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Different harvest intensity and soil CO₂ efflux in sessile oak coppice forests

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Soil CO₂ efflux accounts for about 45-80% of total ecosystem respiration and is therefore an important part of the ecosystem carbon cycle. Soil CO₂ efflux has been poorly studied in forests managed in the ancient coppicing manner. In our study, soil CO₂ efflux, temperature, and moisture were measured in sessile oak stands with different harvesting intensity (control: 0% intensity; V1: 75%; V2: 80%; V3: 85%; and V4: 100%) during the fifth and sixth years after harvesting. Soil CO₂ efflux was in the range 2-8 μmol CO₂ m⁻² s⁻¹ and indicated an increasing pattern with increasing harvesting intensity. The slope of that pattern became less steep from the fifth to the sixth year after harvesting, thus indicating gradual recovery of soil carbon dynamics in the coppiced stand toward the equilibrium state existing before harvesting. Temperature sensitivity of soil CO₂ efflux ranged between 2.1 and 2.8, with the lowest values measured in the control stand. Soil CO₂ efflux in the control stand was more sensitive to changes in soil moisture than was that on harvested plots. By our calculations, 6.2 tC ha⁻¹ was released from the control stand and 6.2-6.8 tC ha⁻¹ from the harvested stands during the sixth year after harvesting. If mean temperature were to rise by 1 °C, the amount of soil carbon released would increase by 7.7% in the control stand and, depending on harvesting intensity, by 9.0-10.8% in the harvested stands.

Keywords: Low Forest, Soil Moisture, Soil Respiration, Temperature Dependence

Introduction

The increase of the atmospheric concentration of anthropogenic greenhouse gases is recognized as one of the main factors causing global warming during recent decades (IPCC 2014). Soil respiration constitutes a predominant part of ecosystem respiration. After photosynthetic carbon assimilation, it comprises the second largest flux of carbon between terrestrial ecosystems and the atmosphere (Raich & Schlesinger 1992). Therefore, soil respiration is one of the key determinants of net ecosystem carbon exchange. It is not surprising

that much research attention has been devoted to CO₂ release from soils, especially with studies interpreting the fate of carbon and evaluating soil as a source or sink of atmospheric CO₂ in various ecosystems.

Whether an ecosystem corresponds to a sink or source for CO₂ can be estimated from the balance between total net photosynthesis and gross respiration during a given time period. As soil respiration accounts for about 45-80% (Law et al. 1999, Bolstad et al. 2004, Guan et al. 2006) of total ecosystem respiration, it significantly influences temporal (annual and interan-

nual) variability of the net ecosystem carbon balance (Wu et al. 2012, Matteucci et al. 2014). Quantification of soil CO₂ efflux is important for understanding the carbon dynamic of terrestrial ecosystems and predicting possible future scenarios.

Forest ecosystems today cover about 44% of Europe's total area. Soil carbon balance within those ecosystems is predominantly affected by climatic conditions, such as temperature or soil moisture (Inclan et al. 2010), and by the developmental stage and management of forests. As forests age, several structural and physiological changes occur that influence soil respiration. Increasing leaf area and gross primary production during forest growth enhance soil CO₂ efflux through increased supply of assimilates (Hogberg et al. 2001). Changes in root density with stand age affect soil CO₂ efflux due to the amounts of respiring roots, rhizomicrobial biomass, and dead residues (Fang et al. 1998). Canopy cover and understory plants change the soil's microclimatic conditions by reducing solar radiation and precipitation reaching the soil surface as well as the amount of litterfall (Raich & Tufekcioglu 2000). The amount and quality of litter affects microbial composition and the decomposition rate of soil organic material (Fang et al.

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1998, Cleveland et al. 2014). Different studies have described increase (Luan et al. 2011) and decrease (Saiz et al. 2006) of soil CO₂ efflux with forest stand age.

Clear-cutting leads to higher rates of soil CO₂ effluxes (Londo et al. 1999) and decline in soil carbon stocks (Guo & Gifford 2002). On the other hand, afforestation increases total soil carbon stocks (Jandl et al. 2007). The effects of clear-cutting, afforestation of non-forested areas, and stand age on soil CO₂ fluxes have been addressed in several studies. Unlike these effects, the impact of forest management in the ancient coppicing manner on soil carbon fluxes has been poorly studied.

