanted to assess the effect of low-intensity prescribed fires on soil respiration in sandy soils in Doñana National Park. Our results showed that soil respiration changed seasonally, and the values in burned plots closely followed the respiration in unburned plots during the two years after fire. The CO_2 flux in the burned plot was significantly higher than in the unburned plot only in the fall one year after fire, which corresponded mainly to the end of the dry season; the rest of soil respiration values did not differ significantly from the values in the unburned plots.

We expected variations in soil respiration just after fire and after the first year after fire, as previous studies in the area showed significant effects of the prescribed fire in different soil components after the first year. Specifically, significant increase in fungus communities, such as saprotroph activity, was observed during the first six months after fire [64]. In addition, significant alterations in soil variables, such as pH, N, K and P, have also been observed, but most of these parameters recovered one year after the burning [42,64]. However, we did not find that soil respiration was modified just after fire, but around one year later, and for a short time (one season), before recovering to previous values.

Variation in soil respiration after fire, including both increases and decreases in respiration values, is supported by other works, such as [42,46,60,73,74]. For example, Muñoz-Rojas et al. [42] showed significant changes in microbial communities in the first year after fire when soil nutrients become available. Fuentes-Ramirez et al. [31] also reported that one year after the fire, the soil nutrients N, P and K significantly increased, as well as the abundance of bacteria and fungi, and microbial activity. Fire-generated necromass can serve as a substrate for the surviving organisms. On the other hand, autotrophic soil respiration can decrease due to root mortality shortly after the fire [74], but the heterotrophic soil respiration increases owing to the probable faster recovery of microbial biomass compared to the vegetation growth after the event [42,75]. In pine plantations in the Sierra Nevada, USA, experimental burning reduced soil respiration by approximately 14% at 5 months after fire [62]. The author suggested that burning results in an increased relative contribution of heterotrophic respiration to total soil respiration. Thus, our observations of no significant changes in soil respiration after burning during the first year could be explained by a reduction in autotrophic soil respiration due to root mortality that could have been compensated by the increase in heterotrophic soil respiration due to the increase in fungus activity detected during the first year [64].

Moreover, the prescribed fire in our study did not reach high temperatures (no more than 50 °C in the soil). It has been reported that when the severity of the fire is low, controlled burns in Mediterranean maquis, pine forests and oak forests do not have significant effects on belowground respiration up to two years after fire [76–78]. In particular, the low conductivity of sand grains in semi-arid ecosystems could act as a thermal insulator and inhibit heat penetration into the soil, lessening fire effects in these soils [76]. This work also suggested that the high resistance of endemic species to water stress and high temperatures led to their rapid recovery. This could explain why in Doñana at one year after burning, the respiration did not significantly increase or only slightly increased, and not drastically, as occurs when the fire intensity is high (e.g., [76]). In other ecosystems, such a Swiss chestnut forest, the authors also showed that a low fire intensity had no significant effect on soil respiration or microbial biomass, but a higher-intensity burning with double the fuel load increased soil respiration from the first 20 h after fire and for the next 6 months, when it returned to the pre-fire level [77]. However, the goal of prescribed fires at Doñana National

Park is to prevent and protect the area from fire, and at the same time, have a low impact on the soils. Our results show that soil respiration seems to be resilient to prescribed fires of low severity, at least during the first year after burning.

After one year without significant changes in soil respiration values between the burned and unburned plots, we observed a sudden significant increase in these values in the following fall, one year after the fire and at the end of the first dry season. This could be due to the recovery of the fungus community [64], acting in synergy with the likely recovery of the rhizosphere that accompanies plant biomass regrowth. In fact, continuous monitoring of the CO_2 efflux from the soil over two years allowed us to observe seasonal variations (e.g., [78]) owing to the possible control that soil moisture and temperature have on this flux (e.g., [44,79]). Effectively, the main factors controlling CO_2 flux in Mediterranean ecosystems seem to be temperature and soil moisture (e.g., [43–45,80–83]), which are inversely related in these ecosystems: maximum temperatures coincide with minimum precipitation and soil moisture [44]. At the ecosystem level, temperature is one of the best predictors of soil respiration, followed by precipitation, and can be explained by the differences in vegetation types [84]. It has been highlighted that the fire effects on soil respiration could also be dependent on the microclimatic conditions [84,85]. However, in relation to the growing seasons, differences between warm and cold seasons or between dry and wet seasons have been shown. For example, it has been shown that the temperature dependency of soil respiration is higher during the warm season than in the cold season (e.g., [83]). With respect to the effect of fire, ref. [57] showed that the soil respiration was more affected by fire during the wet season than in the dry season. Although we found higher values in the wet season compared to the dry season, this occurred only in the control plots. In contrast, in the burned plots, the soil respiration values were higher in the dry season than in the wet season. It could be that the effect of soil temperature was predominant over other factors, such as in [83], and that temperature was very high because vegetation cover was burned and the remaining ashes darkened the sandy soils, resulting in higher soil temperatures during the dry season than in the control plots where scrubland provided vegetation cover (see Figure 2a).

Daily variation has been much studied, especially in order to assess the reliability of snapshot measurements of soil respiration (e.g., [86]). The day–night pattern detected is explaining by both the absence of plant activity and the higher temperatures that are normal during the day. Although the soil respiration values were higher in the burned areas compared to unburned areas, this effect was independent of the day–night pattern.

The study of soil respiration as a measure of ecosystem response after burning is an issue that needs to be studied more thoroughly, considering the characteristics of the prescribed fire and the specific vegetation and fauna, as well as the climatic conditions of each ecosystem, as not all ecosystems respond in the same way. Although assessing fire effects on gas effluxes from soil seems to need the consideration of multiple factors such as the characteristics of the prescribed fire and the microclimatic conditions of each ecosystem, we attribute the increase in soil respiration to the survival and recovery of the rhizosphere and plant biomass regrowth around one year after the fire. Additionally, it could be explained by the high resilience of the micro- and macrofauna, as similarly occurs in fire-prone pine ecosystems [87]. Belowground organisms and microorganisms should follow similar trends after burning, with their fast recolonization possibly enhanced due to favorable changes in soil properties, such as nutrient availability. However, further analyses on soils would be needed to accurately explain the increases in soil respiration and the final consequences of prescribed fire on the ecosystem.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land13101706/s1. Figure S1: Soil respiration values (CO_2 efflux values) and temperature values obtained from the automated soil CO_2 flux chambers at the soil surface.

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draft preparation, M.C.R.-T.; writing—review and editing, M.C.R.-T., E.A., R.C.S., J.M., F.S.-R., X.C. and J.C.; visualization, M.C.R.-T., E.A., R.C.S., X.C. and J.C.; supervision, J.C.; project administration, J.C.; funding acquisition, X.C. and J.C. All authors have read and agreed to the published version of the manuscript.

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