Title

Higher soil respiration under mowing than under grazing explained by biomass differences

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Abstract

Different management practices may change the rate of soil respiration, thus affecting the carbon balance of grasslands. Therefore, we investigated the effect of grazing and mowing on soil respiration along with its driving variables (soil water content, soil temperature, above and below ground biomass, vegetation indices and soil carbon) in adjacent treatments (grazed and mowed) at a semi-arid grassland in Hungary (2011-2013). The average soil respiration over three years was higher in the mown (6.03±4.07 µmol CO_2 m^{-2} s^{-1}) than in the grazed treatment (5.29±3.50 µmol CO_2 m^{-2} s^{-1}). While soil water content and soil temperature did not differ between treatments, mowing resulted in 20 % higher soil respiration than grazing, possibly due to 17% higher average above ground biomass in the mowed than in the grazed treatment. Inclusions of vegetation index VIGreen in the soil respiration model in addition to abiotic drivers improved the explained Rs variance by 16% in the mowed and by 5% in the grazed site, respectively. VIGreen alone proved to be a simple and fast indicator of soil respiration (r^2=0.31 at grazed, r^2=0.44 at mowed site). We conclude that soil respiration is responsive to the combined effect soil water content, soil temperature, biomass and soil carbon content as affected by the management (grazing vs. mowing) practice.

Introduction

Grasslands contain 20 percent of the world's soil carbon stock (Conant 2010) and act as an important sink for carbon (Soussana *et al*. 2007). However, improper management of grasslands e.g. overgrazing (Smith *et al*. 2008), drought (Nagy *et al*. 2007), land use change (Soussana *et al*. 2004), ploughing (Necpálová *et al*. 2014) or degradation (Zhang *et al*. 2011) can lead to a net loss of carbon (C) from the soil as well as from the ecosystem. Loss of C from these ecosystems increases atmospheric carbon-dioxide concentration (CO_2), thus accelerating climate change (Davidson and Janssens 2006; Lal 2008). To mitigate C losses linked to agricultural managements it is necessary to reduce CO_2 emissions by the proper managements of agricultural lands (Smith *et al*. 2008).

Soil respiration (Rs) is the loss of carbon from the soil to the air from the respiration of roots, mycorrhizae, microbes and soil fauna and via the decay of litter and soil organic matter (Lou & Zhou, 2006). Rs generally increases with increasing soil temperature (Ts) and soil water content (SWC) (Lou & Zhou, 2006; Shrestha *et al.* 2004). However, Rs is reduced at high Ts (above 35 C°) - due to limited transport of sugars, oxygen and water to the roots (Atkin *et al*. 2000) and at high SWC - due to limited oxygen supply for root and microbial respiration (Moyano *et al*. 2013, Burri *et al*. 2014). Besides abiotic drivers, Rs is affected by the soil C content (Hou *et al*. 2014, Fóti *et al*., 2014) and the amount of below and above ground biomass (Curiel *et al.* 2004). Respiration from below ground plant biomass is tightly linked to the photosynthesis of above ground biomass as below ground plant biomass consumes nearly half of the total assimilated carbon (Högberg & Read, 2006). A number of studies thus suggest that photosynthesis dependency (e.g. above ground biomass) should be included in models estimating or predicting Rs (Bahn *et al*. 2009; Balogh *et al*. 2011; Huang and Niu 2012).

Vegetation indices from remote sensing are good estimates for biomass (Silleos and Alexandridis 1996) and photosynthesis (Guanter *et al*. 2014) and may accordingly allow the estimation of soil respiration at larger (regional) scales (Huang and Niu 2012). Besides satellite images, vegetation indices can be measured by handheld digital cameras (Sakamoto *et al*. 2012), providing a fast and cost effective way to capture biomass over a spatial scale of 5 to 50 meters (field-scale). Digital images allow the green vegetation index (VIGreen) representing the vegetation cover to be derived (Gitelson *et al*. 2002).

Grassland management practices such as grazing and mowing have been shown to affect both the above and below ground biomass dynamics (Gong *et al*. 2014), and biomass was found to be one of the driving factors behind Rs (Högberg and Read 2006, Bahn *et al*. 2008). In short term (days) Rs decreased after clipping and grazing due to a reduction of biomass i.e. assimilate supply (Bahn *et al*. 2008). At annual time scale Rs was found to be higher at mowed sites compared to grazed sites; however, at mowed sites the annual average temperature had also been higher; therefore, it was not possible to separate effects of management from those related to temperature (Bahn *et al*. 2008). Biomass is preferred to be high at livestock supporting grassland; however, with increased productivity Rs also increases (Bond-Lamberty and Thomson 2010). Estimating the partitioning of drivers (biomass, SWC, Ts) in shaping the yearly Rs flux is important to find an optimal grassland management. For example grazing, depending on animal stocking rate, either decreases or increases Rs, while mowing usually decreases Rs compared to unmanaged (no grazing or mowing) grasslands (Lou and Zhou 2006). Optimal management could lower the loss of carbon from soil thus preserving soil quality and reducing climate change forcing (Luo 2007). There is a large mitigation potential in managed grasslands as grazing areas for livestock production occupy 25% of terrestrial land (Stehfest et al 2009). Optimal grazing intensities compared to under or over grazing increases carbon sequestration to soils (Smith *et al.* 2008). Temporal variability (i.e. seasonal) of soil respiration affected by management (grazed vs. mowed) has been rarely investigated in previous studies (Frank *et al*. 2006, Lou and Zhou 2006) and especially at paired sites (sites in vicinity of each other i.e. similar vegetation cover and identical meteorological conditions). Therefore, paired sites (in a close spatial distance) are necessary to investigate the exclusive effect of different grassland management (i.e. grazing vs. mowing) on carbon loss of soil and to identify the main drivers behind them.