Coppicing is an ancient type of forest management that takes advantage from the vegetative propagation and rapid regeneration of broadleaf tree species when shoots emerge from stumps or roots shortly after the main tree has been cut (Evans 1992). The harvest is usually repeated after a defined time, depending on tree species and site conditions. Compared to trees emerging from seeds, coppiced individuals have roots already established from the previous generation or rotations and therefore grow faster than planted trees (Herrero et al. 2014).

In the past coppice management represented a flexible and diverse system and a good source of income that could be adjusted in response to almost annual changes in labor availability and demands for timber, wood and pasture (Peterken 1993). The extent and importance of coppicing was changing over time. In the second half of the 20th century, coppicing almost disappeared from many parts of Europe, as the firewood got replaced by the fossil fuels (Sieferle 2001), and changes in silvicultural practices led to modern

forestry (Rackham 2008). In some European countries, especially in the Mediterranean region, coppicing still represents an important form of forest management because of the extreme site conditions; for example in Albania (55%), France (47%), Greece (68%), Hungary (29%), Italy (56%), Portugal (37% - UN/ECE-FAO 2000), Bulgaria (48%), Croatia (22%), and also Macedonia (60%). In other parts of Europe, most coppice woods have been transformed into high-forests or left to overgrow (Peterken 1993, Logli & Joffre 2001). Coppiced trees were often reduced to one or two large trunks ("singled out"), felling cycles were prolonged and canopy structure became more uniform.

In recent years, interest in coppice forest management across some EU countries increases (Nielsen & Moller 2008) and has also indicated the possibility of reintroducing this forest practice for both ecological and economic purposes: as part of nature conservation, where the natural regeneration is compromised by environmental conditions and as a source of sustainable energy (Merckx et al. 2012) in countries with limited forest resources for the renewable source of energy.

Coppicing, like other forest management practices, has a significant impact on carbon budget of the forest ecosystem. Due to preservation of root system from the previous generation and according to fast sprout regrowth ability, the response of the ecosystem would differ from the ordinary clear cutting and would be milder. Another open question is the long-term coppice management effect over several rotations on the same site.

The beneficial effects of restoration coppicing are however not guaranteed in all cases. Coppicing can also represent threats

to biodiversity by enhancing the spread of ruderal species of native origin or the invasion of aliens (Radtko et al. 2013). Problems may be related to environmental changes and also insufficient knowledge on coppicing (Verheyen et al. 2012).

To correctly evaluate this management, more information about coppices and their ability to sequester carbon under different harvesting practices, forest regrowth and repeating stand rotations is required.

The aims of our study therefore were: (1) to describe relationships between soil CO₂ efflux in coppiced sessile oak (*Quercus petraea* [Matt.] Liebl.) forest stands with different tending intensities and soil properties (temperature, moisture); and (2) to compare soil CO₂ efflux among the same coppiced forest stands.

We hypothesized that harvesting will significantly increase soil temperature, soil moisture and soil CO₂ efflux. Moreover, we expected no significant differences in the studied parameters among the harvested variants.

Materials and methods

Study site

The studied forest, located 2 km southwest from Sobesice in South Moravia (Czech Republic – 49° 14' 43" N, 16° 35' 60" E), has been managed with a lower coppiced layer and a higher one of seed origin. The stand was 76 years old in 2013 and predominated by sessile oak (*Quercus petraea* – 96%). Stand density was 716 trees ha⁻¹ growing on Cambisol (FAO). Annual mean temperature of the site is approximately 7.5 °C and annual mean precipitation is 550-560 mm.

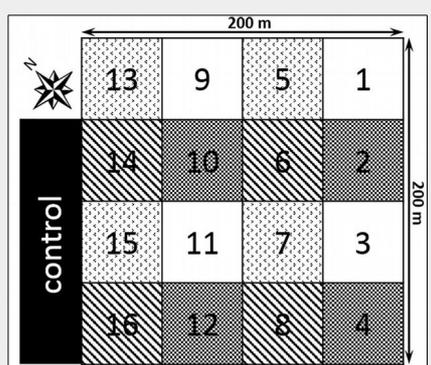
Soil CO₂ efflux measurements were performed in the undisturbed stand and in coppiced stands during the fifth and sixth years after tree harvesting (2008) on a square of 4 ha. The square was divided into 16 plots, each 50 × 50 m with four different harvest intensities, where the number of remaining trees was as follows: V1 at 176 trees ha⁻¹; V2 at 139 trees ha⁻¹; V3 at 97 trees ha⁻¹; V4 was clear-cut. The control plots (V_c), established in the undisturbed part of the stand at the northwestern edge of the harvested plots, had 716 trees ha⁻¹. The design and characteristics of the plots are presented in Fig. 1 and Tab. 1.

