

Temporal variability of CO₂ and N₂O flux spatial patterns at a mowed and a grazed grassland

Szilvia Fóti^{a,*}, János Balogh^b, Marianna Papp^a, Péter Koncz^a, Dóra Hidy^a, Zsolt Csintalan^b, Péter Kertész^b, Sándor Bartha^{c,d}, Zita Zimmermann^{b,c}, Marianna Biró^c, László Hováth^e, Erik Molnár^f, Albert Szaniszló^f, Krisztina Kristóf^f, Györgyi Kampfl^f, Zoltán Nagy^{a,b}

^aMTA-SZIE Plant Ecology Research Group, Szent István University, 2103 Gödöllő, Páter K. u. 1., Hungary,

^bInstitute of Botany and Ecophysiology, Szent István University, 2100 Gödöllő, Páter K. u. 1., Hungary,

^cInstitute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány u. 2-4., H-2163 Vácrátót, Hungary,

^dSchool of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

^eHungarian Meteorological Service, Gilice tér 39, H-1181 Budapest, Hungary,

^fInstitute of Environmental Science, Szent István University, Páter K. u. 1., H-2100 Gödöllő, Hungary,

*Corresponding author: tel: +36309655801, fax: +3628410804, e-mail: foti.szilvia@mkk.szie.hu

Abstract

Spatial patterns of ecosystem processes constitute significant sources of uncertainty in greenhouse gas flux estimations partly because the patterns are temporally dynamic. The aim of this study was to describe temporal variability in the spatial patterns of grassland CO₂ and N₂O flux under varying environmental conditions and to assess effects of the grassland management (grazing and mowing) on flux patterns. We made spatially explicit measurements of variables including soil respiration, aboveground biomass, N₂O flux, soil water content, and soil temperature during a four-year study in the vegetation periods at grazed and mowed grasslands. Sampling was conducted in 80×60 m grids of 10 m resolution with 78 sampling points in both study plots. Soil respiration was monitored nine times, and N₂O flux was monitored twice during the study period. Altitude, soil organic carbon, and total soil nitrogen were used as background factors at each sampling position, while aboveground biomass, soil water content, and soil temperature were considered as covariates in the spatial analysis. Data were analyzed using variography and kriging. Altitude was autocorrelated over distances of 40–50 m in both plots and influenced spatial patterns of soil organic carbon, total soil nitrogen, and the covariates. Altitude was inversely related to soil water content and aboveground biomass and positively related to soil temperature. Autocorrelation lengths for soil respiration were similar on both plots (about 30 m), whereas autocorrelation lengths of N₂O flux differed between plots (39 m in the grazed plot vs. 18 m in the mowed plot). Grazing appeared to increase heterogeneity and linkage of the spatial patterns, whereas mowing had a homogenizing effect. Spatial patterns of soil water content, soil respiration, and aboveground biomass were temporally variable especially in the first 2 years of the experiment, whereas spatial patterns were more persistent (mostly significant correlation at $p < 0.05$ between location ranks) in the second 2 years, following a wet year. Increased persistence of spatial patterns after a wet year indicated the recovery potential of grasslands following drought and suggested that adequate water supply could have a homogenizing effect on CO₂ and N₂O fluxes.

Keywords: CO₂ efflux, kriging, N₂O flux, semivariance, spatial pattern, temporal persistence

Abbreviations: AGB – aboveground biomass, ALT – altitude, DEM – digital elevation model, IDW – inverse distance weighting, R_s – soil CO₂ efflux, SWC – soil water content, SOC – soil organic carbon content, TSN – total nitrogen content, T_s – soil temperature

1 Introduction

Soil carbon dioxide (CO₂) and nitrous oxide (N₂O) fluxes are the two main components of grassland greenhouse gas cycles and their rising atmospheric concentrations have important effects on global warming (IPCC 2014). Being a potential source of uncertainty related to greenhouse gas flux estimates, the spatial variability and patterns of these fluxes have been widely studied (e.g., Kosugi and others 2007; Knohl and others 2008; Rodeghiero and Cescatti 2008; Herbst and others 2009; Porcar-Castell and others 2015). Nevertheless, our knowledge about how and why these spatial patterns change in time or persist for a longer period is still imperfect.

Soil CO₂ efflux, i.e., soil respiration (R_s) originates from the autotrophic (roots, root-associated microbes and fungi) and the heterotrophic (bulk soil microorganisms) respiration activities. It is the second largest CO₂ flux in ecosystems after photosynthesis (Kuzuyakov 2006) moving large quantities of carbon (C), sometimes as much as 50-90% of the total annual uptake by photosynthesis (Bahn and others 2008) from the soil into the atmosphere. However, soil N₂O fluxes can be bi-directional resulting from different production and consumption processes taking place in the soil (Flechard and others 2005). N₂O is produced by nitrification, nitrifier denitrification and denitrification with the contributions of the different pathways varying considerably depending on the soil types (Kool and others 2009) and their moisture contents (Turner and others 2008). Nitrous oxide has natural sinks since it can be removed from the soil air by denitrifiers induced by low soil temperature, anoxic conditions and low NO₃⁻ availability (Flechard and others 2005; Chapuis-Lardy and others 2007). Soil N₂O sink activities could be substantial with more than 40% of the total N₂O fluxes being negative in temperate grasslands (Flechard and others 2005).

