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Effect of different dolomitic limestone dosages on soil respiration in a mid-altitudinal Norway spruce stand

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The study focuses on the effect of chemical amelioration of dolomitic limestone (doses of 0, 2, 3, 4, 6, 9 and 26 t ha^{-1}) on soil respiration in a Norway spruce monoculture in mid-altitudinal elevation during one-year period after application. Firstly, the soil respiration was measured *in situ* as monthly CO_2 efflux from the soil surface horizon in the period May to October 2016. Secondly, basal respiration, microbial biomass carbon and metabolic quotient of the organic H and organo-mineral A horizons were assessed under laboratory conditions within one year after the treatment. Soil CO_2 efflux increased by 3 to 31% and by 29 to 98% for the ameliorant of 2 and 26 t ha^{-1}, respectively, compared to the unlimed control treatment. The CO_2 efflux was significantly driven by external conditions such as soil moisture and temperature, especially in the last seasonal months. Basal respiration of the H horizon increased up to a dose of 9 t ha^{-1} but decreased at 26 t ha^{-1}. In the A horizon, microbial activity increased in all the limed variants compared to the non-limed variant. A similar trend was observed in microbial carbon and the metabolic quotient of the soil. Our results prove that the ameliorant doses commonly used in the forestry sector (3-4 t ha^{-1}) substantially increase the soil microbial activity during (soil CO_2 efflux) and after (laboratory data) the first year after application. This results in the accelerated mineralization of soil organic material and subsequent loss from the forest ecosystem.

Keywords: Amelioration, Basal Respiration, Liming, *Picea abies*, Soil CO_2 Efflux

Introduction

Lime treatment of forest stands has had a fairly long history in Central Europe (Seibt 1977). Historically, lime was used to reduce soil acidification as a negative effect of acidic deposition; it is currently used as a method of supplying the missing nutrients that are blocked in the forest floor (Srámek et al. 2014a). Liming in the Czech Republic reached the highest intensity during the air pollution crisis in the 1970s and 1980s (Hunová & Ostatnická 2004). In particular, it was applied on mountain areas of the Czech borders in the dose of 3 t ha^{-1} (Srámek et al. 2014b). Within the early 21st century, liming was also targeted to mid-altitudinal forests to improve nutrient supply. In addition to the well-known immediate effects of liming on soil pH and nutrient supply, liming widely influences many aspects of the soil environment, which have not been well identified so far (Paradelo et al. 2015, Binkley & Högberg 2016), such as mineralization rate, microbial biomass, metabolic quotient, etc. However, while liming may only be a temporary solution, it is still commonly applied.

Liming results in a number of alterations, mostly in topsoil (Frank & Stuanes 2003). Liming influences the soil sorption complex by increasing the base saturation (Löfgren et al. 2009), especially *via* bivalent base cations (Ca^{2+} and, in case of dolomitic limestone use, Mg^{2+} – Hindar et al. 2003), and increasing of pH. Nevertheless, liming involves risks brought about by antagonism with potassium (K^+), which is susceptible to leaching and blocked for nutrition availability (Weis et al. 2009) and organic matter mineralization. The latter one results from an increase in microbial activity and influences the soil water regime and water retention capacity (Moravčík & Cienciala 2005), mineral nutrient mobilization (Saarsalmi et al. 2011) and nitrogen dynamics (Corre et al. 2003). Liming can also end in the redistribution of fine roots towards the topsoil, which especially in Norway spruce forests (Kakei & Clifford 2002) increases the risk of drought stress (Majdi & Viebke 2004) and uprooting.

The influence of liming on soil chemistry is manifested by edaphon functional group composition and biological activity (Paradelo et al. 2015). An increase in bacterial populations leads to a decrease in the fungi-to-bacteria ratio (Bååth & Anderson 2003) and an increase in the mineralization intensity of organic matter, which can be measured as a release of nutrients and increase in soil respiration/CO_2 efflux (Huber et al. 2006). The response of soil biota to liming can be assessed by monitoring of soil respiration (Nilsson et al. 2001), microbial biomass carbon and metabolic quotient reflecting energy maintenance (Aye et al. 2016). The soil microbial activity is closely related to temperature and moisture (Berryman et al. 2015), thus it can be presumed that the effect of liming will differ under the influence of climate when measured in the field.

Some studies (Augusto et al. 2002, Lee et al. 2007, Binkley & Högberg 2016) found liming as an ambiguous, temporary but rather effective amelioration management.

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Only a few studies in the literature deal with the influence of liming on soil biota; therefore, a critical question regarding the significance of liming on soil respiration and related parameters is still unsolved. Indeed, soil biota response is estimated rather than precisely measured and the response will probably differ according to doses of the ameliorant, especially using extreme amounts.

The aim of the study is to quantify the effect of liming on the biological activity of topsoil in relation to the different doses of dolomitic limestone (0, 2, 3, 4, 6, 9, 26 t ha^{-1}). The hypotheses were the following: (1) soil respiration will increase after liming; and (2) this effect will increase with a limestone dosage.

The respiration was measured (i) *in situ* as CO_2 efflux from the soil surface monthly from May to October 2016 in the year following the application of the ameliorant (November 2015); and (ii) in the laboratory as soil basal respiration using gas chromatography at one year after applying the ameliorant. As supplementary data, the microbial biomass carbon and metabolic quotient were determined. The study is unique from the point of view of the following aspects: (1) the mid-altitudinal elevations (previous studies focused on mountain forests); (2) the wide range of doses of the ameliorant; and (3) the high number of selected investigated parameters (*in situ* soil CO_2 efflux, soil moisture and temperature, basal respiration, microbial biomass carbon, metabolic quotient, soil pH).