We studied soil CO_2 emissions under different grassland managements within a livestock system. We hypothesized that there is a difference in the soil respiration response between grazed and mowed managements due to the differentiating effects of the co-variation by above and below ground biomass with soil water content and temperature. The contribution by these factors was tested by different soil respiration models. Furthermore, we expected to identify the differentiating factor in Rs response between grazed vs. mowed sites. Finally, we aimed to provide recommendations for management options to reduce soil carbon loss and to provide applicable methods improving estimations of soil respiration at regional scale. To test our hypothesis and to meet our goals we assessed the effect of grazing and mowing on Rs in relation to differences in abiotic (SWC, Ts) and biotic (above and below ground biomass, leaf are index and VIGreen) driving variables in a three-year study in Hungary. VIGreen index was used to develop a simple and fast model to estimate soil respiration at field scale. Effect of grazing and mowing management on farm scale greenhouse gas budget (carbon-dioxide, methane and dinitrogen-oxid fluxes) was also measured between 2011 and 2013. Results may contribute to a formulation of a management method to reduce greenhouse gas emission at farm scale.

Methods

1. Study area and management

Our study was conducted on semi-arid sandy grasslands in Hungary (Bugac, 46°41'28"N, 19°36'42"E, relatively flat area with 1-2 meters of undulations, 114 m a.s.l.) (Figure 1). The area is managed by the Kiskunság National Park. The climate is dry continental with an annual mean precipitation of 575 mm and an annual mean temperature of 10.4°C (2003-2014). The soil is chernozem type sandy soil with high organic carbon content (Nagy *et al*. 2011). The vegetation is closed sandy steppe. The grassland i.e. the grazing management unit (1074 ha) is permanent and has been used as pasture for at least in the last 40 years. The grazing period of grey cattle (*Bos taurus primigenius podolicus*) usually lasts from June to July (1.06 cattle ha^{-1}) and from October to December (1.35 cattle ha^{-1}) (2002-2013) at the grazed site (2-3 ha) (Figure 1a). This is an extensive grazing management and represents the local management practice according to the National Park restriction where rotational grazing starts in late May and ends in December with a stocking density around 1 livestock unit (LU) ha^{-1}. From April 2011 onwards 1 ha was fenced to exclude grazing and used for mowing (Figure 1a). This site was mowed once per year according to the management practice in the region (10th of August in 2011, 24th of June in 2012 and first of July in 2013). Mowing height was around six centimeters. No fertilization, irrigation, tillage or other managements was applied on either site.

Due to the vicinity of the two sites (250 meters apart) (Figure 1a) the major climatic conditions (photosynthetic active radiation, precipitation, temperature) were assumed to be identical for the two treatments. Based on a vegetation study conducted in 2012, species composition and abundance did not differ between the two management sites (Koncz *et al*.

2014). The most common species and their relative abundances on the grazed and mowed sites were *Poa* spp. (12.4±5.8%, 13.2±6.9%), *Carex* spp. (11.4±7.8%, 13.0±9.3%), *Cynodon dactylon* (L.) Pers (9.9±8.0%, 15.1±3.9%), and *Festuca pseudovina* Hack. ex. Wiesb. (10.4±6.0, 8.4±7.7), respectively. The species composition at the study area was typical of dry grasslands in the region (Molnár *et al.* 2007; Singh *et al*. 1983). Similarities in the climate and vegetation cover between the two managements provided a baseline to focus on the singular effect of management (grazing vs. mowing) on Rs. Measurements started in April 2011 and ended in December 2013.

2. Experimental design

Rs, Ts, SWC, above and below ground biomass, leaf area index (LAI) and VIGreen index were measured in 0.4 x 0.4 m sampling quadrates at each meter along a 5-meter-long transects (40 cm wide) at each sampling occasion at both sites (Figure 1b). The sampling transect was shifted by 2 meters at every measurement campaign to assure a representative sample over the area and year (Figure 1a and b). Measurement campaigns (between 11:00 to 15:00 hours) took place fortnightly during the growing season (April to October) and about every three to four weeks during winter (a total of 54 measurement campaigns during 2011-2013). Precipitation (ARG 100 Tipping Bucket Raingauges, Waterra Ltd.) and air temperature (HMP35AC, Vaisala) were recorded by the meteorological station at the grazed site throughout the whole study period (Figure 1a).

