



Effect of tree harvest, silvopastoral practices, and microclimate conditions on forest floor CO₂ efflux in a sessile oak (*Quercus petraea* agg. [Matt.] Liebl.) forest

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Abstract

Key message Forest floor CO₂ efflux (R_f ; consisted of soil and potential vegetation) increased after forest harvest, but this response was changed by actual weather (especially drought and rains).

Context Soil respiration is a large source of CO₂ released to the atmosphere and is sensitive to forest management practices and weather.

Aims To determine effects of harvest, ancient practices and weather in a newly established coppice forest on R_f .

Methods R_f , temperature, and moisture were measured during 1 year before and 2 years after harvest.

Results Pasturing and raking had no effect on R_f . It tended to increase during the first season after harvest. In the second year after harvest, differences in R_f between control and harvested plots became much greater because of intensively developing herbaceous vegetation on harvested plots. No difference between the control and harvested plots was found during severely dry conditions. Following intensive rain pulses, R_f was larger in the control than in the harvested plots.

Conclusion Findings indicate that the R_f response is not uniform in time and depends on microclimate, particularly on soil moisture. This may be crucial for estimation of the harvest impact on soil processes especially under changing climate.

Keywords Harvest · Litter raking · Pasture · *Quercus petraea* · Soil respiration · Soil water content

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1 Introduction

Forest ecosystems are considered to be substantial carbon sinks, as they bind more carbon dioxide (via photosynthesis) than they release into the atmosphere (by respiration). Therefore, these ecosystems may retard CO₂ accumulation in the atmosphere and, hence, climate change. Carbon is stored mainly in tree biomass and in soil. Forest soils

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contain approximately 39% of the global soil carbon (Bolin et al. 2000), and soil respiration is the second-largest flux of carbon between terrestrial ecosystems and the atmosphere (Raich and Schlesinger 1992). On an annual basis, soil respiration can return over a half of carbon fixed by photosynthesis (Bond-Lamberty et al. 2018), and it contributes with more than 50% to total ecosystem respiration (Bolstad et al. 2004; Yuste et al. 2005).

Soil respiration consists of roots' respiration (autotrophic fraction) and that of microbes in the rhizosphere and in soil (heterotrophic fraction) (Kuzyakov 2006). The most important factors driving soil respiration in time are assumed to be temperature and soil water content. The relationship between temperature and soil respiration is described as exponential (Davidson et al. 2006). Soil water content has the strongest impact especially under conditions when soil moisture is low, resulting in substrate limitation of the respiration (Suseela et al. 2012), or too high, when it causes oxygen supply to be limited (Freeman et al. 2001). The first case may actually be strongly connected to the dry weather occurring more frequently in relation to climate change (IPCC 2018). Under dry conditions, soil moisture becomes the driving factor because soil respiration may then become independent of temperature (Yuste et al. 2003). The threshold at which volumetric soil water content becomes the driving factor for soil respiration is in the range between 12 and 15% (Xu and Qi 2001; Yuste et al. 2003; Darenova and Čater 2018). Therefore, with changing climate, soil moisture is becoming more and more important as a factor influencing temporal patterns of soil respiration that may affect current estimations and models based on preceding climate conditions.

Carbon flux in forest ecosystems is very sensitive to disturbances and forest management. Forests are usually a substantial sink of CO₂ but clearcut result in rapid reversal to become a large CO₂ source (Larson and Axelrod 2017). Despite that new assimilation ceases to be a supply for tree root respiration, microbial respiration increases severely after harvest (Londo et al. 1999; Mayer et al. 2017; Darenova and Čater 2018; Čater et al. 2021) and results in large losses of long-term accumulated soil organic matter (James and Harrison 2016). Such CO₂ losses from soils of harvested areas, therefore, contribute substantially to increase of CO₂ concentration in the atmosphere (Van Der Werf et al. 2009). The current climate with frequent dry periods may, however, reduce soil carbon losses after harvest.

Sessile oak (*Quercus petraea* agg. [Matt.] Liebl.) forest are widespread at altitudes in the Atlantic and Continental regions of Europe. This species readily colonizes anthropogenically disturbed sites, and it is expected to become more abundant under changing climate conditions thanks to its drought tolerance (Fitzgerald and Lindner 2013; Bobiec et al. 2018). Sessile oak has the ability to resprout from stumps shortly after the main tree has been cut. This

ability is used in the silvicultural management called "coppice." Coppicing was once a traditional method of forest management across Europe, but it nearly disappeared during the twentieth century (Sieferle 2001). Coppicing takes advantage of vegetative propagation and rapid regeneration of broadleaf tree species when shoots emerge from stumps shortly after the main tree has been cut (Evans 1992). This allows a short rotation time between consecutive harvests. Compared to trees emerging from seeds, coppiced individuals have roots already established from the previous generation and therefore grow faster than trees regenerated from seeds (whether planted or from natural regeneration) (Herrero et al. 2014). This may give coppice forests an advantage in severely drought-affected areas. On the other hand, the produced wood is not of the high quality and is used mostly as fuel wood. Moreover, the rotation time in coppice management is shorter than for high forest, and, therefore, the disturbance of soil resulting from harvest practices occurs more frequently and the soil is endangered by soil carbon and nutrient depletion (Šrámek et al. 2015).

Implementation of ancient silvopastoral practices into coppice forests, such as litter raking and livestock grazing, can be used to increase species' floristic diversity (Debussche et al. 2001), but decomposition of leaf and plant litter is the major pathway for transfer of nutrients between plants and soil. Therefore, removal of the litter or herbaceous vegetation leads also to altered organic substrate for soil respiration and soil microclimate, and even severe soil organic matter loss (Zhao et al. 2011). The silvopastoral system should be, therefore, well-managed and taking into account both advantages and negative impacts (Amézquita et al. 2010). Recently, these practices are little applied in Europe but they have been currently actively promoted in the EU (Rodriguez-Rigueiro et al. 2021), and they can be found rather in north-western or Mediterranean areas (McAdam 2005; Castro 2008).