Materials and methods

Site description

The experimental plots were established at the Field Research Station Rájec-Němčice, Drahanská vrchovina region (Czech Republic – 49° 26′ 32″ N, 16° 41′ 52″ E; 623 m a.s.l.; flat terrain; moderately warm and humid climate; mean annual temperature 8.15 °C; mean annual precipitation 631 mm). According to the FAO classification system (IUSS-WRB 2015), the soil was classified as Haplic Cambisol with acid granodiorite as bedrock. Potential vegetation in terms of forest site complexes (Viewegh et al. 2003) was classified as *Fagetum mesotrophicum* (nutrient-medium Beech); actual vegetation is composed of 100 % Norway spruce monoculture (*Picea abies* [L.] H. Karst) aged 110 years with 70-75% coverage in the first generation and with 30% undergrowth coverage of Small balsam (*Impatiens parviflora*).

In November 2015, the study plot was sampled prior to the treatment. The soil was characterized by extremely acidic pH and unsaturated soil sorption complex (Tab. 1). The H humus horizon thickness was 3.0-4.5 cm, the A organo-mineral horizon thickness was 1.5-2.5 cm, stock of organic matter in the surface organic horizons was 94.05 t ha^{-1} on average (standard deviation = 19.65).

Experimental design and soil sampling

The homogeneous 35 × 20 m experimental plot was divided into 7 sampling subplots of 5 × 20 m, which were mutually isolated using PVC foil to the depth of 50 cm. Each subplot was spread with a different dose of finely ground dolomitic limestone (the doses of 0, 2, 3, 4, 6, 9, 26 t ha^{-1}). The doses of 2, 4 and 6 t ha^{-1} were used to monitor the soil response near the standard dose of 3 t ha^{-1} (Srámek et al. 2014a, 2014b); the doses of 9 and 26 t ha^{-1} were used to study soil response under the extremely high amounts of the ameliorant. At each subplot, in the longitudinal axes, seven PVC rings were pre-installed for the duration of the experiment (15 cm high, embedded 3 cm deep in the soil; 49 rings in total) at the distance of 3 m to measure CO_2 efflux (see below).

One year after liming (November 2016), a total of 21 soil samples were taken both from the horizons H (organic horizon of humification) and A (organo-mineral horizon), 3 from each lime treatment variant for the H and A horizons. The samples were sieved through a 2-mm sieve and conserved fresh at 4 °C for the time period of two weeks prior to laboratory analysis (assessment of basal respiration and microbial biomass carbon); the soil samples were air-dried and sieved through a 2-mm sieve for the subsequent assessment of pH.

To avoid measuring any CO_2 incoming from the $CaCO_3$ chemical dissolution, we verified the presence/absence of free carbonates in the soil using volumetric quantification with 4 mol HCl according to ISO-10693 (1995).

Measurement of soil CO_2 efflux in situ and expression of R_{10}

In the time period May to October 2016, soil CO_2 efflux was measured from 08:00 to 11:00 a.m. at the end of every month. The CO_2 efflux was measured using a portable system LI-COR LI-8100A® (Li-Cor, Lincoln, NE, USA) with a 20-cm-diameter chamber, fitted on the pre-installed PVC rings. After closing a chamber, a period (dead band) of 15 s was set to allow steady mixing of the air in the chamber. During the following 60 s, the CO_2 concentration was measured repeatedly at 1-s intervals, and a linear approach was used to calculate the soil CO_2 efflux.

During each measurement, the soil temperature (°C) at 1.5 cm (TPD32 penetrate thermometer, Omega, Stamford, CT, USA) and soil moisture (%vol) in the 0-6 cm profile (ThetaProbe ML2x®, Delta-T Devices, Cambridge, UK) were measured at a distance of 5 cm outside the PVC ring for a minimum of three points for each measurement position.

Within the forest stand close to the experimental plots, the continuous measurements of soil CO_2 efflux were carried out applying an automated closed (non-steady-state through-flow) system (developed at the Global Change Research Institute in Brno, CZ) with six chambers. The design and installation were described by Darenova et al. (2016). Within each chamber, the soil temperature (thermometers PT-100®, Treston a.s., CZ) was measured simultaneously with soil CO_2 efflux at the depth of 1.5 cm. Data from the continuous measurements were used to determine the temperature sensitivity of soil CO_2 efflux during the periods of individual manual measurement periods.

Soil CO_2 efflux (R_s) from the continuous measurements by the automated system from one week containing the measurement campaign was plotted against soil temperature (Temp) and this was expressed by an exponential regression curve with the regression equation (eqn. 1):

$$R_S = \beta \cdot e^{\alpha \cdot Temp} \quad (1)$$

where α and β are the regression coefficients. Mean Q_{10} (the proportional change in CO_2 efflux in relation to a 10 °C increase

Tab. 1 - Selected soil properties characterizing the initial state in horizons H and A - November 2015. (sd): standard deviation; (n): number of repetitions; (pH/H_2O): active soil pH; (pH/KCl): exchangeable soil pH; (Corg): organic (oxidizable) carbon content; (Cmic): microbial biomass carbon; (BasResp): basal respiration; (qCO_2): metabolic quotient; (CEC): cation exchange capacity; (BS): base saturation; (C/N): carbon-to-nitrogen ratio; (dw): dry weight.

