Introduction

Human transformation of the former semiarid, forest-steppe vegetation into agricultural fields in Hungary has left restricted areas of loess steppe and loess steppe oak forest. Most of these stands are strictly protected for several decades. Moreover, their small semi-natural fragments are often encountered by agricultural fields, isolating them from natural species pools and influencing them by management practices (e.g., fertilizer accumulation, grazing) (Archer et al. 1995), or lack of the former activities (Costello et al. 2000). Degradation process of semiarid grasslands is often characterized by shifts in species composition and the cover increase by woody species (Breshears et al. 1997, Jackson and Caldwell 1993) and organic materials (Hirobe et al. 2003), as well as the intercanopy communities, that is the herbaceous assemblages between shrubs. The extremity of this process occurs in deserts, where ‘fertility islands’ develop after the establishment of shrubs (Schlesinger et al. 1990, Reynolds et al. 1999, Schlesinger et al. 1996, Schlesinger and Pilmanis 1998). The response in floristic composition, structure, species richness and diversity of the herbaceous layer to shrub induced heterogeneities (López-Pintor et al. 2006) is well-documented, as well as the microbial processes of decomposition (Schlesinger and Pilmanis 1998). Spatial range of the effects of woody species on their micro-environment varies from a few centimetres (Kelly and Canham 1992, Jackson and Caldwell 1993) to tens of meters (Schlesinger et al. 1996, Hirobe et al. 2003), depending on the property investigated, the spatial resolution of the study, and the sampling design (López-Pintor et al. 2006).

Ecophysiological properties of species after changes in land use (e.g., during secondary succession) have been also investigated (Wolffahrt et al. 2003). However, little information is available on the micro-scale (a few dm² large patches)
physiological responses, for example on CO₂ gas-exchange of the intercanopy communities. Large temporal and spatial variability (Stoyan et al. 2000) of CO₂ exchange of loess steppe under study have already been described (Czóbel et al. 2000, Fóti et al. 2002, Fóti et al. 2004) by the commonly used term of coefficient of variation (Jensen et al. 1996, Yim et al. 2003, Buchmann 2000). However, fine-scale spatial pattern of SR is not known, nor the stability of spatial functional structures, i.e., we do not know whether the scale of similarity changes under e.g., a drought stress, or remains the same irrespective of the change in environmental conditions. Spatial scale of patterns of other, integrated physiological characteristics, biomass and normalized difference vegetation index (NDVI) was larger under water shortage than under good water supply (Chen and Brutsaert 1998, Henebry 2003, Cheng et al. 2007). Study of spatial variability model of SR on a Brazilian bare soil showed high uncertainty in the description of the pattern even within a relatively short measurement period (within a few days) (La Scala et al. 2000).

Our study includes occasional soil CO₂ flux measurements over a 6 years period with the aim of describe the study soil’s CO₂ efflux activity in time, and the investigation of the spatial pattern of SR by means of three replicate measurement campaigns at a small stand of loess grassland encountered by shrubs. Data for spatial pattern investigation of SR were analysed by basic statistics, geostatistics and punctual kriging. Environmental factors, like SWC, the main constraining factor in xeric vegetations, and soil temperature (Ts) were also measured, as well as the response by physiological activity integrated over longer time period, like NDVI. We hypothesized that Ts would be the main determining factor of long-term CO₂ exchange, SR activity, but the actual SR spatial pattern would be dependent mostly on SWC.

Materials and methods

Site description

Formerly, loess grasslands (Zólyomi and Fekete 1994) covered large areas in the Carpathian Basin, nowadays they are important heritages of the Hungarian natural-semi-natural vegetation cover. The sample xeric temperate loess steppe is located near Isaszeg (47°34’N 19°2’E, 230 m a.s.l.). The site is lime-impregnated chernozem (CAMBISOL) with a thick, humus- and nutrient-rich A layer. The basic climatological parameters at the site for the investigated period were: mean annual precipitation 560 mm, mean annual temperature 9.1°C and large annual range of mean daily temperatures (22 °C). The grassland is vertically well structured (60-80 cm height), species-rich, several of them is broad-leaved, dicotyledonous. It is dominated by Festuca rupicola and the shrub, Chamaecytisus australis. The sample area was encountered from the north-west side 8-10 m apart by Crataegus monogyna and Rosa canina shrubs of 2-3 m height. These species are typical invaders in abandoned grasslands.