This study focused on the response of forest floor CO₂ efflux (consisted of CO₂ efflux from soil and herbaceous vegetation; R_f) to harvest of a mature oak forest and the effect of pasturing and litter raking in a newly established coppice-with-standards stand. We were able to catch both severe drought conditions, which have recently started to occur frequently, and periods after heavy rain. These conditions have a strong impact on soil respiration, and therefore, it is necessary to determine their joint effect with forest practices. We hypothesized that (i) harvest would increase R_f through changing soil microclimate and developing herbaceous vegetation; (ii) litter raking would decrease R_f only during the first year post harvest, after which the litter on the non-raked plots would become more or less decomposed; and (iii) pasturing would have minimal effect on R_f .

2 Materials and methods

2.1 Site description

The study site is located at the Training Forest Enterprise Masaryk Forest Krtiny, within the Bilovice Forest District, in the southeastern part of the Czech Republic (49° 25' N, 16° 68' E). Elevation is 285–340 m a.s.l. The site is characterized by mean annual temperature of 9.9 °C and mean total annual precipitation of 534.0 mm (2015–2019).

The predominating tree species are sessile oak (*Quercus petraea* [Matt.] Liebl.), European hornbeam (*Carpinus betulus* L.), and European beech (*Fagus sylvatica* L.) between 26 and 66 years old and with average representation of 58.0%, 20.3%, and 14.0% of stems, respectively. There is also small admixture of *Tilia cordata* Mill., *Prunus avium* (L.) L., *Larix decidua* Mill., and *Pinus sylvestris* L. The stand height was around 13 m and standing stock volume 149 (± 32 , SD) m³ ha⁻¹ before harvest (Kadavý et al. 2019). Herbaceous vegetation in 2017 (before harvest) was very sparse, and dominant species were *Melica uniflora* Retz., *Carex pilosa* Scop., *Dentaria bulbifera* L., and *Carex digitata* L. In 2018, vegetation started to develop and consisted mainly of *Fallopia dumetorum* (L.) Holub, *Galium odoratum* (L.) Scop., *Melica uniflora* Retz., *C. pilosa*, *Scrophularia nodosa* L., *Eupatorium cannabinum* L., *Rubus idaeus* L. In 2019, the vegetation was dominated by *Coryza canadensis* (L.) Cronq., *R. idaeus*, *Galium aparine* L., *Hypericum perforatum* L., *C. pilosa*, and *M. uniflora*.

In 2017, soil analyses were carried out (Kučera et al. 2021) and soil was classified as Eutric Cambisols (Siltic or Loamic, event. Ruptic) altering with Stagnic Luvisols (Loamic, Ruptic). Humus form was classified according to French classification system (Jabiol et al. 1995) with dominance of Eumoder (48%), followed by Oligomull (22%) and Hémimoder (12%). Remaining humus forms (Dysmull, Amphimull and Dysmoder) represent ca 18%. The obvious

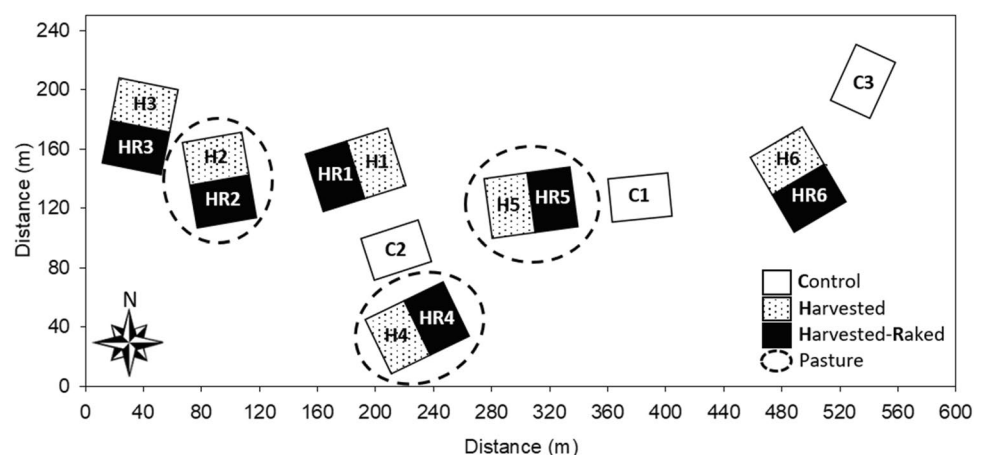
forest floor heterogeneity with thickness 4 cm in average and 11 cm in maximum was given by such local conditions as tree species composition under which the humus form developed and by microtopography. The pH (H₂O) of the soil was 5.58, C/N ratio 15, the organic carbon and total nitrogen was 4.56 and 0.31%, respectively, and the phosphorus content was 45.3 mg kg⁻¹.

2.2 Experimental design

In 2017, fifteen plots (30 × 40 m) were established within the forest stand (Fig. 1). The three plots were left undisturbed as a control, the trees on the remaining plots were harvested in March 2018, and all the plots were fenced. Harvest was carried out also on a 20 m buffer zone around each harvested plot. The harvest intensity was 88% of the stock volume and 92 oak standards left per hectare with regular spacing, and the harvest increased canopy gap fraction from 13 to 88% (Darenova and Čáter 2020). On three plots, litterfall was raked and completely removed in April 2018 and 2019. These raked plots were always adjacent to one non-raked one. Total weight of litter dry mass removed was 30.5 t ha⁻¹ in 2018 and 1.4 t ha⁻¹ in 2019. Three of the harvested plots were pastured between June and September 2018 and between June and October 2019 by a small sheep flock rotated from plot to plot. At first in 2018 there were just 4 sheep for 14 days per plot, but the impact was small. Therefore, the number of sheep was increased to 6 and the time they stayed at one plot was set to 10 days. In 2019, there were 8 sheep for 14 days per plot.