Fluxes of CO₂ and N₂O show large temporal (Konda and others 2010; Livesley and others 2011) and spatial (Jungkunst and others 2008; Fang and others 2009) variability at field scale (within tens of meters) due to the complexity of pathways described above, which all are under the influence of spatio-temporally varying drivers. In general, spatial heterogeneity can be related to complex geomorphological conditions (Ohashi and Gyokusen 2007; Fang and others 2009; Konda and others 2010), which, in turn, may determine the most important driving factors of the fluxes such as soil water content (SWC) (Clemens and others 1999) and soil aeration (Konda and others 2008), soil temperature (T_s), the availability of substrates, i.e., mineralizable C and nitrogen (N) (Yao and others 2009; Horváth and others 2010) and soil organic matter contents (Jungkunst and others 2008; Konda and others 2008). Most of the European grasslands are managed (Soussana and others 2007) and the types, intensity and timing of the different management practices may affect these driving factors through the additional N-input, removal of biomass, trampling etc. (Skiba and others 2009; Lin and others 2010; Burzaco and others 2013). Another important aspect is the potential effects of summer droughts – likely to be more frequent in the future in East-Central Europe (Bartholy and Pongrácz 2007) – on the coupling of C and N turnovers with consequences regarding the recovery capacity of the ecosystem (Evans and Burke 2013) or the linkage of the patterns (Fóti and others 2016). Changes in the magnitudes of the drivers may result in changing spatial patterns of CO₂ and N₂O fluxes (Domisch and others 2006; Ohashi and Gyokusen 2007; Luan and others 2012; Li and others 2013). The degree of temporal constancy of R_s patterns was found to be high within one day (Graf and others 2010; Teixeira and others 2011; ArchMiller and others 2016), over several months (Søe and Buchmann 2005) or even seasons (Ohashi and Gyokusen 2007), whereas it was also reported to be very low on consecutive days (La Scala Jr. and others 2000). These findings all suggest that more detailed knowledge is to be gained in long term studies carried out under various environmental conditions in order to reveal the underlying causes of temporal variability in spatial patterns and to interpret spatial dynamics. Besides reducing uncertainties deriving from spatial variability in greenhouse gas flux studies, this knowledge could help us to find the drivers behind the functional stability of the ecosystems in which the asynchrony of species' responses to environmental fluctuations is a stabilizing mechanism (Loreau and de Mazancourt 2013).

The studies conducted to reveal the spatial patterns of these fluxes often use geostatistical tools (variography and kriging). However, relatively few studies are available investigating N₂O spatial patterns in grasslands (e.g., Yao and others 2009; Imer and others 2013), as opposed to the more thoroughly studied cultivated and arable lands (Röver and others 1999; Yanai and others 2003; Konda

and others 2008, 2010; Li and others 2013, cf. also the review of Li and others 2013). As a result, studies on field-scale spatial variability could provide valuable information in this respect, too.

The aim of this study was to describe the temporal variability of grassland CO₂ and N₂O flux spatial patterns and to assess which modifications can be attributed to the effects of different management regimes such as grazing and mowing. We hypothesized that patch structures in our study plots were determined by small (within 1.5 m) elevation differences due to the undulating surface (altitude: ALT) where wind and water erosion may move the topsoil from the crests into the depressions with a consequently larger soil organic carbon content (SOC), total nitrogen content (TSN) and wetter soil conditions prevailing in the depressions than on the crests. Furthermore, due to the uneven water and organic matter distribution and the semi-arid character of the ecosystem with frequent droughts the depressions are characterized by larger aboveground biomass (AGB) and cooler temperatures compared to the crests. The effects of all these driving factors may govern the R_s and N₂O fluxes, which are expected to be larger in the depressions than on the crests, as the ecosystem under investigation can be described as soil moisture and substrate limited rather than temperature limited.

2 Materials and methods

2.1 Study plots

The study plots can be found in the Kiskunság National Park, at Bugac (46.69° N, 19.6° E, 114 m a.s.l.). The vegetation, which is a semi-arid sandy grassland, is dominated by *Festuca pseudovina* Hack. ex Wiesb., *Carex stenophylla* Wahlbg. and *Cynodon dactylon* L. Pers. The mean annual precipitation in the 2004-2014 period was 562 mm and the annual mean temperature was 10.4 °C, with 422 mm precipitation and 15 °C temperature in the vegetation period. According to the FAO classification (Driessen and others 2001) the soil type is Chernozem with a relatively high organic carbon content, the soil texture is a sandy loam with a sand:silt:clay ratio of 81:11:8 % in the topsoil layer (Balogh and others 2015).

The grazed study plot has been under extensive grazing for decades. Grazing intensity was 0.66±0.18 Hungarian Grey cattle animal ha⁻¹ year⁻¹ during the measurement period of 2012-2015. The grassland may potentially turn into a source of carbon in drought years (Nagy and others 2007) with the annual C-balances ranging from -171 (sink) to +96 (source) g C m⁻² (Pinter and others 2010).

The 1 ha area of the mowed study plot was fenced within the grazed grassland in 2011 to prevent grazing. This part was mown once a year in summer (except in 2014 when it was cut twice due to the high AGB production) with no fertilizers applied. Significant differences were not detected in the botanical composition between the grazed and the mowed management regimes until now (Koncz and others 2014). The same pedo-climatic and botanical conditions of the two study plots allowed us to describe the effects of mowing and grazing on the spatial patterns.

2.2 Environmental conditions in the study period

Meteorological data (e.g., in Figure 1) were available from a paired eddy covariance system functioning at Bugac continuously from 2002 and 2011 in the grazed and mowed plots, respectively. The yearly average air temperature and sum of precipitation for the investigated period were as follows: 2012: 10.8 °C, 431 mm, 2013: 10.9 °C, 590 mm, 2014: 11.5 °C, 813 mm, 2015: 11.2 °C, 523 mm, respectively. Annual precipitation sum was lower by 23% in the driest (2012) and higher by 45% in the wettest year of the study period (2014) than the ten-year average.