Sampling for temporal variability

SR was measured occasionally in the 2001-2004 time period using a closed dynamic system composed of an IRGA (LI-6200, Li-Cor, Lincoln, NE, USA) with a plexi hemisphere chamber of 20 cm diameter. This chamber was 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. In the 2005-2007 time period LI-6400 (Li-Cor, Lincoln, NE, USA) with its own soil respiration chamber was used. Soil collars were not applied. Leakage was prevented by the fact that relatively flat surfaces were sampled and the litter was intact after the removal of live standing biomass. SR was measured on three different plots each time. Grass was cut at each plot two hours before starting the measurements. Our previous studies (unpublished data) have shown this period, necessary to wait after cutting, i.e., SR rates to stabilized. NDVI was calculated from digital photographs before cutting the grass off, using an ADC camera (Dycam Inc. CA, USA). Ts and SWC at 5 cm depth were measured by an infrared thermometer (Raytek MX4, Raytek, Santa Cruz, CA, USA), and a TDR reflectometer (ML-2, Delta-T Devices Co., Cambridge, UK), respectively.

SR was fitted against Ts and SWC using a response function after Kenneth et al. (2005):

\[
SR = -a_1 \exp(a_2 \cdot Ts) \exp \left[ -0.5 \left( \frac{\ln(SWC/\alpha_4)}{\alpha_4} \right)^2 \right]
\]

where \( a_i \) are coefficients of the 3D exponential fit. In addition to this, the influence of NDVI on SR was also estimated by fitting NDVI against the residuals from regression using eq. 1.

Sampling for geostatistical analysis

Measurements for spatial pattern analysis were conducted on 18th of June 2004, 26th of June 2006, and 11th of October 2006. The early summer is the period of the peak biomass in this grassland. The third measurement in autumn reflects senescing period of the stand. The sample area was about 15*15 m large. Soil CO₂ efflux from both autotrophic and heterotrophic respiration, Ts and SWC were measured as described above at every 20 cm along the perimeter of a 4.8 m diameter circle (75 replicates). The measurements were conducted in the early afternoon hours, which is the most convenient period of the day for this type of study (Knapp et al. 1998) because of the relative stationarity of influencing circumstances in time. Measurement on one position lasted less than 1 minute, so the 75 measurements were performed within 1 – 1.5 hours. NDVI was calculated on 20 cm by 20 cm squares along the transects as described above.

Statistical analyses of spatial data

Basic statistics, like mean, standard deviation, coefficient of variation, minimum and maximum values of the measured variables were calculated, as well as Kolmogorov-
Smirnov tests for normality before multiple comparisons (ANOVA or Kruskal-Wallis test) or correlation analysis (Pearson- or Spearman-tests) of the data. Semivariance was calculated according to:

\[ \gamma(h) = \frac{1}{2N(h)} \sum_{i} \left[ z(s_i) - z(s_i + h) \right] \]

(2)

and cross-semivariance:

\[ \gamma(h) = \frac{1}{2N(h)} \sum_{i} \left[ z(s_i) - z(s_i + h) \right] \left[ z(r_i) - z(r_i + h) \right] \]

(3)

where \( z(s_i) \) and \( z(r_i) \) are data values at a particular location, \( h \) is the separation distance between data pairs, and \( N(h) \) is the number of pairs of data values a distance of \( h \) apart (Dale 1999). Several semivariogram models (exponential, Gaussian, spherical) were tested on the calculated values. The exponential model approaches the sill asymptotically, the spherical raises more quickly, both of them displays linear behaviour near the origin. The Gaussian one has parabolic response in this region. Relationships with the highest level of significance will be reported. Punctual kriging was performed on the basis of this semivariogram’s parameters. We estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m sample area (including the 4.8 m diameter sample circle). We estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m sample area (including the 4.8 m diameter sample circle). We estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m sample area (including the 4.8 m diameter sample circle). We estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m sample area (including the 4.8 m diameter sample circle). We estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m sample area (including the 4.8 m diameter sample circle). We estimated values for 121 points of a 5*5 m sample area (including the 4.8 m diameter sample circle) by 0.5*0.5 m sample area (including the 4.8 m diameter sample circle).

