Harvesting intensity and tree species affect soil respiration in uneven-aged Dinaric forest stands

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Abstract

Forest management, especially thinning and harvesting measures, has a significant impact on the forest carbon balance especially in the forests with long-term continuous cover history. We measured soil CO_2 efflux (Rs) in three forest complexes of mixed, uneven-aged Dinaric forests with predominating silver fir (Abies alba Mill.), beech (Fagus sylvatica L.), and Norway spruce (Picea abies Karst.). Rs was measured after removal of mature forest stands with 50% and 100% intensity of living stock and compared with Rs on the control plots without any applied silvicultural measures. Rs was measured monthly in three consecutive 2012, 2013 and 2014 growing periods. Soil CO_2 efflux increased after harvest of both intensities in all studied forest stands. The biggest increase was measured in beech stands and amounted up to 47 and 69% for 50% and 100% harvest intensities, respectively. The effect of harvest on Rs in spruce and fir stands was similar – up to 26% for 50% harvest intensity and 48% for 100% harvest intensity. Despite the biggest increase after harvest, Rs in beech stands returned the fastest to the level of the uncut forest and this levelling period (LP) took 14-17 months with a little delay of the stands with 100% harvest intensity. The LP for all fir stands, for spruce stands with 50% harvest intensity and for one spruce stand with 100% harvest intensity, was 26-29 months. At two spruce stands with 100% harvest intensity we did not record Rs levelling during our three-year study. This study involved forest stands of three predominating tree species growing under the same conditions, which allowed us to determine the species-specific sensitivity of soil CO_2 efflux to the different harvesting intensities.

Key words: *harvesting intensity, soil CO_2 efflux, silviculture, carbon release, beech, silver fir, Norway spruce*

1. Introduction

The net carbon (C) flux in terrestrial ecosystems results from the balance between photosynthetic CO_2 fixation and its release by ecosystem respiration. Temperate forest ecosystems act as a carbon sink (Lal and Lorenz, 2012) with soil respiration accounting for half of total ecosystem respiration (Yuste *et al.*, 2005; Giasson *et al.*, 2013). The rate of C loss from soil through respiration is, to some extent, a function of temperature and water availability, so the soil C balance is likely to be a sensitive indicator of climate change. This makes soil respiration a crucial component of carbon flux on Earth (Weiman, 2015), as it may release huge amounts of C stored in soil (Jian *et al.*, 2018).

Soil respiration, measured often as CO_2 efflux from the soil surface (Rs) (Maier *et al.*, 2011), consists of respiration from roots, microbes, and soil fauna (Kuzyakov, 2006). The abiotic carbonate-derived CO_2 contribution to soil efflux has been considered of minor importance (Werth and Kuzyakov, 2008; Schindlbacher *et al.*, 2015), but in semiarid and arid environments with carbonate-rich soils, efflux could be significant (Emmerich, 2003; Huxman *et al.*, 2004). Soil CO_2 efflux varies temporally from seconds to inter-annual scale, and spatially on the plot to landscape level. Seasonal variations in Rs, observed in almost all ecosystems, have often been associated with changes in temperature, moisture, photosynthetic production, root growth and their combination (Yan *et al.*, 2011; Acosta *et al.*, 2018; Makita *et al.*, 2018; Zhang *et al.*, 2018). On the other hand, the spatial variability in Rs results from a large variability in soil physical properties, soil chemistry, fine-root biomass, fungi and bacteria, nutrient availability and others (disturbance and weathering) (Hanson *et al.*, 1993; Fang *et al.*, 1998; La Scala *et al.*, 2000; Xu and Qi, 2001; Merbold *et al.*, 2011; Allaire *et al.*, 2012; Dore *et al.*, 2014; De Carlo *et al.*, 2019; D'Andrea *et al.*, 2020). The differences in Rs among stands result also from the prevailing tree species, age and management practices (Peng *et al.*, 2008; Akburak and Makineci, 2013; Wang *et al.*, 2013).

Forest management, especially thinning and harvesting measures, has a significant impact on the forest carbon balance and may even result in altering the forest ecosystem from CO_2 sink to CO_2 source (Larson and Axelrod, 2017). As the forest floor becomes more open to light and precipitation, these conditions can increase the organic matter decomposition, causing substantial loss of carbon soil accumulated for decades. The most affected are organic soil horizons which, according to different studies on clear-cuts of a variety of forests, may lose around 30% of carbon (Nave *et al.*, 2010; James and Harrison, 2016). The enhanced decomposition of soil organic matter may lead to higher soil CO_2 efflux compared to that before the harvest despite a decrease in root respiration resulting from tree harvest (Londo *et al.*, 1999; Darenova and Čater, 2020). A combination of decreased fresh organic input after harvest and increased decomposition of the existing organic material may result in carbon and nitrogen losses (Mayer *et al.*, 2020), changes in C:N ratio (Rosikova *et al.*, 2019), and contributes to an increase in CO_2 concentration in the atmosphere (Denman *et al.*, 2007). Studies about ecosystem respiration and net ecosystem balance of CO_2 development after the harvest (Humphreys *et al.*, 2006; Amiro *et al.*, 2010; Williams *et al.*, 2014) investigated the harvesting effect with soil CO_2 efflux, as a main CO_2 source, but have been performed during only one growing season. Knowledge of the longer-time changes in soil CO_2 efflux after harvest is rare, especially for temperate European areas on sensitive forest soils. The period when CO_2 efflux returns to the original levels after applied silvicultural measures and the time of primary production recovery are crucial factors of the disturbed forest ecosystem to become CO_2 sink again.