3. Soil respiration, soil temperature and soil water content measurements

Rs was measured fortnightly during summer and every three to four weeks during winter (2011-2013) with a portable LICOR 6400 IRGA connected to a 6400-09 type soil chamber (Li-Cor Inc., NE, USA). Rs was measured 1 h after the removal of biomass. The soil chamber was placed on the ground without using collars to avoid soil disturbances and changes in assimilate supply to the roots (Wang *et al*. 2005). Three Rs measurements were taken in 0.4 x 0.4 m quadrates at every meter along the 5-meter-long transect (in total 15 measurements per site at each measurement campaign) (Figure 1b).

Ts was measured together with Rs using a digital thermometer (DET3R, Voltcraft) during 2011-2012 and a handle thermocouple probe (001 MHP-ICSS-316G, Omega Engineering Ltd., UK) connected to the LICOR during 2013 in the upper 5 cm layer.

SWC was measured simultaneously with Rs with a time domain reflectometer during 2011-2012 (ML2, Delta-T Devices Co., Cambridge, UK) and with a time domain soil moisture meter (Field Scout TDR 300, Spectrum Technologies, IL-USA) during 2013 in the upper 5 cm layer. All measurements were executed within a short period around noon, thus diurnal course of Rs, Ts and SWC did not affect our results.

The optimal number of Rs measurements (*Nopt*) at our site was calculated based on a previous study by Fóti *et al*. (2014) (Eq. 1):

$$Nopt = 99.5 \times \mathrm{SWC}^{-0.782} \quad (1)$$

where *SWC* is the three years average soil water content at each site.

4. Biomass and soil carbon measurements

Above ground biomass was sampled by cutting the plants above the litter layer >1 cm in each sampling quadrate along the 5-meter-long transects (grazed and mown site) (Figure 1b). Biomass was separated into dead (yellow, brown) and living (green) parts. Below ground biomass samples were taken by the soil core method (5 cm Ø, 0-30 cm depth) from the middle of each biomass sample quadrate (Figure 1b). Plant materials and soil samples were oven-dried at 85 °C for 48 h. Dry soil was sieved (1 mm Ø) to separate below ground biomass (roots, rhizomes, bulbs) from the soil. The harvested biomass of the mowed site was weighted (Family-Coop Agricultural and Trading Ltd, Kecskemét, Hungary) and subsamples were taken to measure the fresh weight of the hay and to estimate the water content of the hay.

Amount of herbage removed by grazing animals was estimated by equation (2) (Barcsák *et al*. 1978; Vinczeffy 1993):

$$x_g = \frac{DMI \times NLSU \times y}{z} \quad (2)$$

where x_g is the mass of grazed forage [g m^{-2} year^{-1}], *DMI* is the daily dry matter intake (g) (IPCC 2006) of a live stock unit (kg, LSU), *NLSU* is the number of live stock unit), *y* is the number of grazing days over the year, and *z* is the grazing land area [m^2]. Dry matter intake per livestock unit was calculated by equation (3) (IPCC 2006):

$$DMI = LSU^{0.75} \times \left(\frac{0.2444 * NE_{ma} - 0.0111 * {NE_{ma}}^2 - 0.472}{NE_{ma}}\right) \quad (3)$$

where *DMI* is the daily dry matter intake (g), *LSU* is live stock unit [kg], NE_{ma} is the estimated dietary net energy concentration of diet (6.8 MJ kg^{-1}, IPCC 2006)

Live stock unit (LSU) was calculated as:

$$LSU = \frac{m_{average}}{n_{average}} \quad (4)$$

where, m is the total mass of all cattle [kg] and n is the total number of all cattle at the farm (2011-2013). Management data (m, n, y, z) were provided by the Kiskunság National Park. Harvest index (H, in %) was calculated for both grazed and mowed site by equation (5) (Hunt 1990):

$$H = \frac{x_g}{e_g} \quad and \; \frac{x_h}{e_h} \; (5)$$

where x_g is the estimated mass of grazed forage per unit grazing land (g m^{-2}), x_h is the mass of harvested hay per unit mowed area (g m^{-2}), e_g and e_h is the measured peak biomass for the grazed and mowed site, respectively. To obtain biomass data for each day the biomass data were smoothed applying a technique using polynomial regression and weights computed from the Gaussian density function in SigmaPlot 8.0 (moving window with 10% of sampling proportion). Soil organic C content [g g^{-1}] was determined from five root free soil samples per sites taken monthly (April to November) from the upper 30 cm soil layer in 2011 (total of 40 soil samples for both sites) following the method by the Hungarian Standard (1987).

5. Measurements of vegetation indices (LAI, VIGreen)

Leaf area index was measured non destructively; light interception was measured by a CEP-40 ceptometer (Decagon Devices, USA) at each measurement campaign at each sample quadrate along the 5-meter-long transects (Figure 1b). LAI was estimated from light interception data using the methods described by Campbell (1986) and Campbell and Norman (1989). VIGreen index was derived from red, green, blue (RGB) photographs made by a commercial digital camera (Canon Eos 350D) from the same sampling quadrates along the transects (Figure 1b). Light interception and VIGreen were measured before the vegetation was removed. VIGreen index is the normalized difference of reflected green and red light (Gitelson *et al*. 2002) :

$$VIGreen = \frac{Green - Red}{Green + Red} \quad (6)$$

where *VIGreen* is a dimensionless index, *Green* and *Red* are the component values of a digital image. To analyze the digital images *Image_RGB program* was used (de Beurs and Henebry 2005).