Variable	Units	H horizon (n = 13)		A horizon (n = 11)	
		mean	sd	mean	sd
pH/H_2O	-	3.41	0.12	3.42	0.04
pH/KCl	-	2.81	0.15	2.61	0.06
Corg	%	32.24	2.75	9.77	0.9
Cmic	µg C g^{-1} dw	1261.94	131.84	282.22	68.64
BasResp	µg C-CO_2 h^{-1} g^{-1} dw	3.52	0.55	1.31	0.19
qCO_2	µg C-CO_2 mg^{-1} Cmic h^{-1}	2.8	0.5	4.9	1.1
CEC	cmolc kg^{-1}	36.42	2.52	34.61	0.89
BS	%	17.67	3.11	8.26	1.13
C/N	%	23.46	2.06	31.73	2.99

in temperature) from six chambers was calculated according to Lloyd & Taylor (1994 – eqn. 2):

$$Q_{10}=e^{10\cdot\alpha} \quad (2)$$

being α the regression coefficient from eqn. 1.

The Q_{10} values were used to normalize soil CO_2 efflux from each position of the liming experiment for the temperature 10 °C (R_{10}) according to the following equation (eqn. 3):

$$R_{10}=\frac{R_s}{Q_{10}^{\frac{Temp-10}{10}}} \quad (3)$$

Laboratory determination of soil properties

Laboratory analyses were performed in autumn 2016. The basal soil respiration (soil native CO_2 release) was determined according to the soil analyses guidelines published by the Central Institute for Supervising and Testing in Agriculture (Zbíral 2016) and the International Organization for Standardization (ISO-16072 2002). The measurement was performed using the YL 6500GC® gas chromatograph (Soft Clarity Next Generation, YL Instruments Ltd., Anyang, Korea). The incubation was carried out for 24 hours at a constant temperature of 22 °C. The CO_2 concentration was determined using an all-purpose detector PDD (Pulsed Discharge Detector).

Microbial biomass carbon (Cmic) was assessed using the fumigation-extraction method according to Vance et al. (1987) and Joergensen (1995). The samples were analysed as fumigated (24-hour chloroform fumigation) and as non-fumigated. The organic carbon was extracted from all the samples with 0.5M K_2SO_4, and the C concentration was analysed by wet combustion (Yakovchenko & Sikora 1998). Briefly, a mineralization mixture consisting of 25M $K_2Cr_2O_7$, 95% H_2SO_4 and distilled water was added to the leachate. Mineralization occurred at 135 °C for 40 minutes. The soil extract absorbance was measured spectrophotometrically at a wavelength of 340 nm.

The metabolic quotient (qCO_2) was calculated according to ISO-16072 (2002), with qCO_2 [µg C-CO_2 mg Cmic^{-1} h^{-1}] = basal respiration [µg C-CO_2 h^{-1} g^{-1} dw] / Cmic [µg C g^{-1} dw].

Soil pH was determined according to ISO/DIS-10390 (1992). It was assessed as both active (pH/H_2O) and exchangeable (pH/KCl) in water or 1M KCl, respectively, for the air-dried soil samples for a soil:eluate ratio of 1:5 (horizon H) and 1:2.5 (horizon A). For the measurement, a glass electrode WTW SenTix 81™ (Thermo Fisher Scientific, Whaltham, MS, USA) combined with a fluid electrolyte and temperature sensor was used.

Statistical analysis

Analysis of variance (ANOVA) and Fisher's LSD test were performed using the software package Statistica® ver. 12 (StatSoft, Tulsa, OK, USA). One-way ANOVA at a significance level α = 0.05 (95% confidence interval) was used for the comparison of soil properties of the individual liming variants. *Post-hoc* multiple comparisons was used in the case of significant differences among groups, using the Fisher's LSD test.

We tested statistical relations of CO_2 efflux depending on either the categorical variables (lime doses, months) or the continuous variables (temperature, moisture).

Correlation and linear regression were carried out in the R language and environment version 3.3.1 (R Core Team 2018) using RStudio version 1.0.126. The correlation was verified via the Pearson's correlation coefficient using the function "cor()" at a significance level of 0.05 with a critical value of 0.413 for n = 21.

We used a Bayesian version of linear mixed effect models to estimate the effect of limestone addition, time during vegetation season (expressed as the month of measurement) and two more covariates (soil temperature and soil moisture) as well as the significance of these effects. Linear mixed effect models were chosen as measurements for each month on the same plot were repeated (this information was stored in data using plot ID). Plot ID was specified as a random effect in all the models. Variables such as soil moisture, soil temperature, dolomitic limestone dosage and months were considered as fixed effects. All the fixed-effect explanatory variables were considered as continuous, and were scaled before analysis to reduce the multicollinearity of variables when adding the interaction term; scaled estimated coefficients are also directly comparable across models. Limestone dosage values were log transformed (natural logarithm) prior to analysis and the trend of the relationship between limestone dosage and R_{10} was straighter after transformation. Limestone dosage values were back-transformed to the original values for the graphical presentation of the results. Control (zero addition) was kept as zero also for the transformed limestone dosage. We fitted several models, some with just one fixed-effect explanatory variables, others with their combination. We also included the interaction of months and limestone dosages as preliminary analysis revealed that the effect of limestone dosage on R_{10} could differ along the vegetation season. All the models were fitted using the package "brms" ver. 2.6.0 (Bürkner 2017) running in the R environment. Uninformative priors were chosen in all the models (defaults in brms). The fitted models were compared using LOO IC, which is an information criterion based on the "leave-one-out" cross-validation method (Vehtari et al. 2017). Similarly to the well known Akaike Information Criterion (AIC), the model with smaller LOO IC has better fit to the data. Significance of the fixed-effect variables was evaluated using 95% highest definition intervals (HDI) whether zero value lies within credible values, *i.e.*, whether it is within 95% HDI (see more in Kruschke 2011). We also reported LOO adjusted version of Bayesian R^2 as a measure of goodness-of-fit. For the final model, estimates were reported for the version of the model with unscaled fixed-effect variables.