Mixed uneven aged forests with predominating silver fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), and Norway spruce (*Picea abies* Karst.) in the Dinaric region represent the largest continuous forest area in Central Europe (Horvat *et al.*, 1974). Most of these forests were gradually transformed from old-growth conditions and have never experienced clear-cut silvicultural systems and extensive planting ((Boncina *et al.*, 2013). They were managed with close-to-nature continuous-cover silvicultural systems like selection systems, irregular shelterwood or their combination, freestyle technique (Mlinšek, 1969), mimicking natural processes. Such approach helped to preserve a higher share of conifers and forest structure (Diaci *et al.*, 2011) on sensitive, shallow high karst soils. So far, little evidence has been provided as to how disturbances and forest management with different harvesting intensities in these sensitive high karst Dinaric ecosystems affect soil processes, particularly soil CO_2 efflux. The aims of this study were: 1) to determine soil CO_2 efflux shortly after 50% and 100% harvesting intensity; 2) to compare harvesting effect in stands with three different predominating tree species, and 3) to determine the time when soil CO_2 efflux after harvesting would return to the control state.

2. Material and methods

2.1 Site conditions

The research area, located in the southern part of Slovenian high karst Dinaric region (Habič, 1978), is distributed along three forest sites: Trnovo, Snežnik and Rog (Fig. 1), all belonging to *Omphalodo-Fagetum* association (Surina and Dakskobler, 2013) with silver fir, Norway spruce and European beech as predominating tree species with comparable forest structure, soil and climatic conditions (Table 1). All studied forest areas are included in the NATURA 2000 network.

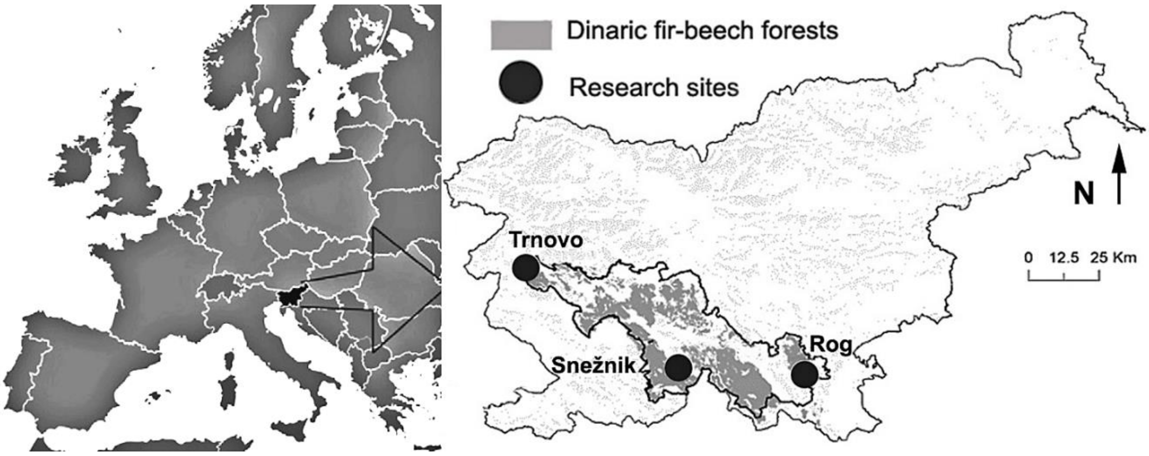

Fig. 1: Location of the research area

Table 1. Research site general characteristics

Site	Trnovo	Snežnik	Rog
Area (ha)	70	70	70
Location (UTM-WGS84)	46° N, 13° E	45° N; 14 ° E	45° N; 15° E
Altitude (m a.s.l.)	772 - 824	731 - 774	799 - 896
Landscape morphology	Karst terrain with sinkholes, ridges and slopes		
Bedrock	Limestone, dolomite		
Soil characteristics	Litosol, Rendzic Leptosol, Cambisol, Luvisol		
Temp $_{med}$ (°C)	9	8	8
Temp $_{max}$ (°C) (avg. warmest month)	12.5	12.5	15.5
Temp $_{min}$ (°C) (avg. coldest month)	4	2.5	2.5
Total annual precipitation (mm)	2300 mm	1600 mm	1700 mm
Forest type	Mixed silver fir, beech and Norway spruce high forests		
Main management type	Uneven-aged		
Cutting - harvesting method	Freestyle, irregular shelterwood system and selective cutting		
Average standing biomass (m^3/ha)	292.0	442.0	351.6
Annual increment (m^3/ha year)	6.2	8.3	9.4
Basal area (average) (m^2/ha)	44.75	42.28	32.54
Stem density (N/ha)	415	379	443

The entire high karst Dinaric region is composed of sinkholes with same orientation due to high karst ontogeny. Little or very shallow soil layers are present on exposed locations at sinkhole edges, particularly where the canopies are fragmented or open. Design with constant distance from the sinkhole centre was the optimal way to perform such study and compare different forest sites. The reason for such small gaps is the principle of close-to-nature forest management, which promotes only small gaps and not large clear-cuts, and also the Slovenian forestry law, which prohibits larger areas of intensive cutting (Forest Act, Official Gazette of the Republic of Slovenia, No. 30/93), given that the forest areas in the Dinaric mountains are dominated by rocky, shallow soils mostly on limestone which makes them sensitive to the effects of temperature extremes, drought and particularly water erosion.

On every site, nine plots were established in sinkholes, each 450m^2 in size, prior to the silvicultural measure - in total 27 plots. Three selected plots were dominated with beech, three with silver fir and three with Norway spruce, with basal area greater than 60%. In the forest stands with a mean canopy cover of over 95%, two logging intensities (treatments) were applied in May 2012: control (0% removal), 50% removal and 100% removal of the growing stock (de Groot *et al.*, 2016) (Fig. 2). Before the treatments, the plots had a basal area between 30.9 and 45.5 m^2/ha. The plots with 50% treatment had a value between 17.9 and 25.7 m^2/ha after the treatment.

