

SMALL SCALE SPATIAL VARIABILITY AND PATTERN OF SOIL RESPIRATION AND WATER CONTENT IN WET AND A DRY TEMPERATE GRASSLANDS AND BARE SOIL

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Abstract

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Spatial variability and pattern of soil respiration and soil water content were examined in uniform patches of two different temperate grasslands and on bare soil. Soil respiration was measured by using hemisphere gas exchange chamber of 20 cm diameter along 15 m long transects at 20 cm spacing. The most simple, but commonly used expression of variability is the coefficient of variation (CV) of the measured variable. The lowest CV of 75 samples of soil respiration was found on the humid mountain meadow (28%), followed by the bare soil (38%) and the dry sandy grassland (45%). More elaborated approach to study the spatial variability of some property is geostatistical analysis, revealing the size of characteristic patches of soil respiration and soil water content. Ranges of spatial autocorrelation for soil respiration were 0.39 m for bare soil, 0.47 m for humid meadow and 0.73 m for sandy grassland, while values of spatial autocorrelation for soil water content were 0.48 m, 0.90 m and 1.08 m, respectively. Our work proved that in dry grassland, where water shortage (drought) is a common feature in the vegetation period, the ranges of spatial autocorrelation and hence the characteristic patch sizes of soil CO₂ efflux and soil water content were larger than in the humid grassland.

Key words: chamber technique; coefficient of variation; semivariance; soil respiration; spatial pattern

Abbreviations: CV – coefficient of variation, SR – soil respiration, SWC – soil water content, T – soil temperature

Introduction

Soil respiration (SR) in grasslands is important considering that large amount of organic matter is contained in the belowground plant parts and in the soil (Rice, Garcia, 1994).

SR displays quite large spatial and temporal variability regardless of the type of ecosystem, and soil processes have scale- and time-dependent features (Stoyan et al., 2000). Several works report on collection of soil core samples for further analysis of the variability of SR, but use of gas exchange chambers in field measurements is more common. Methodological problems related to adequate position (random or nested samples in previously categorized patch types, Epron et al., 2004; Maestre, Cortina, 2003) and number of samples (18 plots in Xu, Qi, 2001, 60 plots in Maestre, Cortina 2003, 72 plots in Epron et al., 2004, 67–85 in Adachi et al., 2005) are usually discussed. Role of the spatial variability of different factors influencing SR and other aspects of ecosystem functioning (nitrogen cycling, trace gas emissions, vegetation gas exchange, etc.), like soil temperature, water content and elevated air CO₂ concentration (Fang et al., 1998; Xu, Qi, 2001; Maestre, Cortina, 2003; Szerdahelyi et al., 2004), distribution of soil organic carbon and hence microbial assemblages (Fang et al., 1998; Bird et al., 2002; Green et al., 2004; Horner-Devine et al., 2004; Xu, Baldocchi, 2004), amount of litter deposition, soil density and porosity, content of different elements, vegetation pattern and dynamism in some community types (Green et al., 2004; Horner-Devine et al., 2004) etc. have also been investigated. Spatio-temporal variability of SR influences both net ecosystem exchange (Czöbel et al., 2005) and source/sink characteristics (Balogh et al., 2005) of grasslands.

Spatial variability and heterogeneity is a common feature of ecosystems (Dale, 1999). The most simple, but commonly used expression of variability is the coefficient of variation (CV) of the measured variable. Two, more elaborated approaches to study the spatial variability of some property are the blocked quadrature variance methods (with successive increase of the sample plot sizes) and the geostatistical analysis, spaced quadrature variance methods (with increasing separation distances between plots of constant sizes). One tool of the latter is the calculation of the semivariance of the investigated property, which method became popular in ecological works. Semivariograms are useful tools to analyze the horizontal spatial structure of the soil biota (Grundmann, Debouzie, 2000; Wallace et al., 2000; Ettema, Wardle, 2002; Franklin, Mills, 2003), the spatial distribution of the size of plant individuals (Wallace et al., 2000), the density (Cosh, Brutsaert, 2003) or genetic diversity (Escudero et al., 2003) of the vegetation from micro-scale to landscape level.