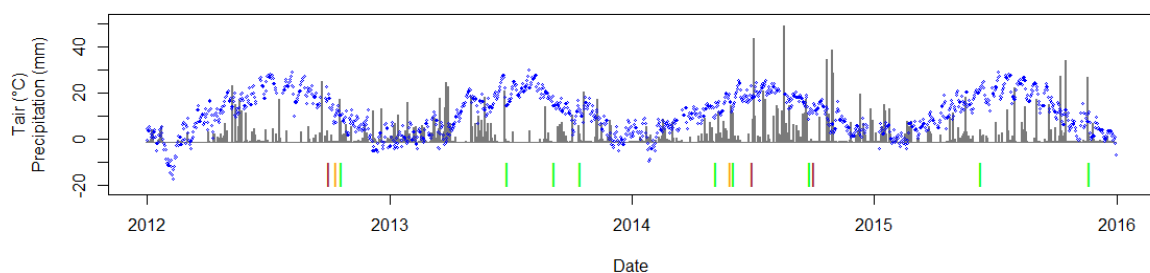


Figure 1. Daily mean temperature (°C) and daily sum of precipitation (mm) in the investigation period 2012-2015. Vertical lines below the chart area show the sampling occasions (green: R_s measurements)

together with AGB, SWC and T_s , orange: N_2O measurements together with SWC and T_s , brown: soil sampling for SOC and TSN).

2.3 Sampling and measured variables

Both plots were monitored in the vegetation periods between 2012 and 2015 for SWC, T_s , R_s , AGB, N_2O , SOC and TSN (Figure 1). The mowing dates were as follows: 24/06/2012, 01/07/2013, 10/06/2014, 29/09/2014, 17/06/2015.

Soil respiration was measured by means of closed chamber systems (Licor 6400, LiCor, Inc. Lincoln, NE, USA and EGM-4 PPSystems, Amesbury, USA) at 78 sampling locations per plot (arranged as a 80×60 m grid; Figure 2) in each measurement campaign. Target CO_2 concentration was set by placing the soil chamber on its side to the soil and monitoring the CO_2 concentration over the surface. Collars were not used with the soil gas exchange chambers to minimize disturbance (Davidson and others 2002; Wang and others 2005) since both measuring systems performed well without collars (Pumpanen and others 2004). Although the sampling positions remained relatively constant for the duration of the experiment, a shift of a few centimeters was applied in selecting the actual patch for measurements. The standing biomass was removed 1.5 hours before starting the soil respiration measurements. To minimize the effects of diurnal temporal patterns the measurements were started at noon and lasted ~1.5 h for one grid. In general, both plots were measured on the same day at the same time with two measuring devices.

A static chamber method was used to determine the soil N_2O emission as described by Horváth and others (2010). Nitrous oxide concentrations were determined with a HP 5890 II gas chromatograph (Waldbronn, Germany) equipped with a Porapak Q column (2x1.8 m, 80-100 mesh) and an electron capture detector (ECD). Equation for the N_2O flux calculation can be found in the Supplementary Material (SM).

Soil water content was measured at the same spots as the gas fluxes by time domain reflectometry (ML2, Delta-T Devices Co., Cambridge, UK; FieldScout TDR300 Soil Moisture Meter, Spectrum Technologies, IL-USA) in the top 0-5 cm layer of the soil. The measurements were performed usually after the R_s measurements in all positions in one run. Soil temperature was determined at a depth of 5 cm by a digital soil thermometer near the R_s chambers in parallel with the R_s measurements. The aboveground biomass was sampled from patches of 10 cm diameter (~80 cm²) (used for R_s measurements) and oven dried for 48 hours before weighing. Soil organic carbon content of the soil samples was determined by sulfochromic oxidation while their TSN by the Kjeldahl method for the 0-15 cm soil depth. These two variables and ALT were used as background factors (cf. SM for some further information about the correlation of the background factors) for all measuring campaigns.

2.4 Spatial data processing

The steps of the spatial data processing, detailed description of variography, inverse distance weighting interpolation, kriging and leave-one-out cross-validation can be found in SM. In brief, we performed variogram analysis (Venables and Ripley 2002; Pebesma 2004; Bivand and others 2014; R Core Team 2014) to (if necessary to fulfill the requirements of variography) temporally detrended and normally distributed (Fox and Weisberg 2011; Meyer and others 2014) data to determine the scale of spatial autocorrelation for each sampling date and sampled variable. Then, when the spatial range or autocorrelation length was larger than half of the maximum lag distance or a sill was not found, we performed surface detrending (detrending in space) with the least-squares method. Residuals were normalized, if non-normally distributed and variography was repeated. The variogram parameters were used in kriging and kriging results were evaluated with leave-one-out cross-validation (Pebesma 2004). The best kriging model (from ordinary kriging, kriging with external drift and ordinary co-kriging) was selected based on the cross-validation and the data were then back-transformed to the original scale for mapping. If kriging was not feasible (e.g., variogram models did not fit the variogram data well or autocorrelation length was less than the minimum grid size: 10 m), we used inverse distance weighting (IDW) for interpolation and mapping. To analyze the spatial correlation between variable pairs we used cross-variograms (Pebesma 2004).

2.5 Temporal persistence of spatial patterns

We used non-parametric Spearman rank correlation coefficients (C_s) to test the temporal stability of the spatial patterns and to determine the extent to which the location ranks persisted over time (Douaik and others 2006; Gao and Shao 2012). For this analysis we used the measured data without any

transformation or detrending and we used only the positions which were measured in each of the 8 campaigns. (Few new measurement positions were added from the second sampling campaign and some positions were lost as some marker sticks were damaged by grazing animals. Therefore, finally we used 55 positions in the grazed, and 72 in the mowed plot, respectively.). The calculation was as follows:

$$C_s = 1 - \frac{6 \sum_{i=1}^n (R_{ij} - R_{ik})^2}{n(n^2 - 1)},$$

where n is the number of locations observed, R_{ij} is the rank of a given variable at location i and in time j , while R_{ik} is the rank of the same variable at the same i location in time k ($k \neq j$). The correlation was calculated for all possible pairs of measuring occasions for SWC, T_s , R_s , AGB and N_2O . A value of $C_s=1$ would signify a perfect temporal stability.