Changes in canopy cover were evaluated by digital hemispherical photographs taken in completely overcast sky conditions with a DSLR Canon EOS Rebel T3i digital camera and calibrated fish-eye lens from Regent WinScanopy. Hemispherical photos were taken prior and after harvesting operations 150 cm above the forest floor. For the evaluation of light intensity before and after harvesting, Gap Fraction (%), Openness (%) and Indirect Site Factor (%) were used, processed with WinScanopy pro-d software (Čater *et al.*, 2012; Čater and Levanič, 2013). Hemispherical photos were taken on every plot and five measurement points (Fig. 2).

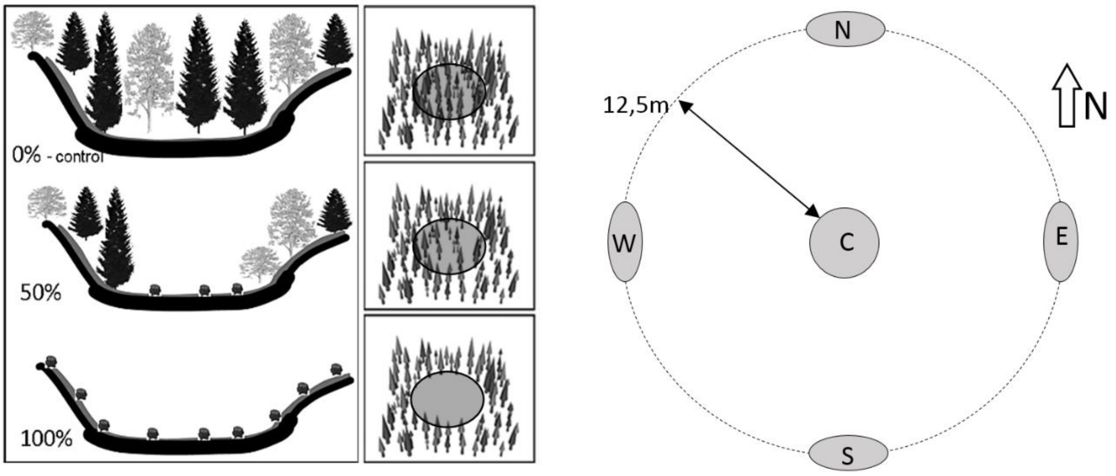

Fig. 2. A scheme of plots with different harvesting intensity (left), and layout of five measurement points (right) within one plot defined according to the aspect position (N, E, S, W and C-center).

2.2 Soil efflux (Rs)

Rs was measured with LI-6400 console and LI-6400-09 Soil CO_2 Flux Chamber, (LI-COR, USA) of 9.6 cm in diameter, placed carefully directly on the soil not to cause overpressure in the chamber headspace but to secure sealing. The chamber concentration was automatically scrubbed to just below an ambient target and measured as it rose slightly above the ambient concentration. This maintained the CO_2 concentration gradient to within a few ppm of the natural, undisturbed value. Following each measurement, the intermediate flux data were fitted with a regression, which was then used to compute the soil CO_2 flux at the target ambient CO_2 concentration (Čater and Ogrinc, 2011). Automated cycling ensured that CO_2 flux measurements were accurate and repeatable. A pressure equilibration tube was used to eliminate pressure differentials and to avoid chamber leaks, whereas air inside the chamber was thoroughly mixed while maintaining a constant pressure to assure consistently accurate data (Čater and Ogrinc, 2011). Soil temperature was monitored simultaneously with soil respiration using a copper/ constantan thermocouple penetration probe (Li 6000-09 TC,) inserted in the soil to a constant depth of 15 cm close to the Rs chamber.

On every plot, five measurement points (centre and 4 celestial sides at the exact distance of 12.5m from the center plot) on a systematic grid have been determined to acquire reliable measurement response under comparable environmental conditions (Fig. 2, right). Five complete measurement cycles were carried out at each celestial side per every month.

2.3 Data analysis

Slopes of linear regression lines between Rs (dependent variable) and soil temperature (T_{soil}) (independent variable) for different tree species (grouping variable) were tested with analysis of covariance (ACOVAR) with program package R. Individual measurements of Rs and soil temperature from control plots and three species on all three sites during three years were used.

Differences between species and different measure (control, 50% harvesting intensity and harvesting 100% intensity) for the Rs were tested with the two-way ANOVA with species and measured as a dependent variable. Measurements from 5 locations (centre and 4 celestial sides) were nested within plots. Analyses of variance (ANOVA) and HSD Tukey post hoc test were made after testing data for normality and homogeneity of variances. No transformation of data was required to fulfil the criteria of normality in all tested parameters. Probability values of $p < 0.05$ (*) were considered significant.

After the applied measures, Rs on plots with 50% and 100% harvesting intensity was significantly higher from the Rs on control plots, however, in time differences became gradually less pronounced. We wanted to determine the time, when Rs on harvested plots would become similar (non-significantly different) to the Rs on control plots. Time between the applied measure and this specific month has been therefore labelled as the observed "levelling period" (LP).

3. Results

3.1 Light conditions

Forest stands indicated similar forest cover all over three forest complexes before harvesting, showing in all plot values of Gap Fraction (%), Openness (%) and Indirect Site Factor (ISF, %) (Table 2) without any significant differences between the studied plots and sites.