These works were relevant to our investigations in the decisions of using as large sample sizes as possible without injure stationarity, collecting T and SWC data parallel with SR and using geostatistics for spatial analysis. The chosen sample size of 75 plots seemed to be enough for the latter purpose (Rossi et al., 1992). T was followed to test for temperature dependence of spatial SR data and spatial pattern of SWC was also recorded because of its important influence on SR pattern in these entities (Casper, Jackson, 1997; Burke et al., 1998; Hook et al., 1994). A few cm ranges of autocorrelation of SR were found in wheat field and poplar plantation at Stoyan et al., 2000, which was in the magnitude of the spatial resolution of our measurements (minimum lag was 20 cm).

Our study was different from the previous ones in several aspects. We investigated micro-scale (from cm to a few m) spatial variability and heterogeneity of SR within different grassland types (sand, mountain meadow) by the same methods. Apparently continuous and physiognomically uniform patches were chosen in each of the studied grasslands (isotropic variograms), and samples were collected along transects on regularly spaced positions, which method allow the description of variability more precisely than random sampling (Podani, 1984). These ecosystems evolved on different soils (neutral sand, loamy) and represent two different moisture levels in the temperate zone of Europe, due to the climate (or also partly to edaphic reasons: properties of sand). Bare soil was also sampled for comparison. These fields were chosen for their differences, to be able to compare different situations.

Our research objectives were (1) to characterize the variability of SR of the investigated sites, (2) to depict the spatial pattern of SR and SWC by semivariograms, (3) to compare patterns of SR and SWC. The study focused on these aims under non-limiting environmental circumstances, at the above-ground vegetation's fully developed stage. The spatial scale of our study was the range of community dynamical processes as well.

We assumed that the bare soil would show the smallest patch size (a few decimeters) or lack of spatial structure of SR and SWC at the measured scales, because of the extremely small scale of microbial processes. We hypothesized a less homogenous/random pattern of patch structure and medium size patches of SR in the meadow, because of its closed, thick vegetation cover and good water supply. Larger scale pattern on the sandy soil with large patches (a few meters) of SR and SWC should be relevant, the characteristic vegetation being less closed (total cover 50–70% in contrast to the other's 100%), vertically less structured, horizontally more mosaic-like than the other grassland.

Materials and methods

Site descriptions

Sand grassland

Sand grasslands cover large areas in the Carpathian basin (Fekete et al., 1988) and well represent the natural, semi-natural, non-forested vegetations (Kemény et al., 2005). The dry sand grassland in the Hungarian Great Plain, Bugac (46.69 N, 19.6 E, 140 m a. s. l.) has chernozem type sandy soil, which has lower water and nutrient holding capacity. The characteristic species of the grassland is *Festuca pseudovina*. Mean annual rainfall is 500 mm, mean annual temperature is 10.5 °C. The study site is a part of the Kiskunság National Park and has been under extensive management (grazing) for the last 20 years.

Mountain meadow

Grassland site of the Experimental Ecological Study Site, Bílý Kříž, Czech Republic (49°29' N, 18°32' E, 854 m a.s.l.) is a regularly mown mountain meadow. Mean annual air temperature is 5.5 °C, mean annual precipitation is 1100–1140 mm. The soil is loamy/sand-loamy with gravel. The grassland's main species is *Festuca rubra* (Pavelka et al., 2007).

Bare soil

Bare soil which has not been used for growing plants for several years (cultivation of maize ceased 5 years ago) but is tilled for weed control in every year is situated in the Botanical Garden of Szent István University in Gödöllő (47.36 N, 19.26 E, 220 m a. s. l.). Mean annual rainfall is 560 mm, mean annual temperature is 11°C. The soil of the Garden is generally calcareous and sandy alluvial with patches of clay.

Sampling

Soil CO₂ efflux from both autotrophic and heterotrophic respiration, soil temperature (T) and soil water content (SWC) were measured at every 20 cm along circular transects of 15 m length (75 replicates). SWC and T were first measured under the standing biomass, to reflect natural patterns of these properties. That was done near midday, in a short time interval (1 hour). Second measurements were always parallel with SR to control temporally constant conditions, in the early afternoon hours (Knapp et al., 1998). T was measured by a thermometer, while SWC with a TDR reflectometer (ML-2, Delta-T Devices Co., Cambridge, UK), both at 5 cm depths.