Results

Temporal variability of SR and its dependence on environmental factors

The minimum and maximum values of SR during the 2006 study period were 0.0903 mmol (0.004 mg) CO₂ m⁻² s⁻¹ on 3rd of March 2006 and 15.7 mmol (0.69 mg) CO₂ m⁻² s⁻¹ on 27th of June 2006, respectively. SWC ranged from 0.041 to 0.296 m³ m⁻³. Average SR values of the growing season 2006 followed Ts (Fig. 1), except for July when high temperature was coupled with low SWC. Dependence of SR on SWC and Ts along of longer time period (from March 2001 to March 2007) showed a good correlation, described by equation (1) (Fig. 2. and Table 1). For this period, NDVI values ranged from 0.02 to 0.7. No correlation was found between the residuals of equation (1) and NDVI for the whole data set of 6 years (including the measurements during the senescent period), but in the case of the investigations of only the main vegetation period from March to June 2006 positive correlation was found (\( n=24, r^2=0.6388, SR_{\text{Residual}}= -0.5543+ 8.705\text{NDVI, see also Fig. 1.} \))

The presented biotic and abiotic factors govern SR in time, but also in space where they determine a dynamically changing spatial pattern.

Spatial variability and pattern of SR

Basic statistics. SWC in summer 2006 transect data was about one and a half as large as in summer 2004, and more than twice as large as in autumn 2006 (Fig. 3). Ts was larger also, to a lesser degree, but the maximum values were not limiting in the point of view of physiological activity (even did not reach 30 °C). In summer 2006, average SR value was about three fold larger, than on the two other measuring dates.

Smaller differences were observed in the case of average values of NDVI (0.65; 0.49; 0.5 at the mentioned measuring dates. The correlation was found (\( n=24, r^2=0.6388, SR_{\text{residual}}= -0.5543+ 8.705\text{NDVI, see also Fig. 1.} \))
Table 1. Estimated parameters from fitting of equation (1) on SWC, Ts and SR from measurements on the loess grassland near Ísa-
szeg, Hungary.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Std error</th>
<th>P</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>a₁</td>
<td>2.1915</td>
<td>0.2942</td>
<td>&lt;0.0001</td>
<td>0.4714</td>
</tr>
<tr>
<td>a₂</td>
<td>0.0553</td>
<td>0.0049</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>a₃</td>
<td>33.0265</td>
<td>12.4673</td>
<td>0.0085</td>
<td></td>
</tr>
<tr>
<td>b₄</td>
<td>1.3224</td>
<td>0.3337</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Nugget (γ₀) and sill (c) variance, range of spatial autocorrelation (a), structural variance ((c-γ₀)/c %) and r squared value of model fitting for the three transect data of SR and SWC in 2004 (summer) and 2006 (summer and autumn) at the loess grassland near Ísa-
szeg, Hungary.