Table 2. Mean values (±SE) of light conditions before and after harvesting of 50% and 100% harvesting intensity

Site	Measure intensity	Gap Fraction (%)	Openness (%)	Indirect Site Factor (%)
Trnovo	before harvest	7.5 ± 1.4	7.5 ± 1.4	11.4 ± 3.2
	control	8.6 ± 0.9	9.4 ± 0.9	10.2 ± 1.4
	50%	22.7 ± 6.7	25.2 ±7.6	44.6 ± 9.9
	100%	46.0 ± 6.5	49.8 ± 6.8	75.4 ± 8.5

Snežnik	before harvest	8.1 ± 2.9	8.2 ± 2.9	12.3 ± 4.7
	control	9.8 ± 1.5	10.7 ± 1.9	15.6 ± 5.3
	50%	19.2 ± 7.2	20.8 ± 8.0	46.3 ± 5.4
	100%	54.4 ± 3.3	56.5 ± 3.2	75.7 ± 8.3
Rog	before harvest	6.4 ± 2.2	6.40 ± 2.2	9.2 ± 3.9
	control	8.9 ± 1.2	10.3 ± 1.3	9.1 ± 1.4
	50%	22.2 ± 4.8	23.3 ± 5.5	49.7 ± 9.6
	100%	49.3 ± 5.6	52.2 ± 8.7	69.2 ± 9.8

Light conditions on control plots were after the applied intervention similar to the conditions before harvesting, without significant differences: on plots with 50% harvesting intensity ISF increased up to 44-49% ISF and on plots with harvesting 100% intensity up to 69-75% ISF, respectively (Table 2).

3.1 Soil temperature

Soil temperatures reached up to 15, 13 and 11 °C at Trnovo, Rog and Snežnik, respectively, including all treatments and species. The differences in soil temperature among stands with the same silvicultural measure at the same site were negligible. Soil temperature was, however, affected by the silvicultural measure. At Trnovo, soil temperature followed the pattern 100%-harvest > 50%-harvest > control for all three studied growing seasons. At Rog and Snežnik, this pattern was observed only during the first growing season, then the differences vanished (Fig. 3).

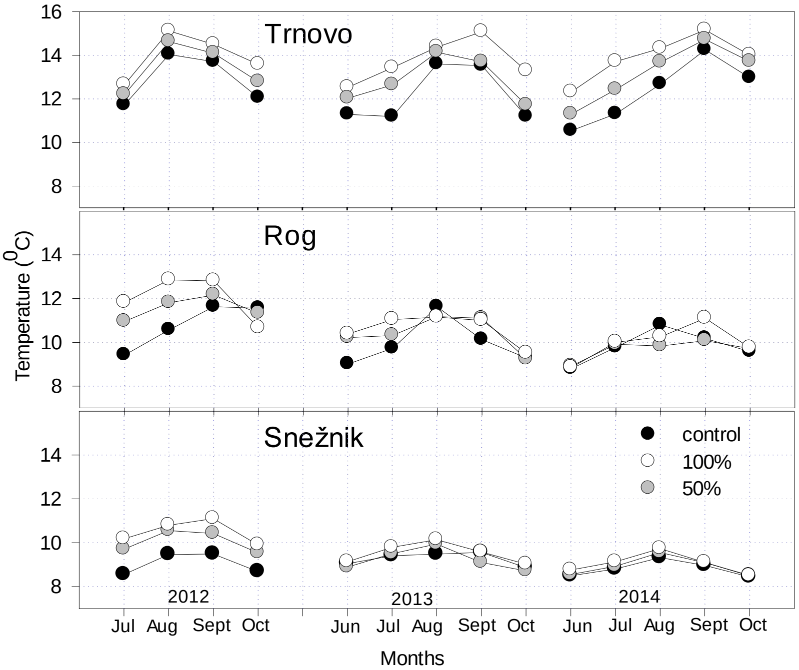

Fig. 3. Mean soil temperature from the stands with the same silvicultural measure at three investigating sites during three growing seasons following the harvest.

3.2 Soil CO$_2$ efflux

Soil CO$_2$ efflux in the control plots ranged between 4.9 and 8.6 μmol m^{-2}s^{-1} (Fig. 4). Generally, the highest Rs was monitored at Trnovo, and the lowest at Snežnik. Comparing the stands with different predominating species, the highest Rs was in beech predominating forest. On average, Rs in spruce and fir stands was by 9.0 and 10.5% lower than that in beech forests; the differences in Rs between fir and spruce forests were smaller than 2%.

Correlation (linear fit) between soil temperature and Rs on control plots over the measuring months in all three years was high in all three forest types; correlation was highest in beech-predominating stands, where also the slope was steeper compared to the linear fit for the Norway spruce and fir (Fig. 4).