3 Results

3.1 Topography of the study plots

The grazed plot had two slight parallel depressions running from the northwest to the southeast and the mowed plot had one crest running from northwest to southeast also with parallel depressions (Figure 2). The overall ALT gradient in both plots was < 1.5 m.

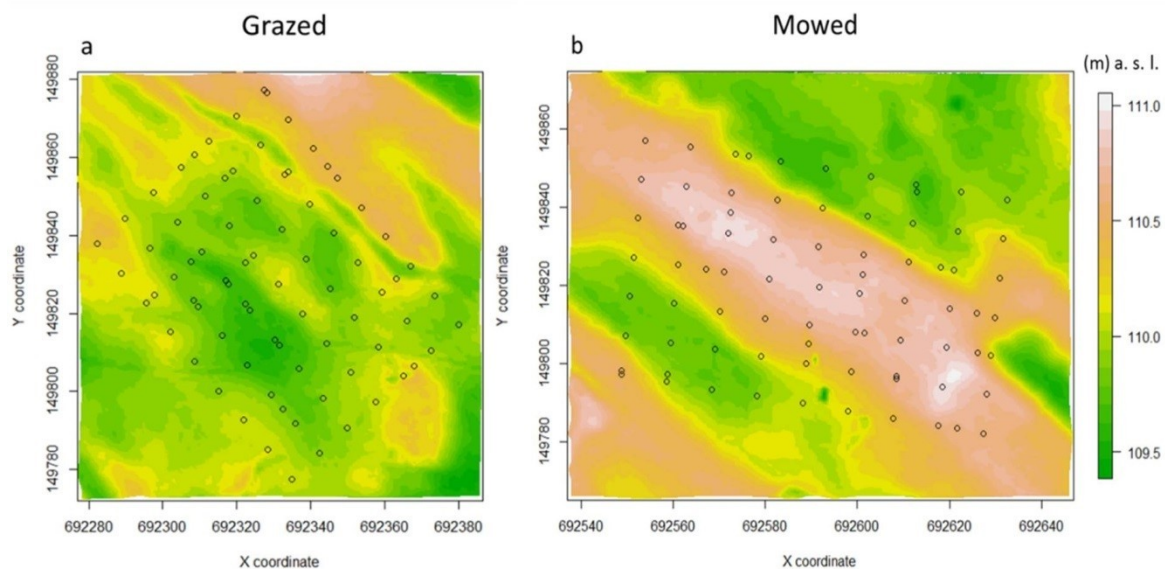


Figure 2. Digital elevation model of the grazed (a) and mowed (b) sampling plots and the sampling positions. Coordinates refer to the Uniform National Projection System (m).

3.2 R_s dynamics: patterns, spatial correlations and their persistence in time

The pattern of R_s showed spatial range, i.e., autocorrelation lengths (cf. definition for the different model variograms in SM Variography) of about 30 m (29.9 ± 13.1 m and 35.1 ± 19.9 m for the grazed and mowed plot campaigns, respectively, Figure 3, for further details of variogram parameters and best fitted models cf. SM Table 3). We detected two nugget variograms in the mowed plot (in May-2014 and June-2014), while all of the 9 variograms reached a sill in the grazed plot. SWC was in positive spatial correlation (SM Table 6) with R_s (an increase in SWC from one position to another was accompanied with an increase in the R_s value) mainly during summer (3 and 4 times in the grazed and mowed plots, respectively). Generally, we detected negative spatial correlation between ALT and R_s (an increase in ALT from one position to another was accompanied with a decrease in R_s), negative correlation between ALT and SWC and positive correlation between SOC/TSN and R_s (SM Table 6). SOC/TSN- R_s correlation was detectable 8 times in the mowed plot, while only 5 times out of 9 in the grazed one. The soil water content-soil respiration joint pattern had a 50.7 ± 14.6 m average length of autocorrelation for the grazed plot, while 3 from the 4 cross-variograms were unbounded for the mowed plot. (It has to be noted that SWC pattern was very homogeneous in the mowed plot with almost exclusively nugget variograms, cf. SM Results, SM Table 1.). The negative T_s - R_s correlation

we hypothesized was detected 5 times in the mowed plot, while only once in the grazed plot where positive correlations were also found in 2 campaigns in autumn.