Vegetation of the plots in the grasslands was cut above ground, which means no green parts remained. SR measurements were started two hours after cutting the grass off. Previous studies have not shown high noise or significant changes in measured values after this period. Timing of studies followed the phenological development of the vegetation at the sites, which highly depends on the beginning of summer drought and heat stress: measurements were conducted near the time of peak biomass, which is the period of intensive growth and also respiration (Frank, 2002), but there is presumably no limitation (water, heat or cold, senescence) yet. Peak biomass was reached earlier in dry sandy grasslands, than in humid regions. Measurements were done 3 times on sand grasslands, 7 times on the meadow and twice on bare soil in 2003–2004. Results of a selected day from each of the sites will be presented in the paper.

Gas exchange measurements were made by using a portable photosynthesis system (LICOR 6200, Li-Cor, Lincoln, NE, USA). Air samples were taken from plexi hemisphere chamber of 20 cm diameter (314 cm² area, 2093 cm³ volume) equipped with two 3 cm diameter fans on the top for inside mixing and with a pressure vent hole for avoiding pressure differences between in- and outside. The SR chamber was very similar to the non-steady-state through-flow chamber (Pumpanen et al., 2004), but no collars were used. Leakage was prevented by the fact that relatively flat surfaces were sampled and the litter was intact after the removal of live standing biomass. Measurement on one position lasted less than 1 minute, so the whole 75 data were collected within 1–1.5 hours.

Statistical analyses

Semivariance was calculated according to:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^n [z(s_i) - z(s_i + h)]^2,$$

where z is a data value at a particular location, h is the separation distance between data pairs, and $N(h)$ are the number of pairs of data values a distance of h apart (Dale, 1999). Several semivariogram models (exponential, Gaussian, spherical, hyperbolic and linear) were tested on the calculated values. The exponential and the hyperbolic model approach the sill asymptotically, while the spherical rise to sill more quickly. Each of them displays linear behavior near the origin except for the Gaussian one with parabolic response in this region. The linear model does not show sill or range, and shows increasing semivariance as the lag increases.

Table 1. Soil respiration, water content and temperature (average, standard deviation, coefficient of variation, minimum and maximum of 75 measured data) on bare soil, mountain meadow and sandy grassland from one day at peak biomass in the early summer vegetation period of 2004 in each stand.

	SR ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			SWC (%)			T ($^{\circ}\text{C}$)		
	bare	meadow	sand	bare	meadow	sand	bare	meadow	sand
Average	1.28	6.32	1.83	16.3	44.1	9.33	21.2	17.9	19.3
St. dev.	0.48	1.76	0.82	2.76	3.42	1.56	0.9	0.43	0.82
CV (%)	38	28	45	17	8	17	4	2	4
Min.	0.28	1.04	0.31	10.6	35.4	4.4	17.9	16.8	17.4
Max.	2.67	10.56	4.1	21.9	50.6	12.8	23.1	18.8	21.4

Results

Measured data

Average SR values increased in the order of bare soil, sand grassland and mountain meadow (Table 1), with the lowest CV on meadow followed by the bare soil and the sandy grassland. Ranges of values were broad. Average SWC was quite low in the sand grassland (Table 1), higher on bare soil and very high on meadow. CVs were relatively low, especially on meadow. Average soil temperature increased from the meadow to the sand grassland and the bare soil with very low CVs and narrow intervals (2–5 $^{\circ}\text{C}$).

Model semivariograms

Several semivariogram models were used on SR and SWC semivariance data. Best fits with the highest structural variance and r squared value (Flanagan et al., 2002) are presented in Fig. 1 and Table 2.

Ranges of spatial autocorrelation of SR and SWC (Table 2) followed the order of bare soil, meadow and sand grassland, with values between 0.39–0.73 m and 0.48–1.08 m, respectively. Sill variance of SR was the lowest also on bare soil, that was followed by sand grassland, and then by meadow (Fig. 1 and Table 2), and that of SWC followed the order of sand grassland – bare soil – meadow, similarly to the order of the measured average values (Table 1). Structural variances were between 26 and 55%.

If we consider range values of SR and SWC patterns together, we had a quite small, similar patch size (< 0.5 m) on bare soil. Larger differences were observed on sand grassland with both values around 1 m, and the largest on the meadow with medium size patches for the two variables.