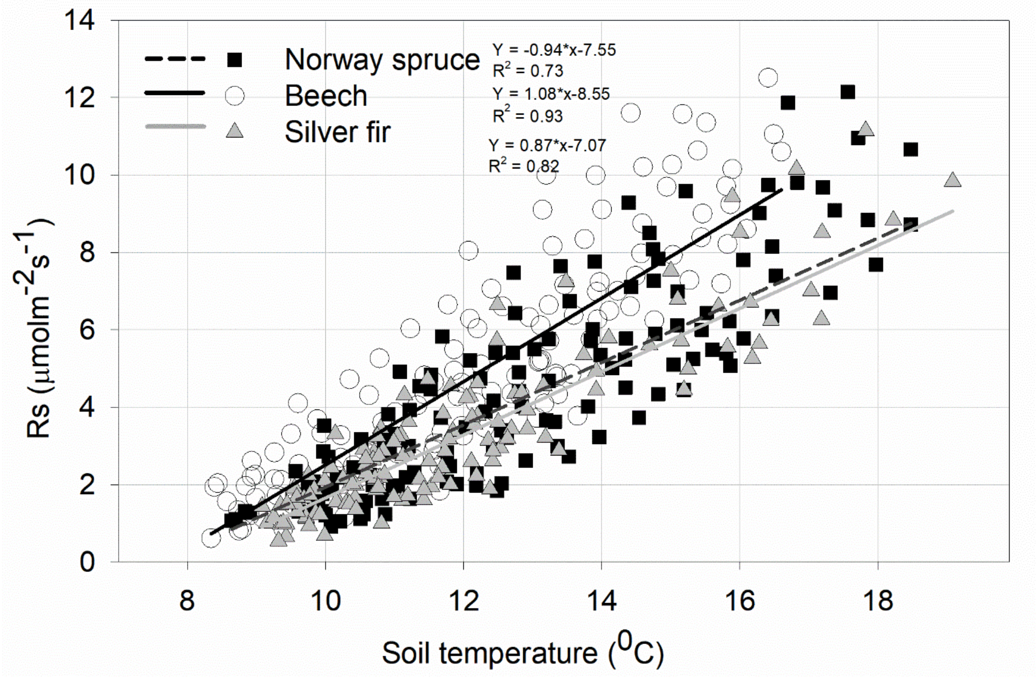

Fig. 4. Soil CO_2 efflux (Rs) over soil temperature in the control stands from Trnovo, Rog and Snežnik with predominating spruce, beech and fir over the 2012-2014 measuring period.

Both slopes and intercept for all tree species were significantly different (Table 3).

Table 3. Results of ACOVAR for difference in slopes and intercept for three tree species – relation between Rs and T soil.

		Slopes		Intercept	
	df	F	p	F	p
Species	2	64.76	2e-16 ***	54.63	2e-16 ***
T soil	1	1286.95	2e-16 ***	1243.98	2e-16 ***
Species: T soil	2	10.02	5.73e-05 ***		
Resid.	624			626	

3.3 Effect of harvesting on Rs

Both applied harvest intensities resulted in a significant increase in Rs during the first measurements after the harvest (Table 4 and 5) with higher increase for 100% harvesting intensity compared to 50% harvesting intensity on all three sites (Fig. 5).

Table 4. Results of ANOVA between measures and species within each studied month for Rs at the Trnovo, Rog and Snežnik forest sites. Probability values of $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p > 0.05$ (ns; non-significant).

		Measure							Species							Measure x Species					
		Trnovo		Rog		Snežnik			Trnovo		Rog		Snežnik			Trnovo		Rog		Snežnik	
Month	$df_{1,2}$	F	p	F	p	F	p	$df_{1,2}$	F	p	F	p	F	p	$df_{1,2}$	F	p	F	p	F	p
Jul 12'	2; 36	166.1	***	87.3	***	571.8	***	2; 36	95.1	***	43.0	***	349.4	***	4; 36	4.7	*	6.5	***	47.2	***
Aug 12'	2; 36	57.1	***	301.2	***	321.2	***	2; 36	46.0	***	171.8	***	226.2	***	4; 36	3.7	*	14.7	***	18.9	***
Sep 12'	2; 36	34.4	***	216.6	***	144.0	***	2; 36	18.7	***	125.0	***	85.0	***	4; 36	3.3	*	16.3	***	9.5	***
Oct 12'	2; 36	28.0	***	57.9	***	202.7	***	2; 36	5.2	*	45.2	***	25.8	**	4; 36	1.2	ns	0.1	ns	5.5	**
Jun 13'	2; 36	142.1	***	112.6	***	285.7	***	2; 36	121.7	***	69.9	***	111.7	***	4; 36	0.8	ns	4.2	**	4.5	***
Jul 13'	2; 36	48.7	***	125.1	***	685.7	***	2; 36	26.8	***	78.5	***	388.4	***	4; 36	0.6	ns	2.5	ns	14.5	***
Aug 13'	2; 36	21.4	***	48.8	***	232.1	***	2; 36	11.8	***	54.6	***	89.7	***	4; 36	0.3	ns	2.1	ns	3.7	*
Sep 13'	2; 36	22.9	***	155.2	***	135.1	***	2; 36	16.8	***	151.9	***	14.1	***	4; 36	0.4	ns	4.0	**	1.8	ns
Oct 13'	2; 36	11.0	***	38.6	***	69.6	***	2; 36	7.8	**	5.1	*	0.8	ns	4; 36	0.2	ns	2.2	ns	0.4	ns
Jun 14'	2; 36	24.8	***	108.6	***	72.3	***	2; 36	73.5	***	9.3	***	9.2	***	4; 36	8.7	***	2.9	*	0.6	ns
Jul 14'	2; 36	22.2	***	175.1	***	68.6	***	2; 36	15.4	***	53.3	***	27.3	***	4; 36	0.4	ns	7.7	***	1.8	ns
Aug 14'	2; 36	13.1	***	39.8	***	26.8	***	2; 36	13.1	***	19.8	***	3.1	ns	4; 36	0.2	***	0.6	ns	0.3	ns
Sep 14'	2; 36	15.7	***	55.9	***	40.6	***	2; 36	22.7	***	30.2	***	6.5	**	4; 36	0.6	ns	1.0	ns	0.6	ns
Oct 14'	2; 36	55.9	***	50.1	***	9.0	***	2; 36	67.3	***	21.5	***	0.6	ns	4; 36	2.3	ns	0.8	ns	0.9	ns

3.4 Time response

Rs on the harvested plots was in all cases higher than Rs on the control plots during the whole period of our observations (Fig. 5); the differences between the harvested plots and the control gradually decreased in time. The month, when difference in Rs between control and 50% (100%) measure intensity remained non-significant has been indicated for every forest site and species. Time between the applied measure and this specific month has been called “the levelling period” (LP). In stands with 50% harvest intensity, the LP was always shorter compared to that in stands with 100% harvesting intensity.