All the graphs were created using the package "ggplot2" version 2.2.1 (Wickham 2016).

Results

Soil reaction after liming

Liming influenced pH/H_2O in both horizons (Fig. 1a, Fig. 1b), but pH/KCl was significantly affected only in the horizon H. The pH/H_2O ratio increased in all the treatments compared to the control; statistical significance was detected in the treatments only in the H horizon (p = 0.0032) at the doses

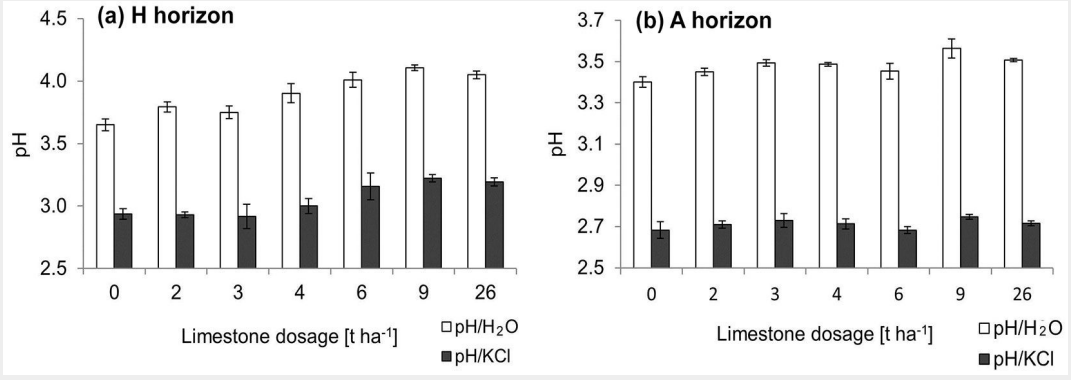

Fig. 1 - Means of active (pH/H_2O – white bars) and potentially exchangeable (pH/KCl – black bars) soil reaction of the horizons H (a) and A (b) for each liming variant one year after the application of the ameliorant. The error bars denote the standard deviation.

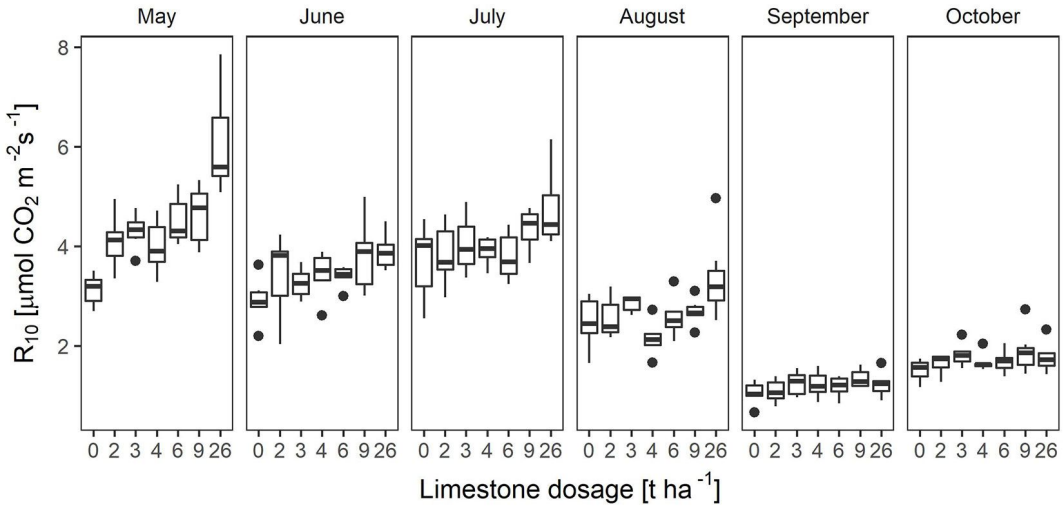

Fig. 2 - Medians of normalized soil CO_2 efflux for 10 °C (R_{10}) by month and application doses of dolomitic limestone. Upper and lower limits of the box (interquartile range – IQR) denote the 1st and 3rd quantile (Q1 and Q3, respectively); minimum and maximum are given by Q1 - 1.5 IQR and Q3 + 1.5 IQR, respectively; points are outliers.

of 4 (p = 0.0236), 6 (p = 0.0028), 9 (p = 0.0004) and 26 t ha^{-1} (p = 0.0013). The pH/KCl ratio increased only in the H horizon, however without statistical significance. The highest pH increase in comparison with the non-limed area occurred within the H horizon the variant 9 t ha^{-1} (pH/KCl: 0.29; pH/H_2O: 0.46). Within the A horizon, the pH increase was very low in response to the ameliorant doses, but the pH/KCl values remained almost unchanged after liming (Fig. 1b).

In situ seasonal measurements

Both soil temperature and moisture profoundly changed during the season. Mean soil temperature ranged 17.9 to 21.1 °C, except for October when it dropped to 7.0 °C. Soil moisture was the highest in May (18.5 %) and the lowest in September when it was only 3.7% (with a minimum of 1.8%, which corresponds to almost dry soil). Otherwise, soil moisture ranged 11.9 to 15.4%.

The seasonal pattern of monthly R_{10} in all the treatments was characterised by the highest values in May and the lowest in September (Fig. 2). The most significant factor affecting R_{10} during the season was the increasing drought at the end of summer. This fact was mostly evident in September when the lowest R_{10} was recorded. In October, an increase in soil moisture resulted in a higher R_{10} compared to September.