In such manner, we obtained five treatments (each with three replicates): undisturbed control plots (C), harvested plots (H), harvested-raked plots (HR), grazed H, and grazed HR (Fig. 1). On each plot, eight permanent measurement positions were established in a row along the longitudinal center line with 4.5-m spacing between permanent measuring points. Thus, there were 120 positions in total.

Fig. 1 Arrangement of the experimental plots. In 2017, the entire area was covered with the same type of forest. In the beginning of 2018, (H) and (HR) plots were harvested. In March 2018, complete litter raking was carried out on HR plots. The circled plots were pastured in summer 2018 and 2019. Control plots (C) were left wholly undisturbed



2.3 Forest floor CO₂ efflux measurements

Forest floor CO₂ efflux (R_f), consisted of CO₂ efflux from soil and potential aboveground biomass, was measured at the permanent positions using a Li-8100 portable non-steady-state through-flow system (Li-Cor, Lincoln, NE, USA) with an opaque 20-cm survey chamber. To ensure sealed connection between soil and the survey chamber, the PVC collars 20 cm in diameter and 15 cm in height (to keep potential vegetation inside the chamber during measurement) were installed 3-cm deep into the soil 1 week prior to the first measurement in each year. The collars were removed before the harvest and raking. The beginnings and ends of all lines were nevertheless visibly marked by small colored stakes to keep the location of the lines and positions as near the same as possible. It was not possible to place collars for CO₂ efflux measurement while excluding the vegetation. No plants were, however, removed from the collars as it would have substantially disturbed the soil, and that could have biased the results. If the vegetation exceeded the height of the chamber (in the second year after harvest), it was gently fold in the chamber space to avoid any damage. Beginning 15 s after chamber closure, CO₂ concentration was measured repeatedly at 1-s intervals for 1 min. CO₂ efflux was calculated using a linear fit of this continuous increase in CO₂ concentration.

The measurements were carried out on a monthly basis during three campaigns in 2017 (26 June, 7 August, and 29 August), eight campaigns in 2018 (23 April, 21 May, 15 June, 20 July, 16 August, 5 September, 18 September, and 15 October), and six campaigns in 2019 (30 April, 30 May, 26 June, 26 July, 27 August, and 24 September). One round on 120 measurement positions was performed on these days between 8 a.m. and 1 p.m. and the sequence of the measured plots was the same during each campaign. The sequence of three small plots and six large plots was divided into three triplets and each triplet contained one control plot and two plots harvested in 2018 (one with and one without pasture) to ensure regular distribution of categories in time. The numbering of the plots (C1-C3 and H(R)1- H(R)6) corresponds with the measurement order.

2.4 Ancillary measurements

During each R_f measurement, soil temperature at a depth of 1.5 cm (TPD32 penetrate thermometer, Omega, Stamford, CT, USA) and soil volumetric water content (SWC) in the profile of 0–6 cm (ThetaProbe ML2x, DeltaT Devices, Cambridge, UK) were measured at one and three positions, respectively, at approximately 5 cm outside each collar.

Air temperature and precipitation were measured and automatically recorded at 1-h intervals using an automatic climate station (EMS Brno, Czech Republic). The station was situated about 500 m from the studied site above a 5-m-high coppice stand.

When herbaceous vegetation started to develop after harvest, photos of each measurement position were taken during every campaign.

2.5 Data analyses

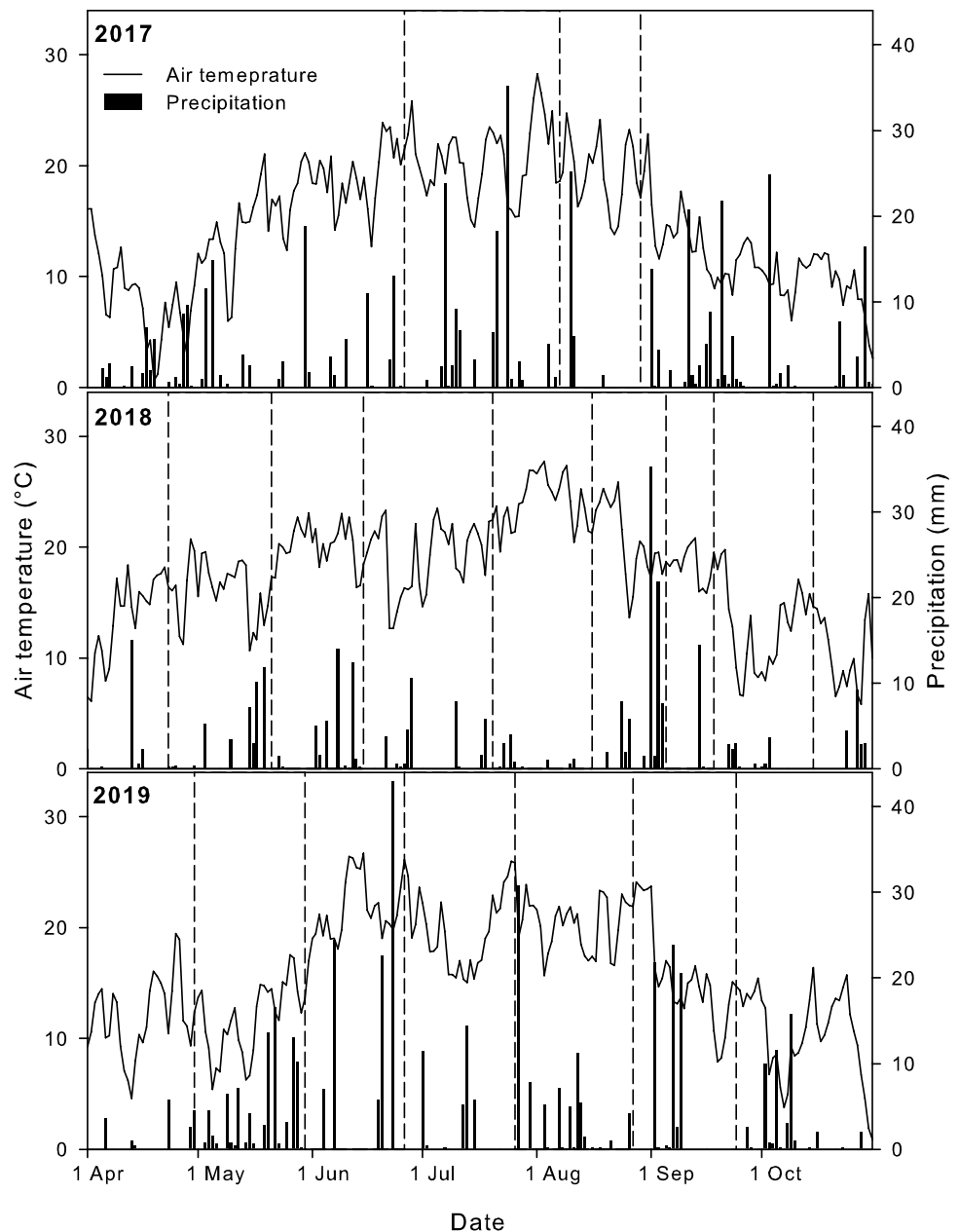
The herbaceous vegetation coverage was determined from the photographs as the percentage proportion of green color within the area of each collar using automated ruleset-based processing in the eCognition Developer software. For each measurement day, R_f was plotted against the vegetation coverage and CO₂ efflux with no vegetation (R_{nv}), which would match with soil CO₂ efflux, was determined as the intercept of the linear fit.