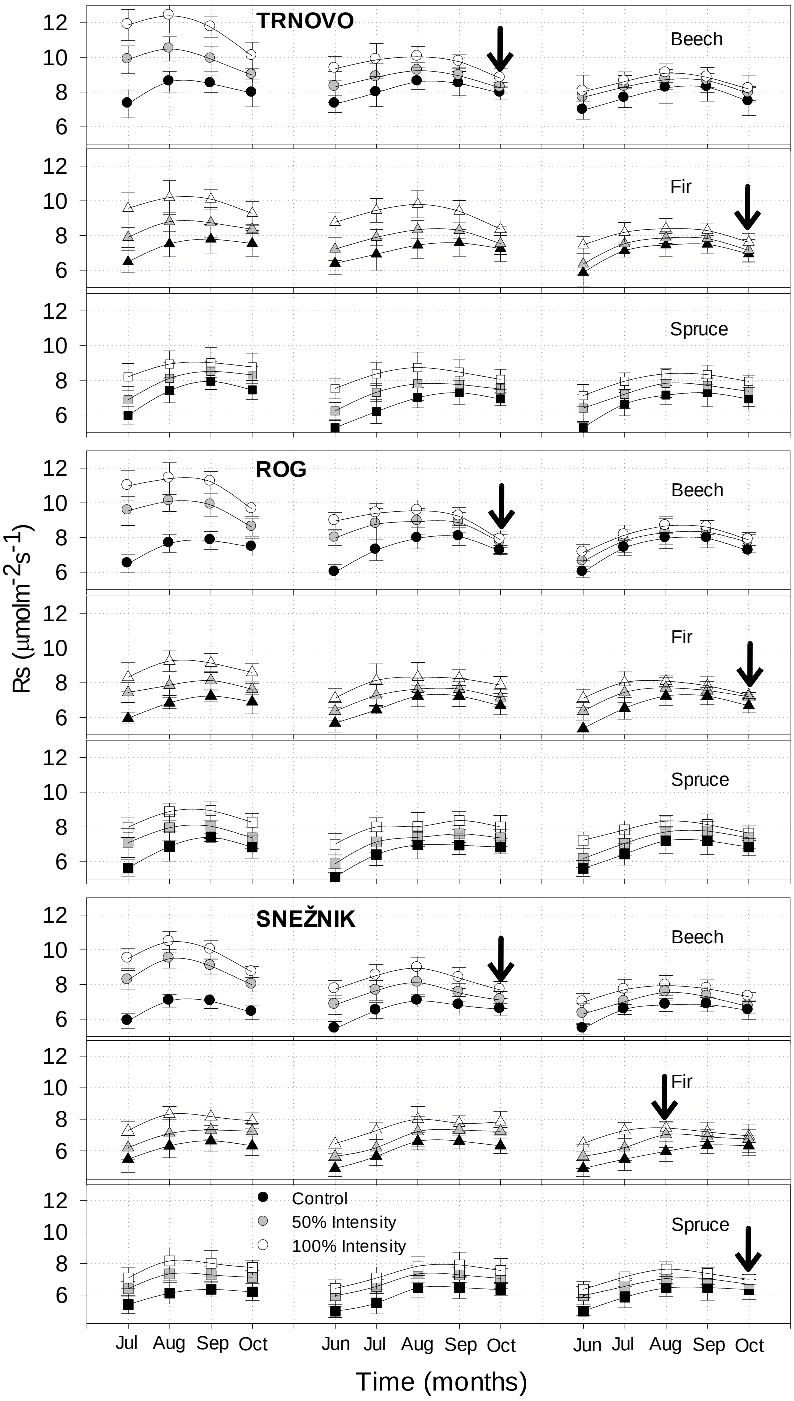

Fig. 5. Soil CO_2 efflux (Rs, means with standard errors) at Trnovo, Rog and Snežnik during the three growing seasons following the harvest. Arrows indicate the months when difference between the harvested and control plots became and remained non-significant: grey colour for 50% harvesting intensity and black for 100% harvesting intensity.

On all plots with the applied 50% harvesting intensity, the shortest LP was observed in stands with predominating beech (14-15 months), followed by stands with predominating fir (26-27 months), and stands with predominating spruce (26-27 months) (Tables 5 and 6).

Table 5. Results of post hoc (HSD) analysis for all three forest complexes for beech, fir and spruce predominating plots by months. Numbers below each species refer to differences in soil CO_2 efflux between 1-2: the control vs. 50% harvesting intensity; 1-3: the control vs. 100% harvesting

intensity and 2-3: 50% vs. 100% harvesting intensity. Bold letters define the month of Rs in 50% and 100% harvesting intensity plots becoming non-significantly different form the control values and the end of soil CO_2 efflux levelling period (LP).

	Trnovo									Rog									Snežnik								
	Beech			Fir			Spruce			beech			fir			spruce			beech			fir			spruce		
Month	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
Jul 12'	***	***	**	***	***	***	**	***	**	***	***	***	***	***	ns	**	***	ns	***	***	***	***	***	***	***	***	***
Aug 12'	***	***	***	***	***	**	**	**	ns	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Sept 12'	***	***	***	***	***	ns	**	*	ns	***	***	***	***	***	***	*	***	***	***	***	***	*	***	**	***	***	ns
Oct 12'	***	***	**	***	**	ns	**	*	ns	**	***	**	***	***	**	*	***	**	***	***	**	***	***	ns	***	***	**
Jun 13'	***	***	***	**	***	***	***	***	***	***	***	***	**	***	**	*	***	***	***	***	***	***	***	***	***	***	**
Jul 13'	**	***	ns	**	***	***	***	***	ns	**ns**	***	**	**	***	***	**	***	***	**ns**	***	***	***	***	***	***	***	***
Aug 13'	**ns**	**	ns	**	***	ns	*	*	ns	ns	***	ns	***	***	*	**	***	ns	ns	***	***	***	***	***	***	***	***
Sept 13'	ns	**	ns	**	***	ns	**	*	ns	ns	***	ns	*	***	***	***	***	***	ns	***	***	***	***	ns	***	***	***
Oct 13'	ns	**ns**	ns	*	**	ns	**	**	ns	ns	**ns**	ns	**	***	**	**	***	*	ns	**ns**	**	***	***	ns	**	***	ns
Jun 14'	ns	ns	ns	**	***	***	***	*	ns	ns	ns	ns	***	***	***	*	***	***	ns	ns	ns	*	***	**	***	***	ns
Jul 14'	ns	ns	ns	**ns**	**	ns	**ns**	***	ns	ns	ns	ns	**ns**	***	***	***	***	***	ns	ns	***	**ns**	***	***	**	***	ns
Aug 14'	ns	ns	ns	ns	**	ns	ns	*	ns	ns	ns	ns	ns	**	ns	**ns**	***	**	ns	ns	ns	ns	**ns**	ns	**ns**	***	ns
Sept 14'	ns	ns	ns	ns	**	ns	ns	***	ns	ns	ns	ns	ns	***	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	***	ns
Oct 14'	ns	ns	ns	ns	**ns**	**	ns	***	***	ns	ns	ns	ns	**ns**	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	**ns**	ns