6. Soil respiration models

Soil respiration data were first fitted using the Lloyd Taylor model (Lloyd and Taylor 1994) (Model 1):

Model (1) $$\mathbf{R_s = R_{10}}\boldsymbol{e}^{\left[\mathbf{E_0}\left(\frac{\mathbf{1}}{\mathbf{56.02}}-\frac{\mathbf{1}}{\mathbf{T_{s-227.13}}}\right)\right]}$$

where R_{10} is the respiration rate at 10 °C, *e* refers to the natural logarithm, *Ts* is the soil temperature at 5 cm in Kelvin degrees, E_0 is the parameter related to the activation energy (in K). This model was modified to simultaneously include SWC (Model 2) (Balogh *et al*. 2011):

Model (2) $$\mathbf{R_s = R_{10}}\boldsymbol{e}^{\left[\mathbf{E_0}\left(\frac{\mathbf{1}}{\mathbf{56.02}}-\frac{\mathbf{1}}{\mathbf{T_{s-227.13}}}\right)\right]+\left[-\mathbf{0.5}\left[\mathbf{ln}\left(\frac{\mathbf{SWC}}{\mathbf{SWC_{opt}}}\right)\right]^{\mathbf{2}}\right]}$$

where *SWC* is soil water content (%), and SWC_{opt} is optimal soil water content (%) for Rs. We modified model (2) to include below ground (roots, rhizomes, bulbs) biomass (*B*) (model 3), above ground (total, including dead) biomass (*A*) (model 4), leaf area index (*LAI*) (model 5), above ground green biomass (*G*) (model 6) and VIGreen index (model 7):

Model (3) $$\mathbf{R_s = R_{10}}\boldsymbol{e}^{\mathbf{B(d)}+\left[\mathbf{E_0}\left(\frac{\mathbf{1}}{\mathbf{56.02}}-\frac{\mathbf{1}}{\mathbf{T_{s-227.13}}}\right)\right]+\left[-\mathbf{0.5}\left[\mathbf{ln}\left(\frac{\mathbf{SWC}}{\mathbf{SWC_{opt}}}\right)\right]^{\mathbf{2}}\right]}$$

Model (4) $$\mathbf{R_s = R_{10}}e^{\mathbf{A(d)}+\left[\mathbf{E_0}\left(\frac{1}{56.02}-\frac{1}{T_{s-227.13}}\right)\right]+\left[-0.5\left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]}$$

Model (5) $$\mathbf{R_s = R_{10}}e^{\mathbf{LAI(d)}+\left[\mathbf{E_0}\left(\frac{1}{56.02}-\frac{1}{T_{s-227.13}}\right)\right]+\left[-0.5\left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]}$$

Model (6) $$\mathbf{R_s = R_{10}}e^{\mathbf{G(d)}+\left[\mathbf{E_0}\left(\frac{1}{56.02}-\frac{1}{T_{s-227.13}}\right)\right]+\left[-0.5\left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]}$$

Model (7) $$\mathbf{R_s = R_{10}}e^{\mathbf{VIGreen(d)}+\left[\mathbf{E_0}\left(\frac{1}{56.02}-\frac{1}{T_{s-227.13}}\right)\right]+\left[-0.5\left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]}$$

where *d* is a model parameter.

7) Statistics

Quality control of the Rs, Ts and SWC data consisted of the removal of out-of-range values (±2.5 standard deviations from the mean). Less than 1.6 % of the data were excluded for Rs, SWC and Ts for both mowed and grazed sites. Data followed non-normal distributions (Kolmogorov–Smirnov test), therefore for comparisons between managements and among years non-parametrical tests were performed using R tools (between managements the Kruskal-Wallis test and among groups the Mann-Whitney-Wilcoxon test was used). Rs model fitting procedures were performed using SigmaPlot 8.0 (SPSS Inc). Graphs were also produced with SigmaPlot 8.0 (SPSS Inc). To test the differences of biomass amongst years and between sites the 14-day average biomass data, centered at the peak biomass (±7days around the maximum) was compared between the sites by using the Mann-Whitney test. To test the differences of Rs, Ts, SWC, above and below ground biomass and VIGreen index between sites we also calculated the significant deviation of paired averages (grazed vs. mowed values for the same date) from the linear regression.