Data were tested for normal distribution (Shapiro–Wilk test). When confirmed, the effects of individual treatments on forest floor CO₂ efflux and SWC were evaluated using *t*-tests at each measurement day. As no effect of pasture was detected, the plots with and without pasture were grouped together. The effect of harvest was then investigated by comparing control and harvested non-raked plots and the effect of raking by comparing harvested non-raked and raked plots. The statistical analyses were made using SigmaPlot 11.0 analytical software (Systat Software, San Jose, CA, USA).

A mixed model was used to assess the change in forest floor CO₂ efflux (R_f) based on treatment and microclimate. The following continuous variables were chosen as potentially significant: volumetric soil water content (SWC), soil temperature (Soil.Temp.) and vegetation coverage (Veg.Cov.). The factor variables chosen were type of treatment (control, harvested, harvested and raked, grazed harvested, grazed harvested, and raked) (Treat.). Data were collected in 3 years during 17 measurement campaigns between 2017 and 2019 on a total of 15 plots with 120 collars (8 collars per plot). After omitting incomplete data records, 1975 individual observations remained. Due to the exponential trend of R_f , it was necessary to linearize the model by logarithm. Due to poor numerical conditionality, it was necessary to standardize continuous variables. For fixed effects, a full quadratic model of continuous variables with interactions was first selected. Both factor variables were then added to the model. The random slopes of continuous and factor variables grouped by plots and random intercepts grouped by measurement year, day, plot, and collar were chosen as random effects. The model was gradually reduced by omitting the least significant term in the formula. The final version of the model form can be written as follows:

$$\ln(R_f) \sim + \text{Treat.} + \text{Soil.Temp.} + \text{SWC} + \text{SWC}^2 + \text{Veg.Cov.} \\ + (\text{Treat.} + \text{Soil.Temp.} + \text{SWC} + \text{SWC}^2 + \text{Veg.Cov.} + ||\text{Plot}) \\ + (1|\text{Year}) + (1|\text{Day}) + (1|\text{Collar})$$

Fig. 2 Mean daily air temperature and precipitation over three experimental growing seasons. Dashed lines indicate days when measurements of CO₂ efflux were carried out



The analysis was performed in the Rstudio environment using the lme4 package (version 1.1–26), estimates of *P* values using the lmerTest package (version 3.1–3).

3 Results

3.1 Micrometeorology

Air temperature during the growing seasons (April–October) ranged between 0 and 30 °C, with maxima occurring in the summer months (Fig. 2). Sums of precipitation

were 449, 283, and 446 mm for the growing seasons in 2017, 2018, and 2019, respectively. Summer 2018 was extremely dry compared to the other 2 years, and precipitation in July and August only slightly exceeded 20 mm per month.

In 2017, when all plots were forested, mean seasonal difference of soil temperature from air temperature was between 4 and 7 °C (Fig. 3A). The smallest difference was during the first measurements and the differences increased as the day went on. Harvest decreased the difference between air and soil temperatures, and the mean differences ranged between 0.9 and 5.9 °C. In several individual cases, however, soil temperature was higher