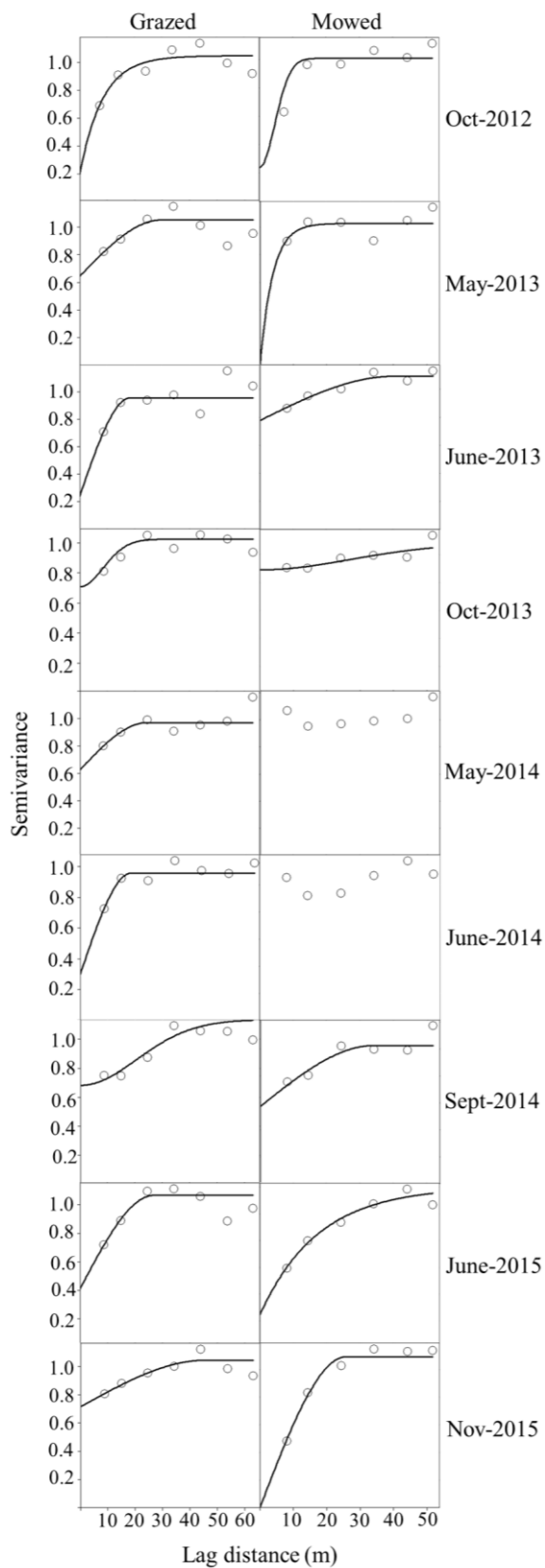


Figure 3. Standardized variograms of R_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the grazed and mowed plots.

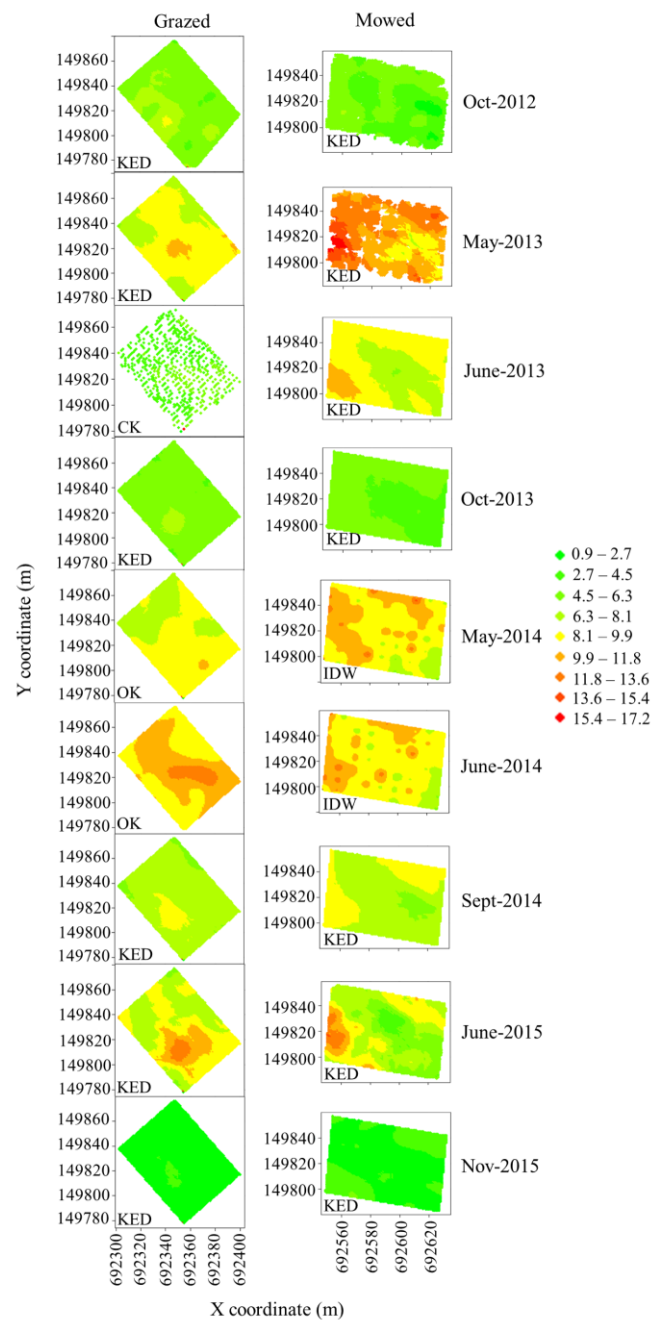
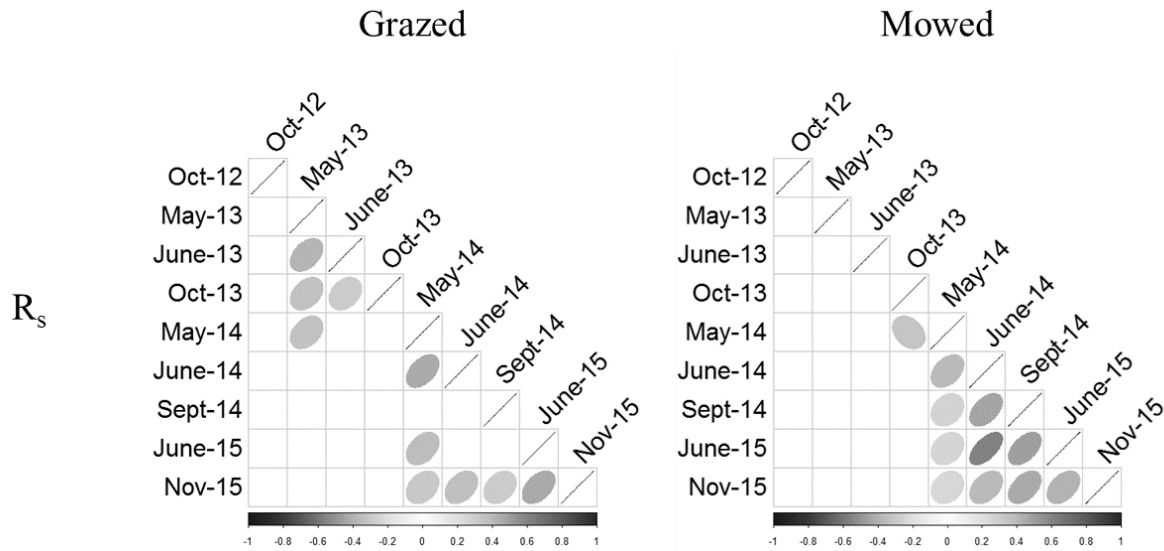