<table>
<thead>
<tr>
<th></th>
<th>Summer 2004</th>
<th>Summer 2006</th>
<th>Autumn 2006</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>γ₀</td>
<td>γ₀</td>
<td>γ₀</td>
</tr>
<tr>
<td>SWC</td>
<td>4.7853 (-0.0001)</td>
<td>10.69 (0.0002)</td>
<td>3.0683 (-0.0001)</td>
</tr>
<tr>
<td>SR</td>
<td>0.74 (-0.0001)</td>
<td>2.44 (0.0001)</td>
<td>1.3766 (-0.0001)</td>
</tr>
<tr>
<td>a</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>c</td>
<td>6.1298 (0.0151)</td>
<td>15.74 (0.046)</td>
<td>3.7983 (0.0457)</td>
</tr>
<tr>
<td>SR</td>
<td>0.9477 (0.006)</td>
<td>3.6 (0.0374)</td>
<td>2.1136 (-0.0001)</td>
</tr>
<tr>
<td>Str. var.</td>
<td>32% (gau)</td>
<td>32% (gau)</td>
<td>32% (gau)</td>
</tr>
<tr>
<td>SWC Str. var.</td>
<td>22% (gau)</td>
<td>32% (gau)</td>
<td>35% (gau)</td>
</tr>
<tr>
<td>SR Str. var.</td>
<td>0.70 (0.0288)</td>
<td>0.70 (0.0288)</td>
<td>0.70 (0.0288)</td>
</tr>
<tr>
<td>r²</td>
<td>0.41 (0.067)</td>
<td>0.41 (0.067)</td>
<td>0.41 (0.067)</td>
</tr>
<tr>
<td>SWC</td>
<td>0.35 (0.047)</td>
<td>0.26 (0.0411)</td>
<td>0.22 (0.07)</td>
</tr>
<tr>
<td>SR</td>
<td>0.31 (0.0032)</td>
<td>0.32 (0.018)</td>
<td>0.32 (0.018)</td>
</tr>
</tbody>
</table>

Figure 2. SR as fitted against Ts and SWC, using eq. (1). Measurements were conducted on the Hungarian loess grassland near Ísa-
szeg occasionally from March 2001 to March 2007. Full sample size was 382.

Figure 3. Average and standard deviation of measured SR, SWC and Ts values of the three replicate measurements for spatial analysis in 2004 (summer) and 2006 (summer and autumn) at the loess grassland near Ísa-
szeg, Hungary.

Figure 4. Semivariances (dots) and model semivariograms (lines) of SR from the three replicate measurements for spatial analysis on loess grassland near Ísa-
szeg, Hungary in summer 2004 (up), summer (middle) and autumn (bottom) 2006.
final decisions (Henebry 1993). This fact must be also taken into consideration in the case of the weak statistically significant correlation between SWC and SR 2004 values (Pearson-test $p<0.05$).

Semivariance, kriging. Differences in the three replicate measurements of SR and SWC for spatial analysis (Fig. 3.) were reflected in the semivariance curves (Fig. 4., SR curves) and the estimated parameters (table 2.). Semivariograms of SR and SWC of summer 2006 (SR: Fig. 4. middle) reached the largest sill, showed the smallest range of autocorrelation, and had almost the largest structural variance. Larger patches (higher degree of heterogeneity) of SWC and SR were found in autumn 2006 (SR: Fig. 4. bottom), and the largest ranges of autocorrelation in summer 2004 for both variables, SWC and SR (SR: Fig. 4. up).

Graphs with kriged values (Fig. 5) show the spatial patterns of SWC and SR of the three measurements campaigns on a larger area. Shrubs were found north-west from the presented areas. The most striking observation was that larger SR (with 4 m of range of autocorrelation, Table 2) and SWC (with 2.6 m of range of autocorrelation, Table 2) were measured on that part of the study site in summer 2004 than on the other one. In the other cases, the patterns seemed to be finer grained, with several smaller patches in the spatial resolution of the measurements.

Discussion

Measured SR values were in good agreement with other studies (from for example a loss of 0.04 to 0.4 mg CO$_2$ m$^{-2}$ s$^{-1}$ in a prairie ecosystem, Ham and Knapp 1998, or between 0 and 0.25 mg CO$_2$ m$^{-2}$ s$^{-1}$ in tallgrass prairie, Mielnick and Dugas 2000). The variability of our SR values (between 20 and 40 %) were also similar to values of previous studies: CV between 10-60% in temperate arable, forest and pasture eco-
systems (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).