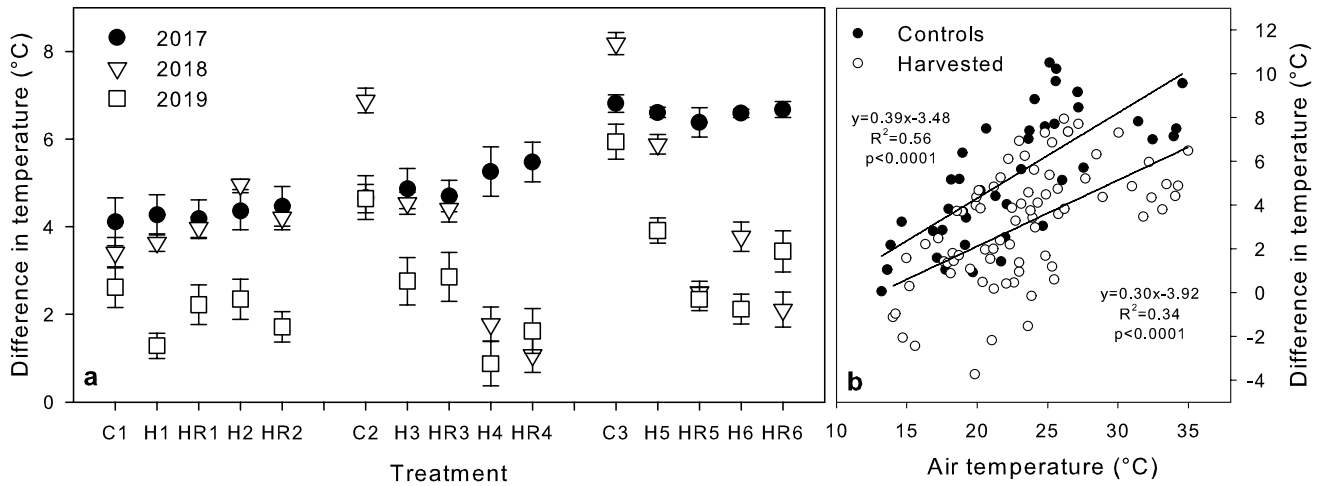


Fig. 3 Difference between soil temperature and air temperature. **A** Mean differences between temperatures on 12 plots in the studied forest. In 2017, the entire area was still covered with the same type of forest. At the beginning of 2018, H and HR plots were harvested. In spring 2018 and 2019, complete litter raking was carried out on

HR plots. Control plots (C) were left wholly undisturbed. Plots were divided into three groups in terms of measurement time, including 1 control and 2 of each H and HR plots. **B** Relationship between air temperature and difference in temperatures in control (C) and harvested (H) plots during 2018 and 2019

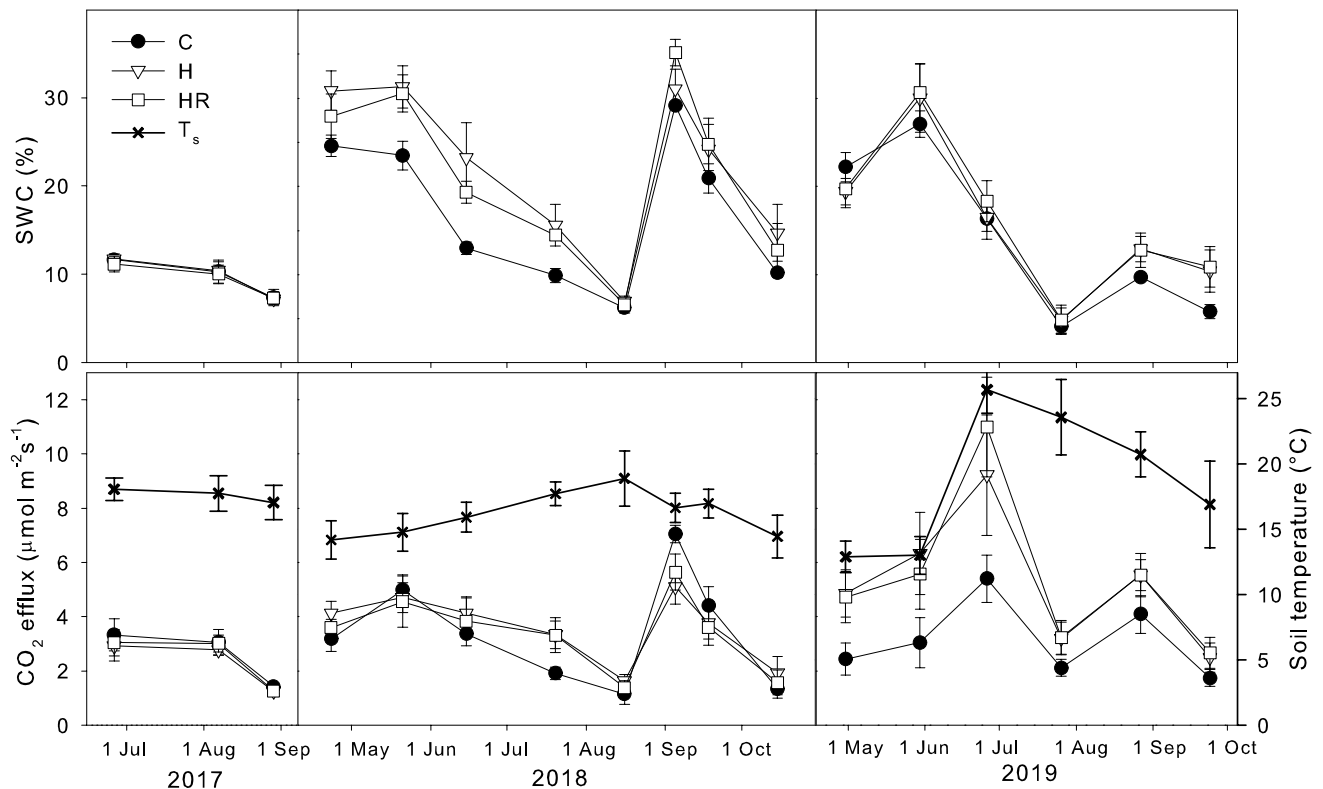


Fig. 4 Mean (\pm SD) soil temperature, soil water content (SWC), and forest floor CO₂ efflux in the control (C), harvested (H), and harvested-raked (HR) plots over three studied seasons. In 2017, the entire area was covered with the same type of forest. At the beginning

of 2018, H and HR plots were harvested. In spring 2018 and 2019, complete litter raking was carried out on HR plots. Control plots were left wholly undisturbed

than air temperature. When we analyzed all measurements separately at control plots (C1, C2, and C3) and harvested plots (H1–H6) during 2018 and 2019, we found that the difference between soil and air temperature significantly increased with air temperature (Pearson correlation, $p < 0.001$; Fig. 3B).