Soil CO₂ efflux, soil temperature and soil moisture measurements

Measurements were performed during the 2013 and 2014 growing seasons. In the middle of each plot, three measurement positions were established at a distance of 8 m each other. In the control plot, four groups of three positions were set. In this arrangement, 12 positions for each variant with three iterations per sample were measured.

Measurements of soil CO₂ efflux on all plots were performed on the following dates: 21 May, 20 June, 1 August, and 5 Sep-

Fig. 1 - Design of the studied area with different harvesting intensities: control (V_c), 716 trees ha⁻¹; V1, 176 trees ha⁻¹ (subplots 2, 4, 10, 12); V2, 139 trees ha⁻¹ (subplots 6, 8, 14, 16); V3, 97 trees ha⁻¹ (subplots 5, 7, 13, 15); V4, clear-cut (subplots 1, 3, 9, 11).



Tab. 1 - Characteristics of the studied subplots with four different harvest intensities designed according to scheme presented in Fig. 1.

Plot number	Variant	Stems before harvesting (n ha ⁻¹)		Stems after harvesting (n ha ⁻¹)		Harvesting intensity (%)	
		Avg	SD	Avg	SD	Avg	SD
2, 4, 10, 12	V1	768	91.6	176	17.2	77	4.8
6, 8, 14, 16	V2	704	52.0	139	7.2	80	1.2
5, 7, 13, 15	V3	688	128.8	97	9.6	86	1.7
1, 3, 9, 11	V4	700	74.4	0	-	100	-

tember 2013 and 18 April, 21 May, 17 June, 8 August, 18 September, and 30 October 2014. The measurements during each day took approximately 4 h, from 9:00-13:00 and were performed in conditions without rain, following the same order each time. In total, 180 measurements were performed in all variants/harvesting intensities.

One month before the first measurement in both years, PVC collars 20 cm in diameter were installed 3 cm into the soil at each position. The green parts of plants were gently removed from the measurement position. Soil CO₂ efflux measurements were performed using a Li-8100[®] portable system (Li-Cor, Lincoln, NE, USA) with a 20 cm survey chamber. After the chamber closed, a period (dead band) of 15 s was set to allow steady mixing of the air in the chamber. During the following 60 s, CO₂ concentration was measured repeatedly at 1 s intervals and a linear approach was used to calculate soil CO₂ efflux. During each measurement, soil temperature at 1.5 cm (TPD32 penetrate thermometer[®], Omega, Stamford, CT, USA) and soil moisture in the 0-6 cm profile (ThetaProbe ML2x[®], Delta-T Devices, Cambridge, UK) were measured 5 cm distant outside the collar at three points for each measurement position.

Data analysis

In 2014, mean soil CO₂ efflux (R_m) measurement was correlated with mean soil temperature (T_m), separately for each treatment, using the following exponential equation (eqn. 1):

$$R_m = \beta \cdot e^{\alpha \cdot T_m}$$

with α and β as the regression coefficients.

The proportional change in CO₂ efflux in relation to a 10 °C increase in temperature, known as Q_{10} , was calculated according to Lloyd & Taylor (1994 – eqn. 2):

$$Q_{10} = e^{10 \cdot \alpha}$$

with α being the regression coefficient from eqn. 1. Q_{10} was calculated individually for each harvest intensity (V_C and V_1 - V_4) in 2014 except for the date 17 June 2014, at which time CO₂ efflux was influenced by severely limited soil moisture. Q_{10} was not calculated during 2013 measurements because of insufficient temperature range. Soil CO₂ efflux was normalized for the temperature 10 °C (R_{10}) according to the following equation (eqn. 3):

$$R_{10} = \frac{R_S}{\frac{T_S - 10}{Q_{10}^{T_S - 10}}}$$

where R_S is the soil CO₂ efflux and T_S the soil temperature measured at each position. For normalization of soil CO₂ efflux on 17 June, Q_{10} was set at 1.2, in accordance with Yuste et al. (2003).