Frank (2002) reported that maximum SR values were measured at the time of the peak biomass in prairie. At our loess grassland site, fluxes were low in the dormant period and increased rapidly from early spring with Ts, which is the main driver of the SR (Lloyd and Taylor 1994, Pavelka et al. 2007) when no water limitation, to June, period of the peak biomass production. SR is also influenced by SWC, which had very low values during summer droughts, which are frequent in climate of Hungary. Grasslands can turn from sink to source of CO₂ in these periods (Nagy et al. 2007), in spite of the respiration processes – including SR - decrease with reduced rainfall (Harper et al. 2005). The role of the phenological status of the vegetation seems to be also very important, because of the root respiration. The ratios of root derived respiration in SR were estimated in wide range: 15-90% (Frank 2002, Raich and Tufekcioglu 2000).

The 3D fit of SWC-Ts vs. SR was statistically significant ($r^2=0.4714$, at n=382), but the rest of the variance may be explained by other factors as found for the NDVI in the present study. Raich and Tufekcioglu (2000) found a good agreement between SR and net primary production. We supposed that the vegetation index of the above ground biomass was related to the active root biomass and hereby SR, in spite of the fact that NDVI is an integrated physiological characteristic for a longer time period. That was supported by our results which also show that soil respiration modelling should consider the condition of the vegetation using biomass or vegetation index data.

Mainly SWC-governed intensity of SR was reflected in summer 2004 dataset for spatial analysis. SR was highly reduced by decreased SWC as compared to the more optimal season of 2006. Ts could also influence these results, but to a lesser degree because of its more similar ranges. However, better environmental circumstances were presumably limited to the period of the measurements (as a consequence of the rainy period preceding the measurements in 2006), because integrated term of NDVI values did not reflect higher long-term physiological activity in 2006 compare to 2004. In autumn 2006, SWC was adequate to this season’s average, and decreased SR activity was the consequence of senescence.

Our measurements returned data with some information (see structural variances in table 2., being low or medium degree according to Makarian et al. 2007) on the spatial autocorrelation of the investigated variables in the spatial resolution applied. Relatively high water content was reflected in the homogeneity (small patch sizes) of SWC and as a consequence, SR patterns in summer 2006. Patterns of the autumn samples reflected the effect of the water loss of the soil during this period, also enhanced by smaller quantity of buffering vegetation cover, but SWC was probably not highly limiting in this period of vegetation development, as compared to the results of summer 2004. Larger range of autocorrelation should be the consequence of increased heterogeneity in SR activity caused by senescence (Ham and Knapp 1998), as well. Severe water stress was reflected in the results of summer 2004 (Schlesinger et al. 1996) which caused the ‘opening up’ (Bartha 2002) of the ecophysiological patch structure of the stand.

Our study reinforced the fact that spatial variability and pattern of SR and SWC were different at any time of sampling (La Scala et al. 2000). It seems that competition was governed by different factors in the three cases, depending on the quantity of the water in the soil, and also phenological state of the vegetation. The switch between “below-ground” (competition for water) and “indeterminate” (competition for nutrients) dominance (Burke et al. 1998) is sustained by the co-occurrence of mesic and xeric coalitions in natural loess grasslands. Water shortage and stress in the soil affected the characteristic patch size and also the position of higher and smaller CO₂ efflux regions in the sample area, accentuated shrub-effect. Cross-semivariance of summer 2004 SWC and SR sustained this observation with positive, increasing values along the investigated scale and with reference of large patches. On the other hand, long-term physiological activity, represented in our study by NDVI, was less influenced. Entities with high species number were found to be able to reach the average biomass of good water supply years under water shortage (Flanagan et al. 2002), while loss of species richness weakened drought-resistance and the ability of return from stress (Tilman and Downing 1994). These are promising signs of the buffering capacity of the vegetation against shrub induced heterogeneity.

Conclusions

In our study we analysed temporal and spatial aspects of loess grassland CO₂ exchange activity. Long-term (6 years) gas exchange performance of the stand was dependent on two main governing factors as SWC and Ts, but another part of the variance was influenced by NDVI which was hypothesized to be related to actively respiring root biomass. The actual spatial pattern of SR was also dependent on the mentioned variables, but mainly on SWC, especially under water stress conditions. In this case, patch size of SR was larger than in well watered situations when nearly random pattern was found.

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