Soil water content in 2017 was only around 10% and did not differ between future established variants (C, H, HR). Tree removal increased SWC compared to the control in 2018, especially until July (Fig. 4). During this time, differences were statistically significant ($p < 0.01$) and ranged in proportion between 25 and 80%. On 16 August 2018, during severe drought, there were no difference between treatments. Later on in 2018 and 2019, however, SWC in the harvested plots was higher compared to the control. Nonetheless, statistical significance was confirmed ($p < 0.05$) only during the last two measurements in 2019.

When comparing H and HR plots, we observed that raking tended to decrease SWC in the first half of the 2018 season, with confirmed statistically significant differences determined on 23 April and 15 June. On 5 September, by contrast, soil moisture in the raked plots was significantly higher compared to the non-raked. Later on, SWC in these two treatments was almost identical.

3.2 Vegetation coverage

In 2017, herbaceous vegetation in the forest was negligible. The harvest in spring 2018 resulted in herbaceous vegetation's development from May (Table 1). During this year, the mean vegetation coverage reached as much as 20%. The next year, the herbaceous vegetation developed even more rapidly than in 2018, reaching higher values already during the first measurement on 30 April. Vegetation coverage peaked at the end of May and in June when its means exceeded 70%.

3.3 Forest floor CO₂ efflux

Forest floor CO₂ efflux (R_f) in the control plots ranged between 1.0 and 7.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ over three study seasons 2017–2019. During 2017, R_f remained low during all three measurements. It peaked at the beginning of September in 2018 and at the end of June in 2019 (Fig. 4).

In 2018, harvest increased R_f on most days, with R_f significantly larger ($p < 0.05$) in harvested plots compared to the control on 23 April, 15 June, and 20 July. We observed two cases, however, when R_f in the control plots was higher than in the harvested ones. On 21 May 2018, R_f in the control plots only slightly exceeded that in the harvested plots, but on 5 September 2018 the difference was highly significant ($p = 0.001$; Fig. 4). For the whole year 2019, R_f on the

Table 1 Forest floor CO₂ efflux (R_f), CO₂ efflux with no vegetation (R_{nv}), percentage contribution of R_{nv} to R_f , and percentage herbaceous coverage of the measured area on the control (C), harvested (H), and harvested-raked (HR) plots during three seasons. Harvest

Year	Date	R_f (\pm SD, $\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			R_{nv} ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$)		% R_{nv}		Vegetation coverage (\pm SE, %)	
		C	H	HR	H	HR	H	HR	H	HR
2017	26 Jun	3.32 (\pm 0.59)	2.91 (\pm 0.53)	3.04 (\pm 0.48)					0	0
	7 Aug	3.05 (\pm 0.46)	2.77 (\pm 0.19)	3.01 (\pm 0.31)					0	0
	29 Aug	1.42 (\pm 0.05)	1.25 (\pm 0.09)	1.26 (\pm 0.15)					0	0
2018	23 Apr	3.18 (\pm 0.46)	4.12 (\pm 0.43)*	3.59 (\pm 0.30)	4.12	3.60	100.0	100.0	0	0
	21 May	4.99 (\pm 0.54)	4.70 (\pm 0.54)	4.47 (\pm 0.84)	4.52	4.22	96.0	94.2	6.16 (\pm 1.44)	4.19 (\pm 0.99)
	15 Jun	3.36 (\pm 0.06)	4.12 (\pm 0.57)*	3.84 (\pm 0.90)	3.69	3.25	89.6	85.2	11.4 (\pm 2.56)	17.4 (\pm 3.54)
	20 Jul	1.91 (\pm 0.23)	3.33 (\pm 0.50)*	3.31 (\pm 0.64)	2.95	2.66	88.4	80.0	10.5 (\pm 2.32)	14.7 (\pm 2.54)
	16 Aug	1.14 (\pm 0.37)	1.51 (\pm 0.30)	1.38 (\pm 0.26)	1.41	1.43	92.2	103.7	16.5 (\pm 3.34)	8.99 (\pm 1.57)
	5 Sep	7.05 (\pm 0.31)	4.98 (\pm 0.62)*	5.64 (\pm 0.67)	4.70	5.48	93.9	97.2	16.5 (\pm 2.77)	21.6 (\pm 3.86)
	18 Sep	4.41 (\pm 0.68)	3.76 (\pm 0.59)	3.60 (\pm 0.66)	3.35	3.42	88.9	95.2	16.5 (\pm 2.77)	21.6 (\pm 3.86)
2019	15 Oct	1.34 (\pm 0.34)	1.92 (\pm 0.60)	1.57 (\pm 0.44)	1.92	1.58	100.0	100.0	0	0
	30 Apr	2.44 (\pm 0.59)	4.85 (\pm 0.87)*	4.71 (\pm 0.94)	2.97	3.34	65.9	70.7	59.4 (\pm 0)	52.7 (\pm 0)
	30 May	3.04 (\pm 0.91)	6.32 (\pm 1.51)*	5.56 (\pm 1.28)	3.74	2.79	66.4	51.5	69.8 (\pm 3.68)	80.1 (\pm 3.12)
	26 Jun	5.39 (\pm 0.87)	9.22 (\pm 2.22)*	11.0 (\pm 1.84)	5.57	7.57	60.6	68.1	61.4 (\pm 3.99)	82.1 (\pm 2.93)
	26 Jul	2.11 (\pm 0.30)	3.20 (\pm 0.59)*	3.22 (\pm 0.63)	2.21	2.51	71.1	77.8	32.1 (\pm 3.69)	40.2 (\pm 3.58)
	27 Aug	4.08 (\pm 0.69)	5.53 (\pm 0.57)*	5.53 (\pm 0.80)	4.95	5.11	90.5	92.4	25.2 (\pm 3.54)	22.4 (\pm 2.88)
	24 Sep	1.74 (\pm 0.30)	2.49 (\pm 0.54)*	2.67 (\pm 0.57)	1.98	2.50	79.9	92.3	33.6 (\pm 3.81)	36.8 (\pm 3.57)

was carried out at the beginning of 2018. Asterisks indicate statistically significant difference between control and harvested plots ($p < 0.05$)