Results

Variability of microclimate

Mean annual temperatures during the study period (10.14 °C, 10.76 °C and 10.79 °C in 2011, 2012, 2013, respectively) were close to the ten-year average (10.4°C, 2003-2013). In 2011 and 2012 annual cumulative precipitations (436 and 381 mm, respectively) were lower, while in 2013 (590 mm) cumulative precipitation was close to the ten-year average (575 mm). The autumn (September-October) of 2012 was relatively wet (87.4 mm) and warm (27.7 °C) compared to the autumn of 2011 (54.4 mm, 26.8°C) and 2013 (80.8 mm, 25.5 °C) (Figure 2c). The inter-annual dynamics of Ts was very similar at the two sites (Figure 2a and 4a); annual averages were slightly lower – although not significantly – at the mowed site compared to the grazed site (Table 1). Ts peaked in mid August in all three years, with a maximum value of 31 °C in the mowed site in August 2012 (Figure 2a). The yearly course of SWC followed the same pattern at the two sites (Figure 2b); it tended to be lower at the mowed than at the grazed site (8 %, Figure 4b) but never significantly (Table 1). SWC peaked in July in 2011 (25.7 % grazed, 24.7% mowed) and in May in 2012 (21.8 % grazed, 25.8 % mowed) and in April in 2013 (25.3 % grazed, April 38.5 % mowed) (Figure 2b). Average SWC decreased from 2011 to 2013, more intensively on grazed (25% decrease) compared to the mowed site (20 %) (Table 1).

Management intensities

The average LSU of grey cattle was 402.37 kg (Eq. 4., 2011-2013), while the average DMI of one LSU was 8.95 kg (2011-2013) (Eq. 3., 2011-2013). The grazing period was twice as long in 2011 than in 2012 or 2013 (Table 2). Therefore, the estimated amount of grazed forage (Eq. 2) was highest in 2011 amongst all years, even though the stocking density was the lowest in 2011 (Table 2). The highest amount of hay was harvested in 2011 amongst all years (Table 2). Each year more biomass was harvested (mowed) than grazed (forage) on a hectare base; hence the harvest index was higher at the mowed than at the grazed site (Eq. 5) (Table 2).

Soil respiration

The annual dynamics of Rs was similar at the two sites and amongst years (Figure 3a). At both sites, Rs was high during the vegetation period and low during winter (Figure 3a). Rs peaked around mid June in all years, at the same time of maximum above ground biomass production (Figure 3a and b), about two months before the peak of Ts (mid August in each year) (Figure 2a).

The yearly mean Rs was significantly higher at the mowed site compared to the grazed site in 2012 and 2013 (Table 1). Mean Rs was 20.23 % higher at the mowed site compared to the grazed site by 2013 (Table 1). The effect of management change on Rs was larger than the inter-annual variability of Rs within sites (differences in mean Rs amongst years within sites was 12.5±6.9% for grazed and 6.98±3.0% for mowed site). Using paired Rs averages from the sites in the three years Rs was 11 % higher at the mowed site compared to the grazed one as shown by the slope of the linear regression (Figure 4c).

Biomass accumulation

The yearly dynamics of above ground biomass growth, until reaching the peak biomass, was similar at the two sites due to the fairly similar timing of the mowing and the beginning of grazing in 2012 and 2013 but not in 2011, when grazing started about 2 month before the harvest (Figure 3b and c). Differences in above ground biomass dynamics were observed mainly after the mowing events and during the grazing periods (summer). Before and after these events at the time of spring growth and during the recovery growth in autumn and decomposition in winter, biomass was similar. Peak above ground biomass was significantly higher in 2011 and 2013 at the mowed site compared to the grazed site but not in 2012 (Table 2). Above ground biomass was significantly higher at the mowed site over a year period based on averages (grazed vs. mowed) paired by dates (Figure 4d). In 2012 autumn the mowed site showed higher regeneration capacity (second growth) after the summer drought compared to the grazed site (Figure 3b), probably due to the coupled effect of the early mowing event in this year (Table 2) and the rainy October (Figure 2b). During this regeneration period Rs was also higher at the mowed site compared to the grazed site, serving a direct evidence of biomass effect on Rs (Figure 3a). On average the VIGreen index was 12% higher at the mowed site than at the grazed site based on the three years data (Figure 4e). Of the three years, the highest average and peak biomass was observed in 2011 (Table 2), which was probably due to the influence of the very wet year 2010 (921 mm annual precipitation sum in 2010, compared to the average of 575 mm during 2003-2013).

Biomass dynamics differed between treatments as shown by Figure 3 due to the different timing of biomass removal (mowing is a sudden event while grazing is periodical).

Below ground biomass, based on smoothed data, peaked later than the above ground biomass in both sites with varying time lags of 39, 26 and 1 days at grazed site and 60, 29 and 16 days at the mowed site during 2011, 2012 and 2013, respectively (Figure 3b). Peak below ground biomass was significantly higher in each year at the mowed site compared to the grazed site (Table 2). On the other hand, significantly higher below ground biomass based on paired averages (mowed vs. grazed) by dates was only observed in 2013 but not in 2011 and 2012 (Figure 4f).