During the observed period, the average R_{10} showed statistically significant differences between liming doses during the period May-August ($p < 0.05$). The largest differences in R_{10} for the liming dosage were found in May ($p < 0.0001$). In each month, R_{10} showed an upward trend with increasing liming intensity. The steepest gradient was found out in May, while the lowest was monitored in September and October (Tab. 2) when the soil CO_2 efflux was more subjected to external factors caused by weather conditions than to liming. The exceptions were found in August at the dose of 4 t ha^{-1} and in September at the doses of 2 and 4 t ha^{-1}, where the lowest R_{10} of all the variants were observed. Overall, the lowest values were found out in September and only slightly higher in October. The overall dynamics of R_{10} had a downward trend during the season and the highest liming effect was found in May with a 98% increase at the extreme doses (26 t ha^{-1}). The reference doses, which are the most frequently used in forestry (2-4 t ha^{-1}), resulted in a 7-17% increase in R_{10} in the all-season average with the lowest response at the dose of 4 t ha^{-1} (Tab. 2).

Soil CO_2 efflux under influence of seasonal factors and treatments

Respiration was significantly affected by both categorical and continuous variables (Tab. 3). The influence of limestone dosage on the CO_2 efflux was affected by external factors. The influence of liming alone was quite weak (M1), while the best fitting model was M11 which combines the limestone dosage, month of measurement and moisture. As both factors condition soil biological activity, the different effect of liming under the influence of seasonal dynamics lies either on moisture, which markedly decreased in September or temperature, which markedly decreased in October (reflected in model M11 by the interaction LimeVol × month).

The best fitted model M11 includes all the studied variables and the interaction LimeVol × month. Tab. 4 shows the relative influence of the scaled variables included in model M11, among which month had the strongest (negative) influence. In the measured season the most intensive CO_2 efflux was in May and the weakest in October under the influence of different factors. The modelled influence of soil moisture on CO_2 efflux, together with doses of lime and season (for months May, July and September) is shown in Fig. 3. An increase in CO_2 efflux with increasing soil moisture (increasing intercept of the curves) is evident, as well as the steeper dependence of CO_2 efflux on liming at the beginning of season (May), where the biological activity was unlimited

Tab. 2 - Mean R_{10} (in µmol CO_2 m^{-2} s^{-1}) by month and doses of dolomitic limestone expressed as the percentage difference (perc) in the month *vs.* the control treatment (LimeVol = 0).

LimeVol (t ha^{-1})	May		June		July		August		September		October	
	mean	perc	mean	perc	mean	perc	mean	perc	mean	perc	mean	perc
0	3.13	100.0	2.91	100.0	3.69	100.0	2.49	100.0	1.13	100.0	1.51	100.0
2	4.09	130.8	3.41	117.1	3.85	104.5	2.56	102.9	1.09	97.1	1.64	108.7
3	4.30	137.6	3.26	112.0	4.04	109.6	2.85	114.3	1.24	110.2	1.82	120.3
4	4.00	127.9	3.44	118.1	3.92	106.2	2.15	86.2	1.10	97.9	1.60	105.6
6	4.52	144.7	3.40	116.7	3.79	102.9	2.57	103.3	1.18	104.9	1.73	114.6
9	4.63	148.0	3.79	130.0	4.35	117.9	2.69	107.8	1.35	119.4	1.88	124.6
26	6.18	197.6	3.89	133.4	4.75	128.8	3.36	134.8	1.22	108.7	1.77	117.2

Tab. 3 - Effect of dosage of dolomitic limestone and other variables (month, moisture and temperature) on R_{10}. All the fitted models are Bayesian mixed effect models with random effect of plot ID. Explanatory variables were scaled before fitting, so the estimated parameters are on scaled scale. (LOO-ajd R^2): LOO adjusted Bayesian R^2; (LOO IC): information criterion – models with lower value of LOO IC had better fit; SD (ID): standard deviation among random effects in the scale of CO_2 efflux. Models are ordered according their LOO IC from the best-fitting model to the worst one. Variables abbreviations: (LimeVol_ln): dosage of dolomitic limestone transformed by natural logarithm; (month): month of measurements; (Moist): soil volumetric moisture; (Temp): soil temperature.

Model No.	Predictor with estimated parameters	LOO-adj R^2	LOO IC	SD(ID)
M11	2.92 + 0.18·LimeVol_ln - 0.85·month + 0.47·Moist - 0.20·LimeVol_ln:month	0.819	474.2	0.30
M9	2.92 + 0.18·LimeVol_ln - 0.86·month + 0.47·Moist	0.787	517.2	0.28
M7	2.92 - 0.85·month + 0.5·Moist	0.786	519.9	0.33
M10	2.91 + 0.30·LimeVol_ln - 1.19·month - 0.22·Temp - 0.21·LimeVol_ln:month	0.726	588.5	0.16
M8	2.91 + 0.30·LimeVol_ln - 1.19·month - 0.22·Temp	0.670	614.9	0.14
M5	2.91 - 1.06·month + 0.28·LimeVol_ln	0.683	628.9	0.13
M6	2.92 - 1.19·month - 0.20·Temp	0.680	632.3	0.34
M2	2.91 - 1.06·month	0.663	645.7	0.33
M12	2.88 + 0.07·LimeVol_ln + 0.60·Temp + 0.91·Moist + 0.15·LimeVol_ln:Moist	0.649	658.5	0.32
M4	2.92 + 0.86·Moist	0.407	803.8	0.16
M3	2.90 + 0.55·Temp	0.158	902.6	0.11
M1	2.90 + 0.29·LimeVol_ln	0.028	941.1	0.08

by moisture and temperature. Therefore, equal response of biological activity on amelioration during the whole season cannot be expected.