Figure 4. Maps (the interpolation method used is signed in each map: OK: ordinary kriging, KED: kriging with external drift, CK: ordinary co-kriging, IDW: inverse distance weighting) of R_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the grazed and mowed plots. Coordinates refer to the Uniform National Projection System (m).

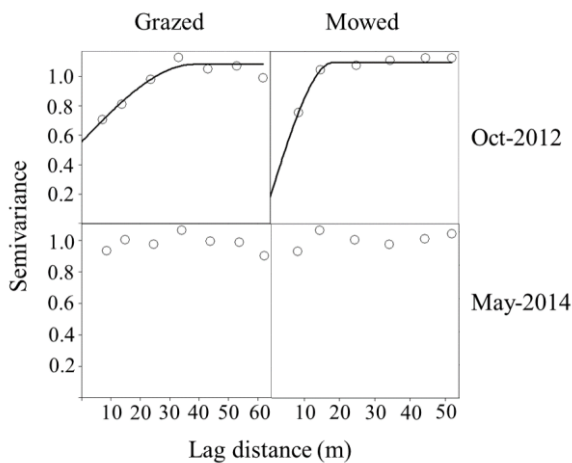
1 Maps of R_s (Figure 4) showed different patterns and different degrees of temporal persistence between
 2 pairs of measurement campaigns (Figure 5). We also detected seasonality in the R_s spatial patterns
 3 with higher R_s values in the summer in areas topographically more depressed and lower R_s values
 4 along the crests, while the autumn patterns for both plots tended to be the most homogenous. Based on
 5 the rank-correlation analysis, the R_s pattern was more stable in the mowed plot in the second half of
 6 the investigation period (after a wet year) in parallel with the stable SWC patterns (cf. SM Figure 3),
 7 while the persistence was less pronounced (Figure 5) and linked to a lesser extent to the SWC stability
 8 (SM Figure 3) in the grazed plot.



9
 10 *Figure 5. Temporal persistence of R_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) spatial patterns for the grazed and for the*
 11 *mowed plots, represented by significant rank-correlations ($p < 0.05$) between measuring campaigns.*
 12 *The darker the color, the more stable the pattern is, while directionality of the symbols represents the*
 13 *sign of the correlation, positive or negative.*

15 3.3 N_2O dynamics: spatial co-patterns and temporal variation

16 We detected positive spatial correlations between N_2O flux pattern and SWC and N_2O flux pattern and
 17 SOC, while negative spatial correlation between N_2O and AGB and N_2O and ALT patterns in the
 grazed plot in Oct-2012 (SM Table 6). The spatial correlation of N_2O pattern was found to be
 positive with both AGB and T_s in the mowed plot in Oct-2012. We did not find any robust spatial
 correlations in the other campaign (May-2014) when none of the N_2O variograms reached a sill
 (Figure 6). In addition, in Oct-2012 N_2O flux showed 39.2 and 18.4 m autocorrelation lengths
 (spherical model both) in the grazed and mowed plots, respectively. The spatial variability of N_2O
 flux was characterized by the largest values of the measured variables (SM Table 5).



32 *Figure 6. Standardized variograms of N_2O*
 33 *flux ($\mu\text{g N m}^{-2} \text{ h}^{-1}$) for the grazed and mowed plots.*

34
 35 Flux maps of N_2O (Figure 7) indicated temporal variability of its spatial patterns, with large
 36 differences between the two campaigns in the two seasons. We could not detect persistence in the
 37 spatial patterns. With only two measuring occasions, distant from each other in time and conducted in
 38 different seasons, we were not able to detect any general co-patterns and their temporal persistence,
 39 other than moderate levels of spatial linkages and temporal variability.

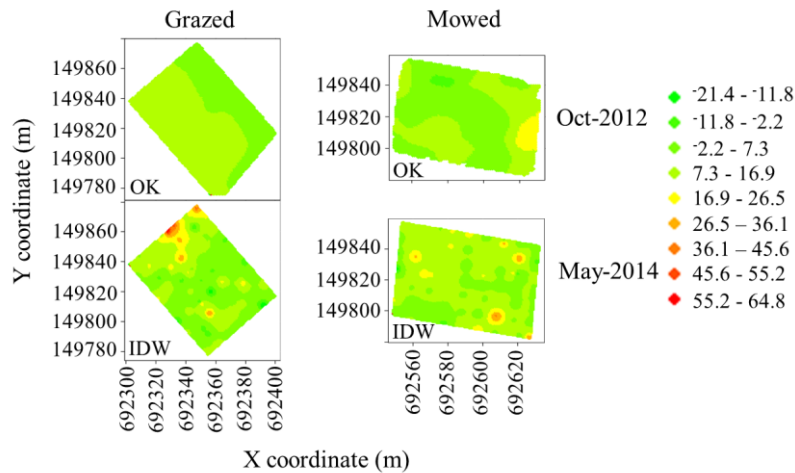


Figure 7. Maps (the interpolation method used is signed in each map: OK: ordinary kriging, IDW: inverse distance weighting) of N_2O flux ($\mu g N m^{-2} h^{-1}$) for the grazed and mowed plots. Coordinates refer to the Uniform National Projection System (m).