A nonlinear model for the dependence of R_{10} on soil moisture was used. R_{10} was

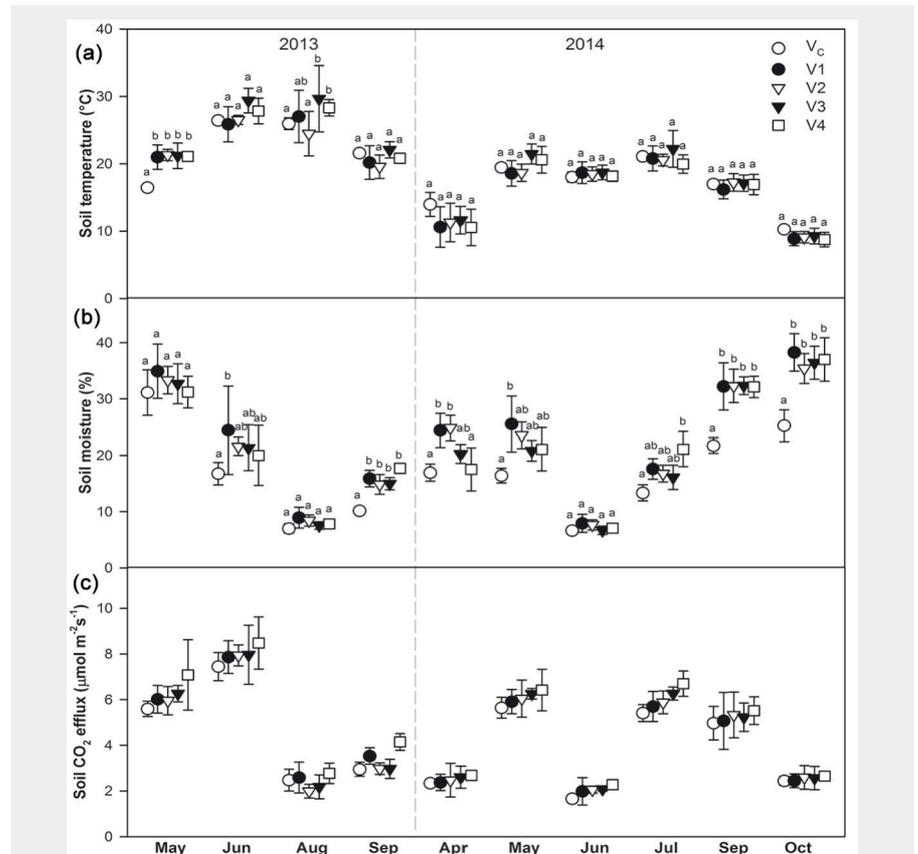


Fig. 2 – Soil temperature at a depth of 1.5 cm (a), soil moisture at a depth of 1-6 cm (b), and soil CO₂ efflux (c) during the 2013 and 2014 growing seasons in the control plots (V_C) with 716 trees ha⁻¹ and the harvested plots V_1 (176 trees ha⁻¹), V_2 (139 trees ha⁻¹), V_3 (97 trees ha⁻¹), and V_4 (clear-cut). The points show mean values with standard deviation indicated by the bars. The small letters indicate statistically significant differences ($p < 0.05$) among the treatments within measurement dates for soil temperature and moisture; for these variables, significant interaction between treatment and date of measurement was confirmed by two-way repeated measures ANOVA.

assumed to follow a sigmoidal function (Graham et al. 2014) of soil moisture (SWC) as follows (eqn. 4):

$$R_{10} = \frac{a}{1 + e^{-\frac{SWC - x_0}{b}}}$$

To evaluate the trend of the tending impact on soil CO₂ efflux, the treatments were ordered from V_C over V_1 to V_4 and values from 1 to 5 were assigned to them on the x-axis. The corresponding means of soil CO₂ efflux were plotted on the y-axis. Finally, the slope from V_C to V_4 was calculated from the linear fit.