Drivers of soil respiration

We found a direct and significant linear relationship between Rs and above ground biomass (r^2=0.23, n=258, p<0.01; r^2=0.50, n=261, p<0.01), green biomass (r^2=0.43, n=257, p<0.01; r^2=0.59, n=259, p<0.01), LAI (r^2=0.27, n=259, p<0.01; r^2=0.43, n=260, p<0.01) and VIGreen index (r^2=0.31, n=247, p<0.01; r^2=0.44, n=242, p<0.01) for grazed and mowed site, respectively. No direct effect of dead biomass or below ground biomass on Rs was observed on either the grazed or mowed sites. Although, no direct effect of below ground biomass was observed on Rs but the growth rate of the below ground biomass (g day^{-1}) showed a correlation with Rs during the growing periods (April-early August). The determination coefficient (r^2) between the Rs and below ground biomass growth rate for the grazed site was significant in 2011 ($r^{2=}$0.42, n=8, p=0.08) and in 2012 (r^2=0.75, n=7, p=0.01) but not in 2013 (r^2=0.43, n=6, p=0.15). At the mowed site the determination coefficient (r^2) between the Rs and below ground biomass was significant in 2011 ($r^{2=}$0.46, n=7, p=0.09), in 2012 (r^2=0.67, n=5, p=0.08) and in 2013 (r^2=0.56, n=6, p=0.08). Also, no direct effect of soil organic C on Rs was observed on either the grazed or mowed sites.

Rs was simultaneously influenced by the combined effects of SWC, Ts and above ground biomass (Table 3). Ts explained 20 % of the variability of Rs at the grazed and 21% at the mowed site using the Lloyd-Taylor model (Model 1). However, when SWC was included in the Rs model (Model 2) the goodness of the model fit (r^2) improved by 55% and 38% in the case of the grazed and mowed site, respectively. When the below ground biomass was incorporated in the model (Model 3) determination coefficient (r^2) for the grazed site decreased in contrast to the small improvement in goodness-of-fit at the mowed site. When above ground biomass, LAI or green biomass was included in the Rs model besides Ts and SWC the goodness of the model fit improved on both grazed and mowed sites. The best model describing the variability of Rs on both grazed and mowed sites was Model 7 which included the VIGreen index. Inclusion of VIGreen index explained an additional 16 % of the variance in Rs at the mowed and 5% at the grazed site compared to Model 2.

No correlation was found between the residuals of the soil respiration Model 7 and the organic C-content of the soil (3.13±1.18% for mowed and 3.74±1.00% for grazed) at either the grazed or the mowed sites ($r^2<0.1$, $p>0.05$).

To estimate whether we had enough number of soil respiration measurements per measurement campaign, we calculated the optimal sample number for Rs (Fóti *et al*., 2014).The sample number taken for Rs was similar to the optimal sample number (we had 15 samples per measurements campaign which is higher than the optimal of 14 for 2011-2013) (Eq. 1).

Discussion

We compared the annual course of soil respiration to that of soil temperature, precipitation, soil water content, above and below ground biomass, vegetation indexes (LAI, VIGreen) and soil carbon in adjacent grazed and mowed sites in a semi-arid grassland in Hungary (2011-2013, Bugac). Due to the vicinity of the two sites their vegetation (Koncz *et al*. 2014) was similar.

Management effects on Rs are often translated through combined effects of SWC, Ts and living above ground biomass (Frank *et al*. 2006; Chen *et al*. 2010). Here we show that seasonal Rs flux was more affected by SWC than by Ts. Ts explained 20% of the Rs variability at the grazed and 21% at the mowed site, whereas SWC accounted for an additional 55 % of Rs variability at the grazed and 35 % of Rs variability at mowed site (Table 3). This was in contrast to other studies, where seasonal soil CO_2 flux was found to be more strongly affected by Ts (explaining 55 % to 83 % of the variability in Rs) than by SWC (Frank et al 2006; Chen et al 2010; Wang et al 2015). Variability of Rs between years was also predominantly caused by differences in annual average SWC at ours sites (Table 1). As the annual average SWC decreased from 2011 to 2013 so did the Rs values (Table 1). SWC decreased more at the grazed site (by 25%) between 2011 and 2013 compared to the mowed site (20%), which was one of the reasons for the larger Rs decrease at the grazed (22%) site compared to the mowed site (10%) during the same time period (Table 1) (decrease in the annual average biomass being one of the other reasons) (Table 2). No differences were observed in the explained variability of Rs by Ts between the grazed and mowed sites. The explained variability of Rs by Ts was lower than for SWC, which indicates that SWC was more important driving factor than Ts. Based on Rs response to SWC the grazed site appeared to be more sensitive to the water content of the soil; however, this response was probably also mediated by covariates (e.g. differences in standing above ground biomass). The optimal SWC for Rs from model fits was equal at the two sites (Table 3). Ts and SWC did not differ between the grazed and mowed sites at any particular year, which could be the reason for their similar effect on Rs at both sites (Table 1).