4 Discussion

Our overall results, which were in accordance with our hypothesis, showed that topographic differences, the patterns of depressions and crests had primary importance in the generation of spatial patterns in the grasslands under investigation. However, we also found that the expected spatial relationships were modified seasonally and the different management regimes may have important effects on them as well.

4.1 Spatial correlations and accuracy of kriging estimates

The autocorrelation lengths of N_2O flux and R_s from our measurements were in good agreement with the findings of other studies carried out at the same spatial scale in non-forested ecosystems (bare soil: Herbst and others 2012, agricultural fields: Yanai and others 2003; Turner and others 2008; Allaire and others 2012; Prolingheuer and others 2014) or in woody vegetation (Kosugi and others 2007; Ohashi and Gyokusen 2007; Konda and others 2008, 2010; Li and others 2013; ArchMiller and others 2016). Furthermore, other studies also found that the spatial patterns were not always detectable (Fóti and others 2016) or the spatial dependency was low (Konda and others 2010; Luan and others 2012; Prolingheuer and others 2014), as the actual characteristics of the patterns and the weights of potential driving factors varied widely from season to season (Ohashi and Gyokusen 2007) or from one study plot to another (ArchMiller and others 2016).

Altitude proved to be an important factor in determining the patterns when there was a correlation detectable with SWC, R_s , AGB and N_2O inversely related to the pattern of ALT in all cases. However, T_s was positively related to its pattern as found in other studies, too (Ohashi and Gyokusen 2007; Konda and others 2008, 2010; Li and others 2013). In general, we found more spatial linkages between ALT and the other patterns in the grazed plot than in the mowed one (ordinary kriging prediction was 3 times more frequent on datasets measured in the grazed plot indicating tight fit to ALT, kriging methods using DEM gave no further improvement in the estimation).

In autumn we detected alterations from the hypothesized pattern linkages. Spatial distributions of the covariates may change in time (Huang and others 2011) but the uncoupling effects of grazing (e.g., effects of browsing on biomass), and/or the effects of the solar radiation may also play a role, as T_s - R_s , T_s -AGB, or SWC- T_s were positively linked. These altered couplings of patterns, however, can be a consequence of grazing resulting in the altered biomass patterns (e.g., N_2O and AGB were negatively linked) rather than a direct effect characteristic of the season because the same exceptions were not observed in the mowed plot at the same measuring date (the only exception was the positive N_2O - T_s correlation in Oct-2012). Grazing may affect vegetation heterogeneity, soil properties and processes depending on the stocking rate (Lin and others 2010). Sensitivity of the spatial patterns to disturbances could increase in autumn, but similar alterations in the spatial correlations can be typical in natural grasslands (i.e., without management) as well in autumn due to the physiological and community dynamical processes taking place (growth of autumn aspect species, regrowth after drought,

1 senescence, temperature-limitation etc.). Furthermore, the alterations taking place in autumn may have
2 relevance in the mitigation strategies of grazed grasslands, provided that the stocking rate is adapted to
3 the seasonality of the ecosystem. Nevertheless, the question whether the co-patterns are modified due
4 to natural processes taking place in autumn or due to the effects of grazing still needs clarification.

5 We could not always verify the potential coupling of AGB and R_s in our study, although in other
6 studies the autotrophic component of R_s was largely influenced by different plant factors (community
7 composition, stand structure etc.) (Søe and Buchmann 2005; Luan and others 2012; Barba and others
8 2013; ArchMiller and others 2016). Even on bare soil the patterns may change in time (La Scala Jr.
9 and others 2000; Herbst and others 2009). In forests the spatial patterns can be very similar temporally
10 and persist for a year (Luan and others 2012) even if the understory vegetation shows some variability
11 in time but has smaller overall importance in the total flux (Søe and Buchmann 2005). Variability in
12 the species' pheno-phases in non-woody vegetation (Mendonça and others 2010) or stands with
13 remarkable heterogeneity (Konda and others 2010; ArchMiller and others 2016), as well as natural
14 grasslands with a high number of coexisting populations can all cause an increased variability in AGB.

15 4.2 Potential effects of grazing and mowing on the spatial variabilities and patterns

16 We detected that mowing, similarly to the majority of other treatments generally used in agriculture
17 (like tillage, fertilization, cf. Konda and others 2010), had a homogenizing effect. The uniform
18 exposure of the surface after mowing and the uniform stand structure along re-growth may further
19 result in decreased fit and linkage of the spatial patterns, which we found in the mowed SWC
20 structure, but also detected in the R_s patterns having nugget variograms in two cases, while sill was
21 reached in every case in the grazed plot. Moreover, in the mowed plot R_s and AGB (cf. also SM
22 Results) were tightly linked to SOC/TSN spatial distributions, whereas in the grazed plot the link was
23 not so pronounced. The reason behind all this could be that the spatial patterns of the background C
24 and N contents in the grazed plot were more strongly mediated by factors other than ALT, including
25 the ones which result from the random effects of grazing (dungs, urine, tread, browsing, biomass
26 variability, litter mixing by trampling etc.), while a more stable background was ensured in the mowed
27 plot due to the lack of animal activity. As much as 40% of the soil carbon is located in the upper 10
28 cm of the main rooting zone and the quantity decreases gradually downward. Furthermore, more than
29 half of the root biomass can also be found here (Balogh and others 2015) forming a rapidly adapting
30 system to environmental constraints. Therefore, the importance of SWC and the regulatory effect of
31 the stand structure on the SWC spatial patterns could be more pronounced in the grazed plot. Changes
32 can take place in the stand structure under prolonged droughts as well (Evans and Burke 2013) leading
33 to alteration of the regulatory processes with important consequences during the recovery period.