Mean soil temperature, soil moisture and soil CO₂ efflux from three positions was calculated for each plot, therefore four values were obtained for each treatment on each date.

To test differences in soil temperature, soil moisture and soil CO₂ efflux over two experimental years, a two-way repeated measures ANOVA was applied with treatment and date of measurement as factors. Statistical significance of the analysis was tested at the level of probability $\alpha = 0.05$.

To confirm permanency of the impact of thinning on soil CO₂ efflux over two experi-

mental seasons, differences in mean soil CO₂ efflux of V_C (treatment without thinning) from soil CO₂ efflux of individual treatments with thinning (V_1 - V_4) were calculated for each measurement day. The differences for each treatment (V_1 - V_4) were compared to zero by applying a t-test. Significance level was set to $\alpha = 0.05$ and Bonferroni's correction for multiple testing was applied.

Statistical analyses were performed using SigmaPlot[®] 11.0 analytical software (Systat Software, San José, CA, USA).

Results

Mean soil temperature from all positions during soil CO₂ efflux measurements ranged from 20.2 ± 2.6 to 27.1 ± 2.4 °C in 2013 and from 9.3 ± 1.1 to 20.9 ± 1.9 °C in 2014, with maxima occurring in the middle of the season.

Two-way repeated measures ANOVA confirmed the statistically significant interaction between treatment and date of measurement. Significant differences among the treatments was, however, found only in May and August 2013 (Fig. 2).

In 2013, mean soil moisture calculated from all positions was the highest in May,

Tab. 2 - P and F values of the two-way repeated measures ANOVA testing differences in soil CO₂ efflux among five treatments and p-values of all pairwise multiple comparison procedures (Tukey's test). Asterisks indicate significant differences between two treatments ($p < 0.05$).

ANOVA Results		Pairwise multiple comparison				
Param	Value	Plots	V1	V2	V3	V4
F	3.4	V _c	0.777	0.816	0.521	0.017*
P	0.035	V1	-	1.000	0.991	0.161
-	-	V2	-	-	0.983	0.142
-	-	V3	-	-	-	0.321

Fig. 3 - Soil CO₂ efflux over soil temperature in 2014 in the control plots (V_c) with 716 trees ha⁻¹ and the harvested plots V1 (176 trees ha⁻¹), V2 (139 trees ha⁻¹), V3 (97 trees ha⁻¹), and V4 (clear-cut). The encircled points are data from June when soil moisture dropped below 10%; these data were not included into calculation of temperature sensitivity of soil CO₂ efflux.

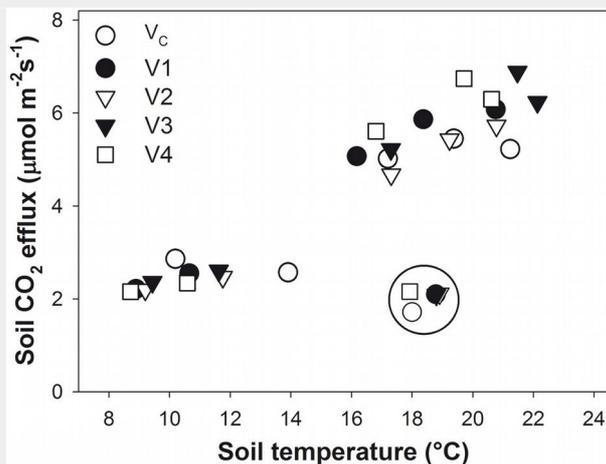
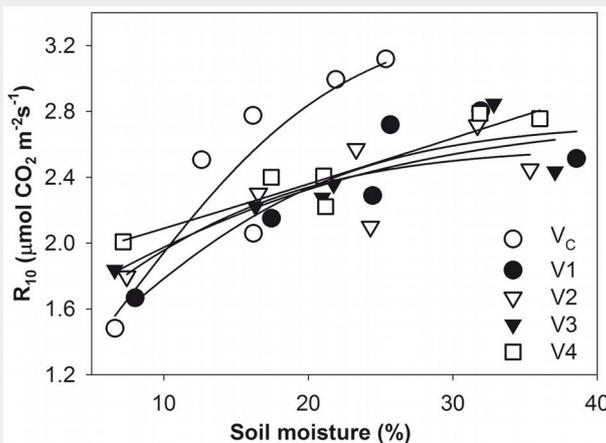