Soil microbial characteristics one year after liming

In the soil samples collected for soil respiration no carbonates were detected, hence all CO_2 measured during the analysis comes from respiration. In one year, the effect of liming was evident within both the H and A horizons (Fig. 4a, Fig. 4b).

For the H horizon, apart from the 26 t ha^{-1} treatment, the values of soil respiration tended to increase depending on the in-

Tab. 4 - Scaled and unscaled parameter estimates for final model M11 together with their highest density intervals (HDI). HDI are Bayesian alternative to confidence intervals with either scaled or unscaled variables. (LimeVol_ln): dosage of dolomitic limestone transformed by natural logarithm; (month): month of measurements; (Moist): soil volumetric moisture.

Variable	Scaled variables (μ = 0; σ = 1)			Unscaled variables		
	Estimate	Lower 95% HDI	Upper 95% HDI	Estimate	Lower 95% HDI	Upper 95% HDI
intercept	2.92	2.81	3.02	3.980	3.409	4.559
LimeVol_ln (A)	0.18	0.07	0.29	1.075	0.793	1.356
Month (B)	-0.85	-0.92	-0.78	-0.322	-0.388	-0.256
Moist	0.47	0.40	0.55	0.085	0.071	0.099
A × B interaction	-0.20	-0.26	-0.14	-0.119	-0.155	-0.083

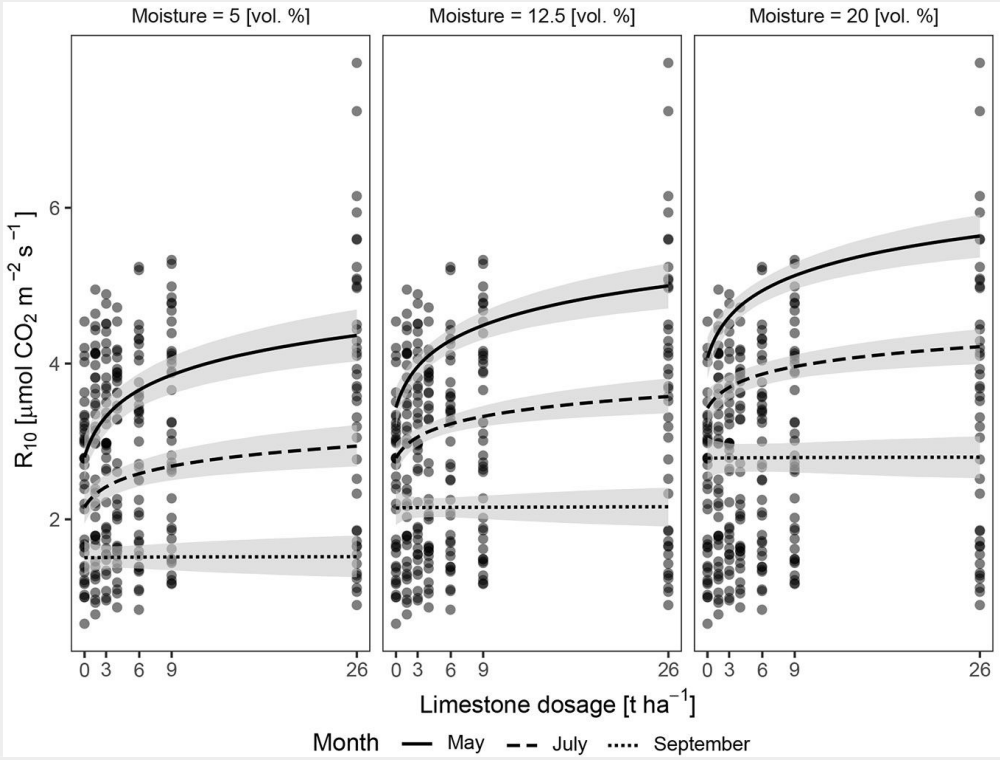

Fig. 3 - Graphic results of the Bayesian modelling. Model M11 values of CO_2 efflux (R_{10}, *y*-axis) in dependence on doses of lime (*x*-axis), in three categories of soil moisture (5, 12.5 and 20 vol. %) and three selected months (May, July and September). The grey belts denote 95 % confidence interval.