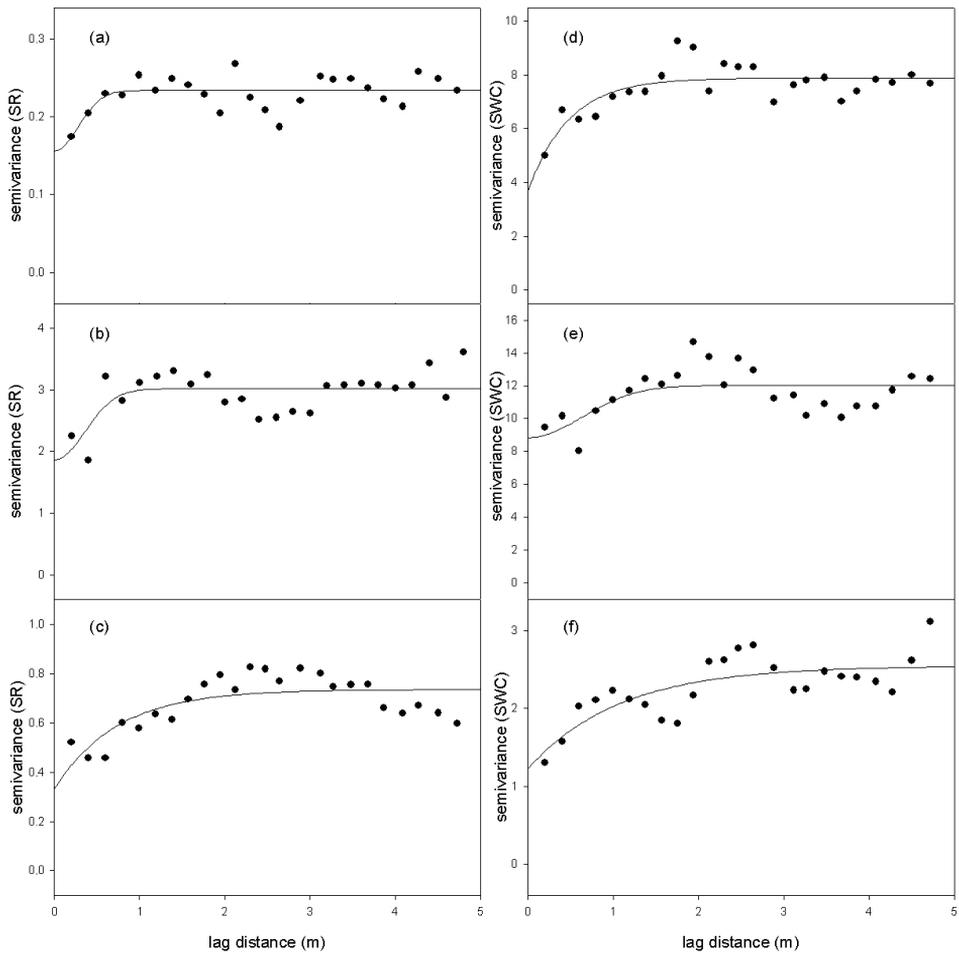


Fig. 1. Example of calculated semivariance (dots) and model semivariograms (lines) of soil respiration and water content on bare soil (a, d), mountain meadow (b, e) and sandy grassland (c, f) from one day of measurement campaigns in 2003–2004 peak biomass vegetation periods.

Discussion

The spatial scale, the size of the sample plots, the sample size and the arrangement of plots (spatial resolution of the sampling) of our measurements seemed to be adequate for studying small (relevant with chamber technique) scale variability and heterogeneity of soil CO₂

Table 2. Parameters of model semivariograms (regression coefficient of fit, nugget, sill and structural variances and range with P values) of soil respiration and water content on bare soil, mountain meadow and sandy grassland, early summer, 2004.

	Model	r ²	P	Nugget variance	P	Sill variance	P	Range (m)	P	Structural variance (%)
SR										
Bare	Gaussian	0.34	0.01	0.16	0.0002	0.24	0.04	0.39	0.02	33
Meadow	Gaussian	0.37	0.0074	1.83	0.0002	3.07	0.0088	0.47	0.025	39
Sand	exponential	0.56	0.0002	0.33	0.008	0.74	0.0011	0.73	0.0338	55
SWC										
Bare	exponential	0.59	<0.0001	3.67	0.01	7.87	0.0032	0.48	0.018	53
Meadow	Gaussian	0.36	0.0086	8.84	<0.0001	12.02	0.0082	0.9	0.014	26
Sand	exponential	0.57	0.0001	1.23	0.0012	2.55	0.0002	1.08	0.042	52

efflux in grasslands. Botanical studies have also proved that using sampling unit size of a few dm² is expected to find the highest variability in species composition of these grasslands (Mucina, Bartha, 1999), or have showed statistically significant association between biomass and species frequencies (Kertész et al., 2001). These above-ground properties of vegetation structure may be relevant in SR by influencing litter deposition (Epron et al., 2004), root respiration or stand canopy microclimate (Prach, 1982).