In agreement with other studies (Craine et al 1999; Bahn et al 2009; Gong et al 2014) we found a strong influence of above ground biomass on Rs. This was confirmed by the improvements of Rs models (3-7) including biotic (biomass, LAI, VIGreen) factors (Table 3). At the mowed site biomass seemed to be a more important driver than at the grazed site as indicated by greater improvement of Rs models when the above ground biomass, green biomass, LAI or VIGreen indices were included (Table 3). Biomass and VIGreen were both higher at the mowed site (Figure 4d and e). Differences in above ground biomass between the grazed vs. mowed sites acted as a differentiating factor in terms of Rs response between the two sites - Rs was higher at the mowed site compared to the grazed site - while no differences were observed in SWC and Ts between the two sites at any particular year (Table 3). Biomass dynamics differed due to the management practices as in 2011 grazing period started earlier than mowing event and in the autumn of 2012 the mowed site had the capacity to recover due to the combined effects of early mowing (Figure 3b) and rainy autumn (Figure 2c). This biomass gain at the mowed site lasted until the spring 2013 showing higher biomass than at the grazed site (Figure 3b). The effect of biomass on Rs was also shown in other studies, where Rs decreased after grazing due to the limited growth of roots (Stark *et al*. 2003; Wan and Luo 2003). Also, Rs decreased after biomass removal via clipping by 19-49% (Bremer *et al*. 1998; Craine *et al*. 1999) due to the reduced supply from photosynthesis (Shahzad *et al*. 2012). On the other hand biomass removal did not change Rs in another study because at the same time SWC increased, which highlighted the dependence of Rs on the multiplicative abiotic and biotic drivers (Jia and Wei 2012).

In our study, there was a strong and direct correlation between the VIGreen index and Rs on both sites. VIGreen explained a higher additional variability of Rs at the mowed site than at the grazed site (Table 3). This corresponds to the results from model 5 and 6 when LAI or the green biomass was included in the soil respiration model (Table 3), indicating the mowed site to be more sensitive to assimilate supply (biomass) in terms of Rs response. Accordingly, remotely sensed vegetation indices (such as VIGreen or NDVI) are likely to be useful variables to improve the goodness of Rs models or for direct estimation of Rs (Huang and Niu 2012). It is important to note that the estimation of Rs still requires SWC and Ts measurements at the same time as the photos were produced (Huang and Niu 2012). However, after calibration (correlation of known Rs flux to VIGreen index) solely VIGreen index i.e. photos could also be used to estimate Rs. The use of vegetation indices in Rs estimates could help to identify the effect of grassland management in soil C loss.

We found only a small direct impact of below ground biomass on Rs in contrast to Geng *et al*. (2012). Also, the Rs model including below ground biomass improved only at the mowed site (Table 3). On the other hand, the growth rate of roots correlated with Rs (except for the grazed site in 2013), indicating the dominance of growth respiration over maintenance respiration of roots in total Rs. It also has to be noted that during the period of fast root growth (Figure 3c) SWC values (Figure 2b) sharply decreased with a negative effect on Rs. Root respiration of grasses was found to be reduced when SWC dropped (Thorne and Frank 2008), and the heterotrophic part of the total Rs was probably also reduced by decreasing SWC.

We found no correlation between the soil organic C content and Rs at both sites in contrast to others (Bahn *et al*. 2008; Hou *et al*. 2014). The reason for this could be that the variability of soil organic C content was low at both of our sites (3.74±1.01 % at grazed and 3.13±1.19 % at mowed site) compared to others where a wider range of soil C content was found to have a significant effect on Rs (e.g. soil C content varied between 3-8 kg m^{-2} by Bahn *et al*. 2008; between 8-13 g kg^{-1} by Hou *et al*. 2014, and between 1-20% by Geng *et al*. 2012).

In summary, we found that the CO_2 carbon flux from soil was higher at the mowed site compared to the grazed site due to the higher biomass under mowing than under grazing. However, the role of Rs in total ecosytem respiration and in net carbon ecosystem exchange (NEE) should be considered before general statement could be drawn about the possible contribution of different managements to climate change mitigation/adaptation practices. Rs is a response to the combined effect of drivers such as SWC, Ts, above and below ground biomass, as well as soil carbon (Geng *et al*. 2012) rather than to the management itself.

Influence of management on biomass dynamics seems to be the main practical option to modify this combined effect to address mitigation/adaptation targets.

Conclusion

We found that soil respiration was higher under mowing than grazing in semi-arid grasslands. The yearly course of soil respiration was mainly influenced by soil water content and to lesser extent by soil temperature and above ground green biomass. We suggest that soil respiration differences between the grazed and mowed sites were linked more to biomass differences between the sites rather than to the insignificant differences in soil water content and soil moisture between the sites. Biomass played an important role in differentiating the two management forms with regard to Rs. Biomass was larger due to management effect (grazing started earlier than mowing in 2011, early mowing and rainy autumn in 2012 favored faster regeneration at the mowed site, compared to grazed site which biomass gain lasted until 2013). In our study we improved the soil respiration model by including the VIGreen index besides soil water content and soil temperature in the soil respiration model. VIGreen index derived from images taken by a digital camera could be a fast and cost effective way to estimate soil respiration over larger spatial scales. Our observations would indicate that grazing should be favored instead of mowing; however the role of soil respiration in total ecosytem respiration and net carbon ecosystem exchange should be quantified before more general statement could be drawn. Nevertheless, net loss of carbon from soil should be avoided to preserve soil productivity and mitigate climate change. Also, soil respiration response to different grassland management practices should be represented in soil respiration models as a mix of soil water content, temperature, soil carbon and biomass response, rather than a direct effect of the management itself.