Table 6. Levelling period (LP) of soil CO_2 efflux after harvest in months - the time between applied measure and the month when the difference between the harvested and control plots became and remained non-significant.

	LP					
	50% harvesting intensity			100% harvesting intensity		
	Beech	Fir	Spruce	Beech	Fir	Spruce
Trnovo	15	26	26	17	29	< 29
Rog	14	26	27	17	29	< 29
Snežnik	14	26	27	17	27	29

On plots with 100% harvesting intensity, the LP for stands with predominating beech (17 months) and fir (27-29 months) was on average two months longer than for 50% harvesting intensity. In spruce stands, we recorded non-significant Rs from control only at the Snežnik site (29 months), while on other spruce sites Rs was significantly higher for the whole study period, indicating a prolonged period (lasting longer than 29 months) (Tables 4 and 5).

4. Discussion

4.1 Soil CO_2 efflux

The study sites are situated in the high karst Dinaric region, where CO_2 can be released not only from organic matter decomposition but also form parent material. Plestenjak *et al.* (2012) reported that the vast majority (78-99%) of soil CO_2 during warm periods between May and October (2008-2010) originated from the organic sources in a Mediterranean karst area and inorganic CO_2 contributed 12 % on average. Similarly, contribution of an inorganic pool of about 17% to total soil CO_2 efflux was found for forest stands on carbonate bedrock in a karst Dinaric area (Čater and Ogrinc, 2011). The variability of the inorganic CO_2 contribution to soil CO_2 efflux, however, varied only in a few percent. Therefore, we can assume that the Rs variability in this study was driven rather by organic sources such as rhizosphere and soil organic matter.

Soil CO_2 efflux followed seasonal changes in soil temperature with maxima in August in all studied forest stands, which is common for temperate forests. Results are consistent with high correlation between CO_2 efflux (Rs) and temperature (Fig. 4) referring that temperature was the main factor driving soil CO_2 efflux under studied conditions. The relationship between Rs and soil temperature is usually described as exponential (Davidson *et al.*, 2006) but any limiting conditions, such as for example drought, would results in deviations from this relationship (Darenova *et al.*, 2016a). While soil moisture above the certain threshold has a negligible effect on Rs, under dry conditions, changes in soil moisture start to drive Rs as much as Rs may become completely independent on temperature (Xu *et al.*, 2004). As the relation between CO_2 efflux and soil temperature did not display any substantial deviation (Fig. 4), we may assume that although no measurements were provided in this study, soil moisture had only a minor effect on soil CO_2 efflux and that the forest ecosystem did not suffer from drought during the study period. This can be also be supported by high annual precipitation that is characteristic of the areas (1600-2300 mm y^{-1}). Temperature can be also responsible for Rs differences among the three forest complexes, as we observed the highest temperature at Trnovo and the lowest at Snežnik, which corresponds to the same pattern of Rs.

The measured light conditions reflect the canopy opening, tree density and the amount of leaf biomass. Canopy opening can affect soil microclimate such as soil's exposure to solar radiation and precipitation throughfall (Mazza *et al.*, 2011; Pang *et al.*, 2013), whereas leaf biomass provides for the supply of new assimilates respiration in the rhizosphere (Finzi *et al.*, 2015), and litterfall for microbial respiration (Pitman, 2013). Light conditions are also closely connected with the stand type which drives soil CO_2 efflux on the spatial scale (Čater and Ogrinc, 2011; Darenova and Čater, 2018).

We observed higher Rs in beech forests compared to fir and spruce. According to Raich and Tufekcioglu (2000) and Mayer *et al*. (2020), soil organic matter decomposition and soil CO_2 efflux are generally higher in broad leaf forest than in conifer stands located on the same soil types by an average of 10%. This trend was also observed in studies with direct comparing of beech and spruce forests. While we found significantly higher Rs in beech stand compared to spruce stands on average by 10.5%, the differences between these two species in other studies are not consistent. In these studies, Rs in beech forests exceeded that in spruce stands by 20 to 65% (Matteucci *et al.*, 2000; Borken and Beese, 2005; Priwitzer *et al.*, 2013). However, Borken *et al*. (2005) or Berger *et al*. (2010) confirmed no difference between the stands at one of the studied sites. Berger *et al*. (2010) considered this to be a result of bedrock as they confirmed the difference only for a base-poor site. A few studies even found opposite trend with higher soil CO_2 efflux in spruce forests compared to beech forests (Vesterdal *et al.*, 2012; Darenova *et al.*, 2016b).