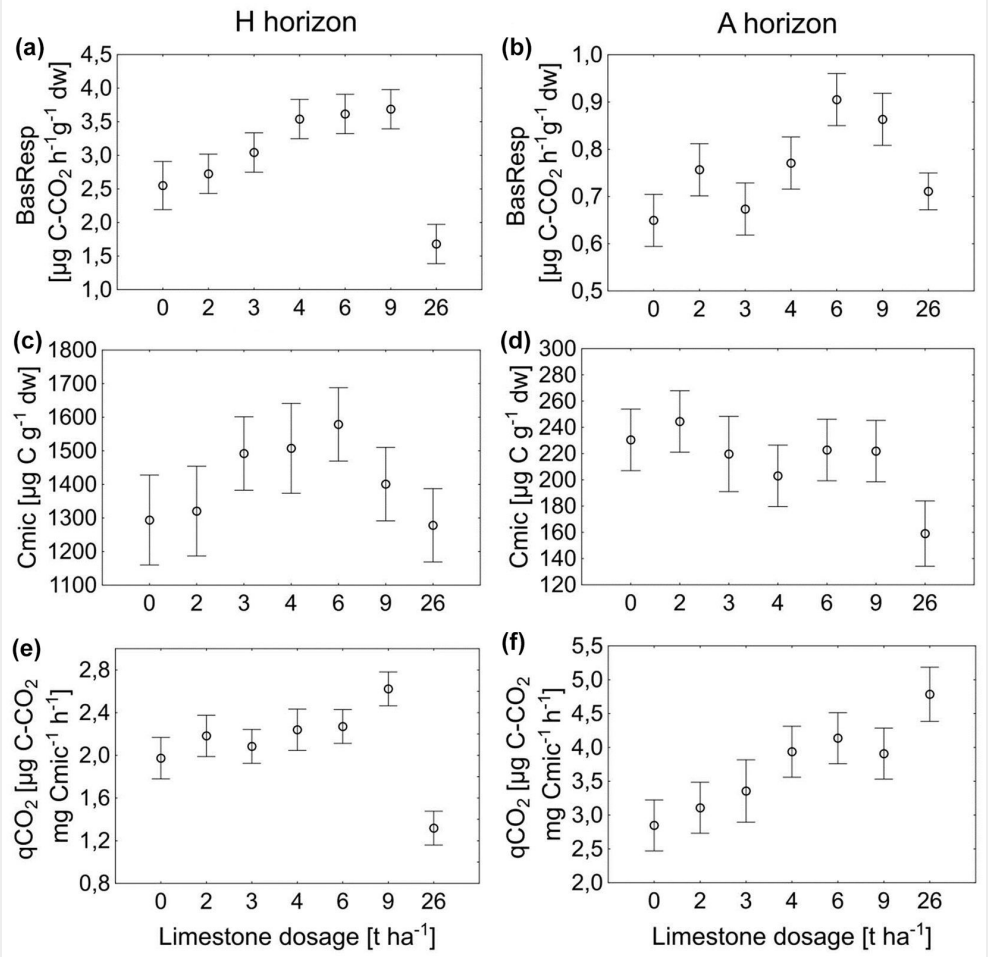

Fig. 4 - Microbial activity expressed by basal soil respiration (a, b), microbial biomass carbon (Cmic – c, d) and metabolic quotient (qCO_2 – e, f) for the horizons H and A. Error bars represent the 95 % confidence intervals.

creasing amounts of the ameliorant. Unlike the CO_2 efflux measured from the soil surface, the 26 t ha^{-1} variant unexpectedly reached the lowest soil respiration level. The highest values were reached for the 9 t ha^{-1} limed area.

The lowest values in the A horizon were reached in the control subplot; compared to them, the different ameliorant doses caused an increase in soil respiration activity. However, the most heavily limed area showed significantly lower soil respiration than did the variants at 9 and 6 t ha^{-1}.

The microbial biomass carbon (Cmic) amount was dependent on ameliorant doses in both horizons. With an increasing ameliorant dose, there is a gradual increase in the Cmic values in the humus horizon, followed by a significant decrease at the doses of 9 and 26 t ha^{-1}, which are even lower than the control (Fig. 4c). In the A horizon, Cmic decreased with increasing the ameliorant dose (except for the variant 2 t ha^{-1} where the increase was non-significant) to the lowest values in the most heavily limed treatment. Therefore, in the control, immediately after the application of the 2 t ha^{-1} variant, it reaches the highest values (Fig. 4d).

In both horizons H and A, the soil respiration was significantly affected by Cmic, (Pearson's r = 0.721, $p<0.05$; and r = 0.517, $p<0.05$, respectively).

The metabolic quotient (qCO_2) was found to be higher in the A-horizon than in the H-horizon (Fig. 4e, Fig. 4f). Moreover, all the treated subplots showed the increased qCO_2 values in comparison with the control, except for the variant 26 t ha^{-1} in the H horizon (Fig. 4e), where a remarkable decrease in qCO_2 was observed.

Discussion

The practice of limestone application may affect various aspects of soil properties and microbial activity. Andersson & Nilsson (2001) demonstrated an increase in pH of the upper soil layers over a period of 12 or more years after the liming doses of 8.8 t ha^{-1}. Conversely, lower pH values in mineral soil 4 years after liming at the dose of 3.25 t ha^{-1} are reported by Lundström et al. (2003). The short-term effect of the soil pH modification is documented by Vavříček & Kučera (2016) who reported a minimum impact on pH 15 years after the application dosage of 26 t ha^{-1}. By contrast, McKie et al. (2006) discussed the potential risks connected with the inappropriately high doses of limestone and consequent substantial pH changes in the humus layer. Soil buffering capacity was demonstrated in our study, when one year after liming there was only a slight pH increase in the two observed horizons (0.4 in H horizon, 0.1 in A horizon), especially when thick humus layers leading to moder and mor humus forms evolve – a situation typical of most of the Norway spruce stands (McCauley et al. 2009).

Both methods applied in this study for determining soil respiration demonstrated the dependence of this parameter on the individual doses of ameliorant. In particular, basal soil respiration in organic horizons showed an increase when increasing the ameliorant dose (Nilsson et al. 2001, McKie et al. 2006), except for the 26 t ha^{-1} treatment, which decreased to values even lower than the non-limed treatments. These results are inconsistent with the general expectations and it is possible that extreme ameliorant doses may have a different impact on soil biological properties compared to lower doses. However, the literature does not provide any examples of the inhibition of soil biological activity due to the application of extreme doses of the ameliorant. Moreover, our results from field measurements did not reveal any decrease in soil CO_2 efflux under the highest limestone dosage. The possible cause is a significant alteration of the microbial community due to the substantial chemical impact (similar to the findings by Shah et al. 1990), leading to changes both in the total volume of microbial biomass and in the related microbial activity.