Table 2 Estimates of the effect of individual parameters on forest floor CO₂ efflux obtained from the mixed model. Asterisks indicate significant effect (p value < 0.05)

Random effect group	Variable	Fixed effect estimate	Variance	Std. Dev	P value
Year	(Intercept)	–	$1.588 \cdot 10^{-8}$	$1.260 \cdot 10^{-4}$	–
Day	(Intercept)	–	$1.440 \cdot 10^{-1}$	$3.794 \cdot 10^{-1}$	–
Collars	(Intercept)	–	$1.234 \cdot 10^{-2}$	$1.111 \cdot 10^{-1}$	–
Plots	(Intercept)	1.09956	$3.510 \cdot 10^{-4}$	$1.874 \cdot 10^{-2}$	$*2.87 \cdot 10^{-10}$
	C	–	$1.353 \cdot 10^{-2}$	$1.163 \cdot 10^{-1}$	–
	H	0.21674	$4.696 \cdot 10^{-3}$	$6.853 \cdot 10^{-2}$	$*1.13 \cdot 10^{-5}$
	HR	0.17703	$1.420 \cdot 10^{-2}$	$1.192 \cdot 10^{-1}$	$*3.18 \cdot 10^{-2}$
	Grazed H	0.24013	$4.468 \cdot 10^{-3}$	$6.685 \cdot 10^{-2}$	$6.14 \cdot 10^{-2}$
	Grazed HR	0.18491	$3.652 \cdot 10^{-2}$	$1.911 \cdot 10^{-1}$	$4.38 \cdot 10^{-1}$
	Soil temperature	0.07281	$2.968 \cdot 10^{-3}$	$5.448 \cdot 10^{-2}$	$*7.18 \cdot 10^{-3}$
	Soil water content	0.09226	$3.712 \cdot 10^{-3}$	$6.093 \cdot 10^{-2}$	$*4.93 \cdot 10^{-3}$
	Soil water content ²	-0.04795	$6.966 \cdot 10^{-4}$	$2.639 \cdot 10^{-2}$	$*3.96 \cdot 10^{-3}$
	Vegetation coverage	0.16755	$2.828 \cdot 10^{-4}$	$1.682 \cdot 10^{-2}$	$*3.19 \cdot 10^{-7}$
Residual		–	$6.209 \cdot 10^{-2}$	$2.492 \cdot 10^{-1}$	–

harvested plots was significantly ($p < 0.05$) larger compared to the control. We found no difference in R_f between raked and non-raked plots on any date.

CO₂ efflux with no vegetation (R_{nv}) contributed 80–100% to R_f in 2018, the lowest values being in July when they reached 88% in harvested and 80% in harvested-raked plots (Table 1). In 2019, the vegetation coverage was higher than in 2018, and that led to a smaller contribution of R_{nv} to R_f , which ranged between 2 and 70% in the harvested plots and between 22 and 82% in the harvested-raked plots.

3.4 The mixed model

All treatments differed significantly except for the effect of grazing which was insignificant in combination with the other two treatments. The mixed model confirmed that R_f significantly increased after harvest, with soil temperature, SWC, and vegetation coverage. On the contrary, R_f also decreased with square of the SWC. This means that respiration did not depend linearly on SWC. The values of the estimated parameters and their variance are summarized in Table 2.

4 Discussion

Forest management practices affect many aspects of the carbon cycle. One of these is the rate at which CO₂ is released from forest floor (R_f). R_f in our study included CO₂ efflux from both soil and aboveground parts of understory vegetation which developed on the harvested plots. In the first year of measurement, when the whole study area was forested, there was no understory. Therefore, R_f consisted solely of soil CO₂ efflux. The

same can be said for control plots during the second and third years of measurement and for the first measurement after harvest (22 April 2018), as no vegetation had yet developed. When vegetation is developed, R_f includes also the respiration of aboveground biomass. That, however, bind CO₂ from the atmosphere by photosynthesis which was not caught with measurements using an opaque chamber. Therefore, the net CO₂ efflux differs from that measured. Soil component of the R_f was, however, dominant (Table 1).

We found no response of R_f to pasturing by sheep. Other studies have shown decrease in soil respiration (e.g., Chen et al. 2016; Wang et al. 2020) due to removal of herbaceous leaves and a decrease in photosynthesis (Liu et al. 2016) and thus diminished carbon intake into the ecosystem and carbon storage (Li et al. 2013). On the contrary, Shi et al. (2019) observed greater soil respiration on grazed plots during the wet period. Those authors explained this as plant compensatory growth stimulation of rhizospheric respiration following release from drought and grazing stress. Moreover, patches of stimulated soil respiration can occur due to inputs of manure and urine (Boon et al. 2014). Studies focused on the effect of pasture on soil respiration have been mostly investigated in grasslands and only rarely in a forest (e.g., Bahamonde et al., 2017). Moreover, such studies usually focus on long-term intensively grazed ecosystems while our study forest was grazed only for two seasons with low intensity, and this was not sufficient to be reflected in soil respiration.