4.2 Effect of harvesting on Rs

According to the previous studies, effect of logging on soil CO_2 efflux is not consistent. It has been reported that harvest decreased or had no effect on soil CO_2 efflux (Mallik and Hu, 1997; Striegl and Wickland, 2011; Olajuyigbe *et al.*, 2012) or, similar to our study, that soil CO_2 efflux increased after the harvest (Schilling *et al.*, 1999; Pang *et al.*, 2013; Darenova and Čater, 2020). The decrease in Rs after harvest can result from larger reduction in belowground root respiration than the stimulation of microbial respiration as suggested by Sullivan *et al*. (2008). Therefore, we may assess that in our case the harvest of both intensities more than compensated the reduced or eliminated root respiration by stimulating microbial decomposition. Shortly after harvest, both partially harvested and clear-cut stands also show higher amount of dead tree roots which become a substrate for microbial respiration (Kohout *et al.*, 2018). Moreover, partial or total tree removal results in alteration of the local microclimate. We observed higher soil temperature in the harvested plots with the highest temperature in the plots 100% harvest intensity. This is because the reduction or removal of the canopy enables more solar radiation to reach the soil surface and this was also confirmed in previous studies (Mello, 2007; Akburak and Makineci, 2016). Moreover, canopy opening can also result in more precipitation reaching the ground and reduction in transpiration leading to increase in soil moisture (Epron *et al.*, 2004; Kang *et al.*, 2014; Darenova *et al.*, 2016a). Increase in temperature and moisture stimulates microbial decomposition of organic material accumulated in the soil from previous decades (Tedeschi *et al.*, 2006) and this soil CO_2 efflux. This makes the forests with long term continuous coverage, like those in our studied area, very sensitive to the intensive harvest management.

The response of Rs depended also on the intensity of the harvest. We found Rs varying significantly among treatments in the order: 100% intensity > 50% intensity > control reported also by Londo *et al*. (1999) and Schilling *et al*. (1999). This can be partly explained by the same pattern of soil temperature. However, when comparing Rs at the same temperature (data not shown), the same pattern was observed. On the other hand, Londo *et al*. (1999) observed such a pattern of measured Rs, but no difference was observed in Rs at a given temperature, which was confirmed between control and partial clear cut, indicating that Rs in the partially cut stand increased mainly due to the increase in soil temperature, while that clear cut increased also due to other factors (e.g. increase in dead root biomass).

4.3 Time response

We found the biggest differences in Rs between control and harvested plots during the first year after harvest and then the differences gradually decreased so much that they became insignificant (Fig 6, Table 4). This can be due to several reasons. The decrease in Rs can be attributed to the gradual depletion of harvested tree dead roots (Schilling *et al.*, 1999; Kohout *et al.*, 2018). Moreover, if soil organic matter starts to be rapidly decomposed shortly after harvest, we may expect that this would lead to a fast reduction of its amount (Achat *et al.*, 2015). Harvest also reduces or eliminates fresh tree litter input. The effect of enhanced soil temperature after harvest also vanishes slowly, which is consistent with our results, as soil starts to be gradually shaded by developing vegetation (Don *et al.*, 2012) or by remaining trees of which leaf area rises due to the lack of competition (Le Dantec *et al.*, 2000).

The canopy opening leads to a rapid development of herbaceous vegetation, which can compensate the decline in tree litter input (Don *et al.*, 2012). We can assume that root respiration and leaf litter decomposition of this newly established vegetation can result in an increase in soil respiration.

Moreover, in the thinned stands, the releasing competition among trees may stimulate root growth and productivity of the remaining trees, which brings more fresh assimilates available for both root and microbial respiration (Wang *et al.*, 2019).

The decreasing trend on the difference in Rs between control and harvested stands results from these opposing processes and we found that the stands with 100% harvest were recovering longer that those with 50% harvest intensity. Moreover, we observed the length of the LP to be species specific. Rs in beech forest stands with both harvest intensities recovered during the second growing season after the harvest (after 14-17 months), while the LP for spruce stands with 100% harvest intensity was recorded at the very end of the third growing season after harvest at Snežnik, but it was not observed at all at other two sites during the three year study period. Beech trees and seedlings responses to higher radiation resulted from opening canopy more sensitively than the other two species. Čater and Diaci (2017) found that leaf production and assimilation rate of beech increased faster with increasing light that those of spruce and fir. This can contribute to the increasing trend of Rs after harvest through rhizosphere respiration as mentioned above and, therefore, to rather postpone the LP in fir and spruce stands. The shortest LP for beech can thus indicate that the decrease in Rs after harvest is driven rather by microbial respiration of accumulated soil organic matter.

There is a limited number of long enough studies to record the Rs trend after the harvest. Ma *et al.* (2013) observed that the increase in Rs disappeared already upon three to six months after the clear cut of a subtropical forest, while Darenova *et al.* (2016a) estimated ten years for Rs to return to its state before harvest in an oak coppice stand.

Conclusions

The study was carried out at sites with long-term continuous forest coverage. Our results point out that soil respiration, and therefore soil carbon stock, of this type of forests is very sensitive to any harvesting operations. We observed a significant increase in soil CO_2 efflux in plots with both 50% and 100% harvesting intensity. In beech stands, the initial increase in soil CO_2 efflux was much bigger that in spruce and fir stands, but the LP when soil CO_2 efflux returned to the level of the un-cut forest took 13-16 months, which was at least one year less that for the other species. Soil CO_2 efflux LP in spruce stands with 100% harvest intensity was not even recorded during the three years of the study at two sites. From our results, we may conclude that dynamics of soil CO_2 efflux after harvest is species specific and is driven mainly by microbial decomposition of dead roots and previously accumulated soil organic matter. Conclusions of this research may help in considering changes of forest carbon balance in the future, should the climate change lead to alteration of coexisting tree species.

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