SR values and ranges of values described well the respiration performance of various temperate grasslands and were in good agreement with other studies (from a loss of 0.04 to 0.4 mg CO₂ m⁻² s⁻¹ in a prairie ecosystem – Ham, Knapp, 1998), that is 0.01–0.12 mg CO₂ m⁻² s⁻¹ on bare soil, 0.01–0.18 mg CO₂ m⁻² s⁻¹ on sand soil and 0.05–0.46 mg CO₂ m⁻² s⁻¹ on loamy soil.

CV values were also similar to values of previous studies (CV between 10–60% in temperate arable, forest and pasture ecosystems, Jensen et al., 1996, average CV 28% in the case of larch plantation SR, Yim et al., 2003 and 40% CV as within-site variability in *Picea* stands, Buchmann, 2000).

Semivariance analysis revealed characteristic patch sizes of the investigated variables. Bare soil without important respiring plant tissues and relatively small amount of degrading carbon-containing organic matter showed a quite homogenous (random) spatial pattern of SR (despite of its relatively high CV), with similarly small patch size to that showed by SWC (0.39 vs. 0.48 m). This suggests that the soil water content should be one of the influencing factors in SR patch size (Maestre, Cortina, 2003), but the low structural variance of SR (33%) and the high nugget effect indicates that other, mainly smaller scale (out of our spatial resolution) below-ground, microbial processes (Grundmann, Debouzie, 2000) were responsible for the other part of the structure.

Under the vertically well-developed vegetation and thick litter layer of the mountain meadow, SR had a few dm² patch size (saturation of the curve at 0.47 m), while that of SWC was greater (0.9 m). In this case, we should conclude that measured driving variable, water in the soil, was homogenous at the scale of SR (it is sustained by the low structural variance: 26%); therefore water had no limiting effect here (Epron et al., 2004), instead, the good water supply caused SR's small size patches as in the case of the random pattern observed on bare soil. Other factors, not measured in this study, may be responsible for the pattern in SR, but large part of the variance (only 38% structural variance) was probably depending on smaller scale processes as well.

These field situations were completely different from those of the sandy grasslands, which are often severely water stressed during the vegetation period. The measuring dates were selected possibly close to time of the peak biomass, but water quantity in the soil was already quite low (Table 1), as compared to the other investigated entities. SR and SWC had the largest patch size on the sandy grassland (0.73 and 1.08 m), and structural variances were high (55 and 52%). These should mean that pattern of water in the soil may have influenced pattern of SR, and the structure was probably explained by other factors out of the measured spatial resolution to a smaller extent, than on bare soil or meadow.

So water limitation of SR was more pronounced on sand. The spatial pattern of SR may be highly influenced and maintained by the extensive management of this pasture (Shyomi et al., 2000), as well as its composition and structure (Kitazawa, Ohsawa, 2002; Milchunas et al., 1988). All of the structural variance values were between 26 and 55%, which means medium level spatial dependence after Makarian et al. (2007, low: < 25%, medium between 25 and 75%, high > 75%).

Conclusion

According to this study, large number of SR samples (we have chosen 75) should be collected for spatial analysis in homogenous fields (without significant temporal variability). This number of samples and the plot size were adequate for characterization of the spatial pattern of SR in different temperate grasslands. Medium level spatial autocorrelation was found in each case (Makarian et al., 2007), but nugget effect may be as high as in our study for more "stable" variables as well, like for example soil nutrients (> 50% Schlesinger et al., 1996, between 10 and 70% Jackson, Caldwell, 1993 and between 15 and 50% Hirobe et al., 2001).

Our expectations were partly sustained by our results: homogenous/random spatial patterns were found on the bare soil and meadow with smaller patches of SR and SWC in the former and larger in the latter case. The largest patches with the highest structural variance characterised the sand grassland's soil. Almost all values were less than 1 m. In dry grassland stand, where water shortage developed in the soil already as early as the time of peak biomass, the ranges of spatial autocorrelation and hence the characteristic patch sizes of soil CO₂ efflux and soil water content were larger than in the well-watered soils.

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