Raking of leaf litter did not affect R_f in our study. Previous research had mostly shown decrease in R_{nv} after litter removal (Han et al. 2015; Gao et al. 2018; Yan et al. 2019). Litter is an important input of fresh organic material into soil, and its exclusion results in a

reduction of soil carbon (Bowden et al. 2014). We may assume that the absence of a difference in R_{NV} between raked and non-raked plots can be because disturbance of the topsoil by raking somewhat resembles plowing. That increases R_{NV} (Stróżecki et al. 2018) due to better soil aeration, and this could compensate for the lack of litter. Later in the season, the litter at non-raked plots was decomposed, thereby narrowing the difference from the raked plots. We may expect that the litter removal can have an effect on soil carbon and nitrogen content, and on microbial community as well as on herbaceous plant community development, which should be the focus of other studies. Such effect will be probably only temporal assuming the rapid decomposition of litter in non-raked plots. Bigger effect could be then expected from repeated removal of litter of which amount starts increase due to growing sprouts.

Forest floor CO_2 efflux on the harvested plots increased compared to R_f at the control plots during the first season after harvest. The majority of R_f during the first year after harvest was due to soil CO_2 efflux (Table 1). Increase in soil CO_2 efflux after harvest has been observed in previous studies (Pang et al. 2013; Čater et al. 2021). Despite reduction of root respiration, decomposition of dead roots and altered soil microclimatic condition can be responsible for this phenomenon (Sullivan et al. 2008; Kohout et al. 2018). Removal of shading canopy leads to greater warming of soil surface, as confirmed also by Čater et al. (2021). This warming, however, depends also on the time of day and actual temperature (Fig. 3), so it is variable in time. We also observed that harvest increased soil water content, and that is consistent with other studies (Londo et al. 1999; Čater and Simončič 2010; Darenova et al. 2016). The largest differences in SWC between control and harvested plots were observed during the first half of the first season after harvest. Later, water demand and transpiration of developing understory resulted in lower SWC and, therefore, smaller difference from SWC in the control plots. Both higher temperature and SWC in the harvested plots constitute more favorable conditions for soil microbes and increase their activity (Ma et al. 2019). We observed two cases, however, when this trend was in the opposite direction, meaning that R_f in the control plots was greater than in the harvested ones. On 21 May 2018, R_f in the control plots only slightly exceeded that in harvested plots, but on 5 September 2018 the difference was highly significant (Fig. 4). The explanation might be that the measurements were carried out shortly after a strong rain. During the 4 days preceding 21 May 2018, there fell 20 mm of precipitation; during the 4 days preceding 5 September 2018, there was even 66 mm of precipitation. Such conditions could lead to wetting of the thick

litter layer in the control plots to such extent as to cause intensive litter decomposition even as litter in the harvested plots, especially in September, was already more or less decomposed. Moreover, respiration of the litter layer is more sensitive than is mineral soil respiration (Wang et al. 2012), and that could contribute to enhancing the difference between control and harvested plots.

These findings indicate that the differences in R_f between forested and harvested stands were not constant during the season and were modulated by actual weather conditions. This view is supported also by measurements on 16 August 2018, when there was a minimal difference in R_f between control and harvested plots even as the difference had tended to increase during the previous two measurements. Measurements on 16 August 2018 were strongly affected by severe drought, and SWC was only around 6.7%. Water shortage strongly limits soil microbial activity, inasmuch as soil respiration becomes independent of, for example, temperature (Correia et al. 2012), which is the main driver of temporal fluctuation in soil respiration. Therefore, we can assume that the effect of harvest on R_f is “covered” by these dry conditions.

The study shows that the soil carbon losses due to increased soil respiration after harvest can be reduced due to more frequently occurring severe dry periods. On the other hand, the slow decomposition during droughts leads to slower nutrient release from organic matter and reduced water supply also inhibits development of herbaceous vegetation. Its important role, among others, is preventing water surface run off and potential erosion, and enabling its infiltration (Miyata et al. 2009) and it represents new carbon input to soil through fresh rhizodeposits and litter which increases soil organic carbon and nutrients in the soil (Pan et al. 2018). Therefore, we may assume the intensively harvested areas may lose less carbon during current dry condition but recovery from that disturbance and reforestation may last longer.

Calculated CO_2 efflux without vegetation, which was considered to be soil CO_2 efflux, remained in most cases greater compared to R_f in the control plots, where no vegetation grew. However, the difference between R_f in the control plots and soil CO_2 efflux in the harvested plots diminished in the second year after harvest. That is the opposite when comparing R_f in the control plots with R_f in the harvested plots, when this difference increased. This supports the assumption that the differences in R_f between the control and harvested plots was caused by respiration of vegetation, especially in the second year after harvest, when the understory developed strongly. The understory vegetation contributes to actual R_f not only by respiration of its aboveground parts but also by increased soil CO_2 efflux due to respiration of its roots, which is, however, eliminated by our method.

5 Conclusions

Our analyses show that short-term pasturing and litter raking had negligible effect on the amount of CO₂ released from soil to the atmosphere, which supports these practices if they are provided with the aim of an increase in local biodiversity.

A significant effect on CO₂ emissions was observed for harvest. That increased both forest floor and soil CO₂ efflux directly and also due to harvest's effects on such microclimatic condition as soil temperature and soil water content. However, a microclimatic condition, in our case heavy rain, caused forest floor and soil CO₂ efflux in the harvested plots to be higher compared to CO₂ efflux in the control. Moreover, under dry conditions, the differences in CO₂ efflux between harvested and control plots were very small. The results, therefore, show that weather conditions can have a substantial effect on the response of CO₂ efflux to harvest and on its estimation under current and future climate. Nevertheless, although dry weather may decrease soil organic matter decomposition after an intense harvest, such conditions can lead to longer soil recovery from the disturbance and reforestation.

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Availability of data and materials The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Ethics approval The authors declare that they follow the rules of good scientific practice.

Consent to participate Not applicable.

Consent for publication All authors gave their informed consent to this publication and its content.

Conflicts of interest The authors declare that they have no conflict of interest.

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