34 The observed homogeneity also appeared in a smaller autocorrelation length of the N_2O pattern in the
35 mowed plot, while heterogeneity due to grazing could be captured in an increased scale (similarly
36 found by Zhou and others 2008, but for overgrazed grassland). The overall very large spatial
37 variability of N_2O flux was due to the 22 (29%), 12 (15%) negative values in the mowed and the 11
38 (15%), 21 (27%) negative values in the grazed plots on Oct-2012 and May-2014(N_2O) measuring
39 occasions, respectively.

40 4.3 Seasonal variability and temporal persistence of the patterns

41 We found that the patterns in the second part of the study period (2014-15) were more stable. The
42 amount of precipitation higher than the average in one year could exert a long-term effect (Evans and
43 Burke 2013) on the spatial patterns, which is also in line with our earlier findings on the homogenizing
44 effects of wet years/good water supply conditions (Fóti and others 2014). This kind of homogenizing
45 effect can also be seen by the R_s nugget variograms occurring uniquely in the wet year of 2014 (but
46 only in the mowed plot) and the N_2O variograms not reaching a sill either. We could not observe any
47 stability in R_s and AGB patterns during the first two years of the study period in the mowed plot, while
48 some stability was detectable in the grazed one for a few consecutive campaigns. On the other hand,
49 after a rainy year, even the persistence of AGB pattern became detectable despite the small sampling
50 patch size (leading to large variability) and the minor topographic differences (1-2 m differences) in
51 the investigated grassland compared to those found in other studies (Ohashi and Gyokusen 2007;
52 Konda and others 2008, 2010; Fang and others 2009; Acosta and others 2013). It was reported that
53 well-developed canopy increased the persistence of R_s patterns (Graf and others 2010) and we found
54 that AGB was slightly larger in the second part of the study period (cf. SM Results).

1 Although we expected more heterogeneity in the AGB patterns in the grazed plot, we detected much
2 higher occurrence rate of negative correlations between temporal AGB patterns in the mowed one,
3 which means that an opposite pattern could develop e.g., after mowing or from autumns to springs and
4 from springs/summers to autumns. The observed negative temporal correlations may potentially be
5 related to phenological growth stages since early and late species would be affected differently by
6 uniform height cuttings. The regrowth potential of plants with larger size and biomass is more affected
7 than plants in earlier growth stages and with smaller size. Higher rates of persistence in R_s patterns
8 were reported under forests with relatively stable stand structure (Søe and Buchmann 2005) and within
9 a day with stationary plant and soil factors (ArchMiller and others 2016). In our study we found higher
10 (longer lasting) rates of persistence in R_s pattern in the mowed plot with more uniform stand structure
11 than in the grazed one.

12 The recovery of the patterns can be a common phenomenon in grasslands where summer droughts are
13 frequent (Nagy and others 2007; Koncz and others 2015) but wet extremes may also occur. The
14 process could be similar to that found in another study at micro-scale (Fóti and others 2014), involving
15 a dynamic opening up and closing of the patterns during drying and wetting with the depressions
16 providing a potential refuge for stable ecosystem functioning during droughts. It seems also that the
17 variability in the R_s spatial patterns could be attributed to the rather dynamic responses of the
18 autotrophic components as the background data were very stable (Jurasinski and others 2012; Li and
19 others 2013) in our study as well. However, the exact processes taking place in the recovery period
20 after drought and the role of the autotrophic components (e.g., canopy closure, phenology) throughout
21 the period remains to be elucidated in further studies.

22 5 Conclusions

23 We found that topographic differences, however small they might be, had primary importance in the
24 generation of spatial pattern in the investigated grasslands where drought is frequent but wet extremes
25 also occur. The main background factors such as SOC, TSN and the covariates like SWC and T_s and
26 also AGB, R_s and N_2O were found to follow the patterns of depressions and crests to varying extent.
27 However, we found that spatial patterns and correlations between them were dynamically changing
28 characteristics: sometimes (in the high-precipitation year and primarily in the mowed plot) the co-
29 patterns were masked, or not detectable at all, other times, primarily in autumn, they were reversed
30 compared to the expectations.

31 Patterns and their persistence were also modulated by the management effects even with the applied
32 low grazing pressure and yearly mowing. These management regimes may create different levels of
33 heterogeneity/ homogeneity possibly due to selective grazing, trampling and the return of N by
34 livestock in the grazed plot and due to the uniform cutting height (differently affecting the
35 community's species) in the mowed plot. Regulatory effect of stand structure on the spatial patterns
36 was present in the grazed plot and less detectable or missing altogether in the mowed plot.

37 Temporal persistence of the spatial patterns was also a dynamic phenomenon. During periods of
38 drought the patterns were more variable, depending on the actual potential and pattern of vegetation
39 functioning, while under well-watered conditions we could detect more stability as well as
40 homogeneity. The recovery of the patterns could be a common phenomenon in similar grasslands
41 apparently affected by annual water supply, which is a factor strongly varying in the region. Minor
42 topographical differences seem to be of high importance in pattern dynamics with surface depressions
43 offering potential refuge for stable ecosystem functioning during drought.

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