Fig. 4 - Normalized soil CO₂ efflux (R_{10}) vs. soil moisture at 1-6 cm depth during the 2014 growing season in the control plots (V_c) with 716 trees ha⁻¹ and the harvested plots V1 (176 trees ha⁻¹), V2 (139 trees ha⁻¹), V3 (97 trees ha⁻¹), and V4 (clear-cut) fitted to a sigmoid curve [$R_{10} = a/(1+\exp(-(SWC-x_0)/b))$]. The parameters are presented in Tab. 3.



reaching $32.5 \pm 5.0\%$. It then decreased to $8.0 \pm 1.7\%$ in August and then increased slightly until the last measurement ($14.7 \pm 3.2\%$). In contrast, during 2014 the highest soil moisture was measured in the autumn (reaching $34.7 \pm 6.3\%$ in October), while the lowest value was detected in June ($7.2 \pm 1.4\%$).

Soil moisture proved significant interaction between treatment and date of measurement. Soil moisture in V_c was in most cases the lowest out of all treatments. Detailed results of statistical analyses are shown in Fig. 2.

Soil CO₂ efflux followed the pattern of soil temperature, with the highest values

occurring in summer when the mean values from all positions reached up to $8.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 2). Exceptions were the days when soil moisture was low, especially in August and September 2013 during the long-term period of drought and also in June 2014.

Soil CO₂ efflux did not proved significant interaction between treatment and date of measurement. Subsequent Tukey's post-hoc test confirmed the significant difference between V_c and V4 (Tab. 2).

Mean soil CO₂ efflux showed an increasing pattern with increasing harvesting intensity (from V_c through V1 to V4) during most of the measurement dates. The mean differences of soil CO₂ efflux in V_c from soil CO₂ efflux in individual treatments (V1-V4) amounted 0.19 ± 0.14 , 0.21 ± 0.28 , 0.36 ± 0.35 , 0.62 ± 0.32 for V1, V2, V3 and V4, respectively, and it increased from V1 to V4. Analyses confirmed that the differences for V1, V3 and V4 were significantly higher than zero ($p \leq 0.001$). P-value for V2 reached 0.068. When measurements in August and September 2013, when long-term drought severely limited soil CO₂ efflux and suppressed the effect of other factors, were excluded, the mean differences reached values of 0.19 ± 0.11 , 0.32 ± 0.15 , 0.49 ± 0.24 and 0.64 ± 0.29 for V1, V2, V3 and V4, respectively, and the significant difference from zero was confirmed for all treatments V1-V4 ($p > 0.001$).

The slope of the increasing curve changed during the studied years: in 2013 the values ranged between 0.21 and 0.23 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while during 2014 they ranged from 0.05 to 0.20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, indicating a decrease in carbon release from the soil as the harvesting effect became weaker.

From exponential regression of soil CO₂ efflux and soil temperature (Fig. 3), values of Q_{10} were determined for each treatment as follows: V_c = 2.05; V1 = 2.55; V2 = 2.47; V3 = 2.46; and V4 = 2.78. Data from June 2014 were not included because of very low soil moisture (the encircled points in Fig. 3). For June 2014, the Q_{10} value was set at 1.2 in accordance with Yuste et al. (2003). Mean R_{10} from all plots ranged between 1.7 and $2.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in 2014. The lowest values were measured in June under water stress conditions. R_{10} increased with rising soil moisture in all treatments. The steepest increase was found for V_c (Fig. 4). The regression parameters for the relationship between R_{10} and soil moisture for each harvesting intensity are presented in Fig. 4 and Tab. 3.

During the 2014 growing season, mean air temperature at the study site was $15.8 \text{ }^\circ\text{C}$ (1 May – 31 October) and according to our observations (Darenova et al. 2014) was approximately $2 \text{ }^\circ\text{C}$ higher than was the mean seasonal soil temperature.

By substituting mean seasonal soil temperature, mean (seasonal) R_{10} , and Q_{10} of each treatment for 2014 into the first equation (eqn. 1), we calculated that approxi-

Tab. 3 - The parameters of the sigmoid fit of the relationships between R_{10} and soil moisture from Fig. 3 [$R_{10} = a/(1+\exp(-(SWC-x_0)/b))$] during the 2014 growing season in the control plot (V_c) with 716 trees ha⁻¹ and the harvested plots V1 (176 trees ha⁻¹), V2 (139 trees ha⁻¹), V3 (97 trees ha⁻¹), and V4 (clear-cut).