The respiration of the plant root system is

also an important factor affecting the resulting soil CO_2 efflux measured in the field (Raich & Tufekciogul 2000). Comstedt et al. (2011) revealed that respiration of the rhizosphere accounted for about 50% of the total soil CO_2 efflux in a mature Norway spruce forest. According to Hanson et al. (2000) the proportion of root respiration can be 10-90 % of total soil respiration, depending on vegetation type and season. However, the subdivision of the total soil respiration in root respiration (autotrophic) and soil microorganism respiration (heterotrophic – Kuzyakov & Larionova 2005) is still unclear (Bhupinderpal et al. 2003, Baggs 2006) and often yielded different results (Bond-Lamberty et al. 2004). Our study dealt with the total soil respiration (CO_2 efflux) which characterises the response of the whole soil ecosystem in our study.

Although field measurement of CO_2 efflux from soil under natural conditions allows for the respiratory activity dynamics to be monitored during the season, the effects of external environmental factors can also be incorporated. These factors substantially drive the temporal (from daily to seasonal) variability of soil CO_2 efflux and include mainly soil temperature and moisture (Davidson et al. 1998). In our study, the reduction of normalized CO_2 efflux at 10 °C (R_{10}) under soil moisture in September was observed, and the corresponding soil moisture was only 3.7 %. Under such conditions, soil CO_2 efflux is almost independent on temperature, and soil moisture becomes the driving factor (Yuste et al. 2003). The R_{10} decline in October can be associated with the decrease in microbial biomass and activity at the end of the season and with permanent low temperatures. Moreover, the increase in respiration during warmer months could lead to the significant interaction between R_{10} and temperature observed in this study (Rigobelo & Nahas 2004).

The largest differences in field measurements were observed for the treatment 26 t ha^{-1} in May, when R_{10} increased by 97.6% compared to the control. However, this enormous difference decreased during the season, and by September, the increase was only 8.7% (Tab. 2). Lundström et al. (2003) reports a 35% increase in soil respiration 14 years after liming the spruce stands at the dose of 8.75 t ha^{-1} compared to the control. In our case, the average R_{10} measured in May increased by 32.4% after 9 t ha^{-1} liming; the lowest increase in this variant was detected in August (7.8%).

In some cases, the expected liming effect on microbial soil activity is also reflected in the increase in the carbon microbial biomass Cmic (Aye et al. 2016) and metabolic quotient qCO_2 (Lorenz et al. 2001). On the other hand, Priha & Smolander (1994) reported no or only minimal changes in the amount of microbial biomass after liming. In our study, we found that the response on liming may differ between the individual horizons and also in dependence on limestone dosage. In the H horizon, Cmic tended to increase after liming, except for the dosage of 26 t ha^{-1}. On the contrary, Cmic slightly decreased after liming the A horizon except for the dosages of 2 t ha^{-1}. Therefore, it may be assumed that in the A horizon, liming acted as an inhibitor, to a certain extent, and the Cmic decreased as the dose of dolomitic limestone increased.

The effect of various liming doses on the metabolic quotient (qCO_2) is expressed as an increase in qCO_2 values according to increasing of ameliorant doses. This can be related to bacterial communities reacting to changes in soil chemistry (Bauhus & Khanna 1999). However, the exception is the 26 t ha^{-1} variant within the H horizon, which showed 33.2% decrease compared to the control. In this case, the extreme doses could lead to a temporal inhibition of microbial activity (qCO_2).

Despite the current application of dolomitic limestone on forest soils, it may be discussed whether liming is a suitable practice to improve soil chemistry. Liming results in an increase of soil biological activity and hence in an increase in mineralization of organic layers. Although this is confirmed by the presented results, there are still unknown aspects regarding the consequences of liming. The following questions still need to be answered: (i) what is the proportion of autotrophic/heterotrophic respiration? (ii) are we able to measure how fast is the organic layer mineralization? (iii) what are the consequences of liming on long-term plant nutrition and soil water regime?

Conclusions

In general, liming increased soil respiration in our experimental forest stand, and this was confirmed by both *in situ* measurements and laboratory analyses. However, the effect of liming *in situ* was mitigated by environmental conditions such as drought or low temperatures.

The hypothesis that the effect of liming will increase with limestone dosage was fully confirmed only for *in situ* measurements of soil CO_2 efflux and qCO_2 in A horizon. For the basal respiration, a decrease for the dose of 26 t ha^{-1} was observed, with values in the H horizon even lower than in the control.

In the H horizon, liming increased the amount of microbial biomass, and a gradual inhibition of microbial development was observed at the highest ameliorant doses. In contrast, microbial biomass development in the A-horizon was inhibited after liming and this inhibition increased with the ameliorant dose.

Our results confirm that the dose of ameliorant commonly used in forest management (3 t ha^{-1}) significantly increases the microbial activity of forest soil even one year after liming. This may accelerate the mineralization of soil organic material and lead to a decrease in soil quality. Future studies based on soil respiration measurement under controlled laboratory conditions will provide a better understanding of the potential response of soil microorganisms to changes in soil chemistry under optimal conditions.

List of abbreviations

(BasResp): basal respiration; (BS): base saturation; (CEC): cation exchange capacity; (Cmic): microbial biomass carbon; (Corg): organic (oxidizable) carbon content; (C/N): carbon-to-nitrogen ratio; (dw): dry weight; (HDI): highest density interval; (LimeVol): liming variant; (LOO-ajd R^2): adjusted R^2; (LOO IC): LOO information criterion; (Moist): soil moisture; (pH/H_2O): active soil pH; (pH/KCl): exchangeable soil pH; (qCO_2): metabolic quotient; (Q_{10}): the proportional change in CO_2 efflux in relation to a 10 °C increase in temperature; (R_{10}): normalized soil CO_2 efflux for 10 °C; (R_s): soil CO_2 efflux; (sd): standard deviation; SD (ID): estimation of variability among random effects in scale of CO_2 efflux; (Temp): soil temperature.

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