Treatment	a	b	x ₀	R ²
V _c	3.085	6.599	6.876	0.74
V1	2.692	8.220	2.737	0.80
V2	2.438	10.64	-3.710	0.84
V3	2.706	10.09	0.397	0.84
V4	2.815	14.74	-2.293	0.71

mately 6.25 tC ha⁻¹ was released from the soil at the control stand during the 2014 growing season (May-October). The calculated amounts of carbon released from harvested stands ranged between 6.17 and 6.84 tC ha⁻¹ during the sixth growing season after harvest. If mean air temperature were to increase by 1 °C as a consequence of global warming, the amount of the soil carbon released would increase by 7.7 % in the control stand and by 9.0-10.8% in the harvested stands, depending on harvesting intensity.

Discussion

Seasonal variations in soil CO₂ efflux have been observed in almost all ecosystems and often have been associated with changes in temperature, moisture, photosynthate production, and/or their combinations. The main controlling factors may depend on the type of ecosystem and climate. Large spatial variability in soil CO₂ respiration results from large variability in such physical properties of soil as soil water content, thermal conditions, porosity, texture, chemistry, biological conditions (e.g., fine-root biomass, fungi, and bacteria), nutrient availability (e.g., nitrogen mineralization), and others (disturbance history and weathering – Hanson et al. 1993, Fang et al. 1998, La Scala et al. 2000, Xu & Qi 2001). Shibistova et al. (2002) showed a close connection between tree density and soil CO₂ efflux in an open boreal forest. Soil CO₂ efflux rates in areas in proximity to trees were about double compared with open areas, thus indicating that the developmental stage of trees (e.g., age and height) can explain some of the spatial patterns of soil CO₂ efflux in forests.

Canopy removal and exposure to increased solar radiation raise soil temperature in harvested stands, as described by Londo et al. (1999) and Pang et al. (2013). Moreover, Mello et al. (2007) observed increased amplitude range in a harvested stand's temperature as compared to that of a mature (control) stand. In our study, however, no clear effect of harvesting on soil temperature in the fifth and sixth year after coppicing was confirmed.

Lower soil moisture was detected in the control plot compared to other plots with different harvest intensity, and this confirms the findings reported by Lopez et al. (2003) and Mello et al. (2007). The change was caused by removal of the tree canopy and opening of the soil surface to solar radiation, as a consequence of which temperature oscillations increased (Pang et al. 2013).

In several studies, increase in soil CO₂ efflux has been observed during the first year after harvest (Londo et al. 1999, Tedeschi et al. 2006). According to Raich & Tufekcioglu (2000), Mello et al. (2007) and Inclan et al. (2010), the increase in soil respiration in coppice forests may therefore be attributed to various reasons:

- interruption of the canopy cover resulting in higher soil temperatures and soil moisture, which may induce an increase in microbial respiration;
- decomposition of the woody debris left on the soil surface after harvest;
- increased fine root mortality and decomposition of dead roots after harvest;
- development of a grass or herb ground layer of vegetation and its leaf litterfall and rapid root turnover.

After five years since harvesting, the impact of debris decomposition and increased root mortality can be assumed having vanished. On the other hand, changed soil properties and grass development may have contributed substantially to the increased soil efflux rates.

The effect of harvesting on soil CO₂ efflux was confirmed as the efflux remained constantly higher in the harvested plots compared to V_C, and the differences of soil CO₂ in V_C from the individual harvested treatments were significantly higher than zero. Moreover, soil CO₂ efflux increased with harvesting intensity from V_C through V₁ to V₄ (Fig. 2).

The steepness of the CO₂ efflux increase from V_C to V₄ declined from the fifth to the sixth year after harvest, thus indicating a gradual return with age of the coppiced stand's soil carbon dynamics to the state of equilibrium existing prior to harvest. Based on the change in steepness, we may speculate that the effect will wear off within another 5 years such that no difference would be evident between the control and harvested stands.

The recovery of soil carbon balance after harvesting in coppice-type stands may be attributed to the strongly developed root system established during previous rotations, binding of CO₂ by rapidly growing aboveground biomass, and transporting of assimilates to the roots (Drake et al. 2009). This constitutes an advantage over sites with pronounced stress conditions due, for example, to soil water content and erosion (Evans 1992). As the established root system preserves carbon for the next generation, the benefits may be evident during its initial developmental stages. This explains why coppice-type management is so effective on extreme sites. If the rotation is too intensive, however, and the carbon stock does not have time to recover, then site conditions may become depleted or even threatened by alien species (Radtke et al. 2013).

Temperature is the driving factor behind soil CO₂ efflux if it is not limited by high water content in the soil – which results in a lack of oxygen (Jassal et al. 2008) – or by low water content (Xu et al. 2004). Because these conditions reduce soil CO₂ efflux and its sensitivity to temperature, determination of a single value of Q₁₀ for the entire season can bias the temperature normalization of CO₂ efflux. In particular, measuring during periods of low soil water content can cause under- or overestima-

tion of R₁₀ (Darenova et al. 2014). Therefore, data from June 2014, when the soil moisture was only 8 %, were excluded from the Q₁₀ calculation. The calculated Q₁₀ was not used to normalize soil CO₂ efflux on that date inasmuch as R₁₀ would have been greatly underestimated. On the other hand, neither should the effect of temperature be fully excluded. Although the topsoil (where soil moisture was measured) was dry, the deeper horizons which do not suffer from such drought also contribute to CO₂ efflux from the soil surface (Borken et al. 2006). The respiration of these horizons would still be temperature dependent. Therefore, we set the Q₁₀ value equal to 1.2 in accordance with Yuste et al. (2003), who had determined this value for forest soil under water stress conditions.

In our study, the temperature sensitivity of soil CO₂ efflux (Q₁₀) was in the range of 2.05-2.78, and that is comparable with findings from other studies on oak forests (Luan et al. 2011, Rey et al. 2002). Q₁₀ was lower in the control plot than it was in harvested plots. That is in accordance with results from Tedeschi et al. (2006), who found higher Q₁₀ several years after coppicing as compared to older stands. Saiz et al. (2006) had described a decrease in Q₁₀ with age from a young to mature forest. The difference between the control and harvested plots could be caused by different microclimatic conditions triggered by canopy removal or by different contributions of CO₂ sources into total soil respiration, as in our case. As heterotrophic respiration is less temperature sensitive than autotrophic respiration (Boone et al. 1998), we can assume greater contribution of heterotrophic respiration to total soil CO₂ efflux on the control plot than in the harvested plots due to the continuous accumulation of organic matter inputs from tree leaf litter (Saiz et al. 2006).

Normalized soil CO₂ efflux (R₁₀) in V_C increased more steeply with increasing soil moisture than it did in the harvested stands. This can be the reason why, despite lower soil moisture in the control compared to the harvested plots, no significant differences between V_C and harvested stands was found in the majority of cases.

Conclusions

Coppicing had no impact on soil temperature in the fifth and sixth year after coppicing. On the contrary, the harvesting increased soil moisture in comparison to the undisturbed control forest, because of probable increased throughfall.

Soil CO₂ efflux showed significant differences only between V_C and V₄. However, soil CO₂ efflux tended to increase with harvesting intensity from the control to clear-cut plots. The slope of the rising CO₂ efflux curve from V_C toward V₄ became less steep from the fifth to the sixth year after harvesting. On the basis of our results, we assume that in about 10 years after harvesting the soil carbon dynamics of the

coppiced stand would return to the balanced stage of the non-harvested stand.

Soil CO₂ efflux in the undisturbed stand showed steeper increase with increasing soil moisture compared to the harvested stands. This resulted in small differences in soil CO₂ efflux between the control and harvested plots despite the significantly lower soil moisture on the control plot.

The results of this study supported our hypothesis concerning effect of harvesting on soil moisture and soil CO₂ efflux, but not the effect on soil temperature. Moreover, differences in soil CO₂ efflux among the harvested variants were not as significant as expected.

From the viewpoint of sustainability and soil carbon preservation, the rapid restoration of carbon flux under coppicing points to a seemingly advantageous style of forest management.

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