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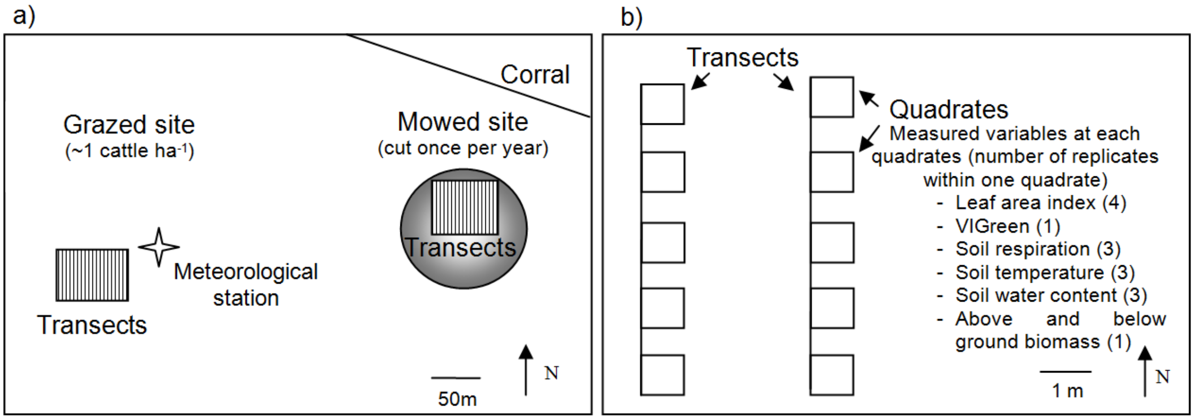

Fig. 1 Study site (a) and experimental design (b) at the cattle farm of the Kiskunság National Park (near Bugac, Hungary).

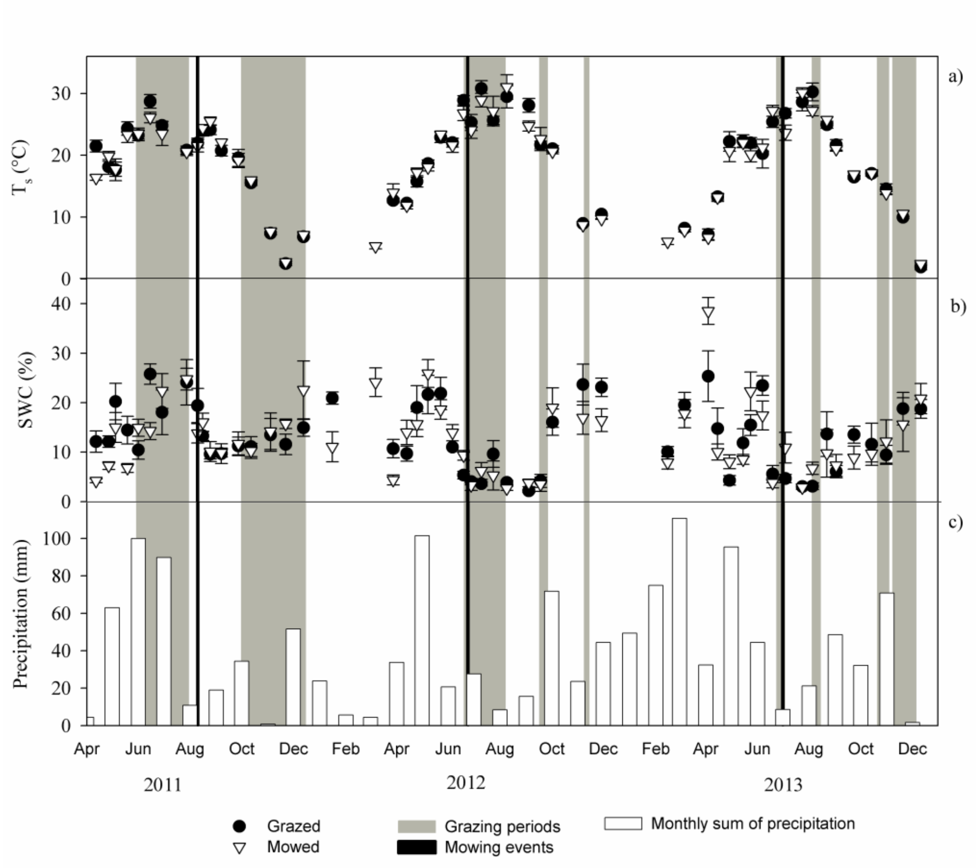

Fig. 2 Temporal dynamics of yearly soil temperature [Ts, °C] (a), yearly soil water content [SWC, %] (b), monthly sum of precipitation [Precipitation, mm] (c) and management at the grazed and mowed sites (2011-2013). Error bars are standard deviations of fifteen measurements.

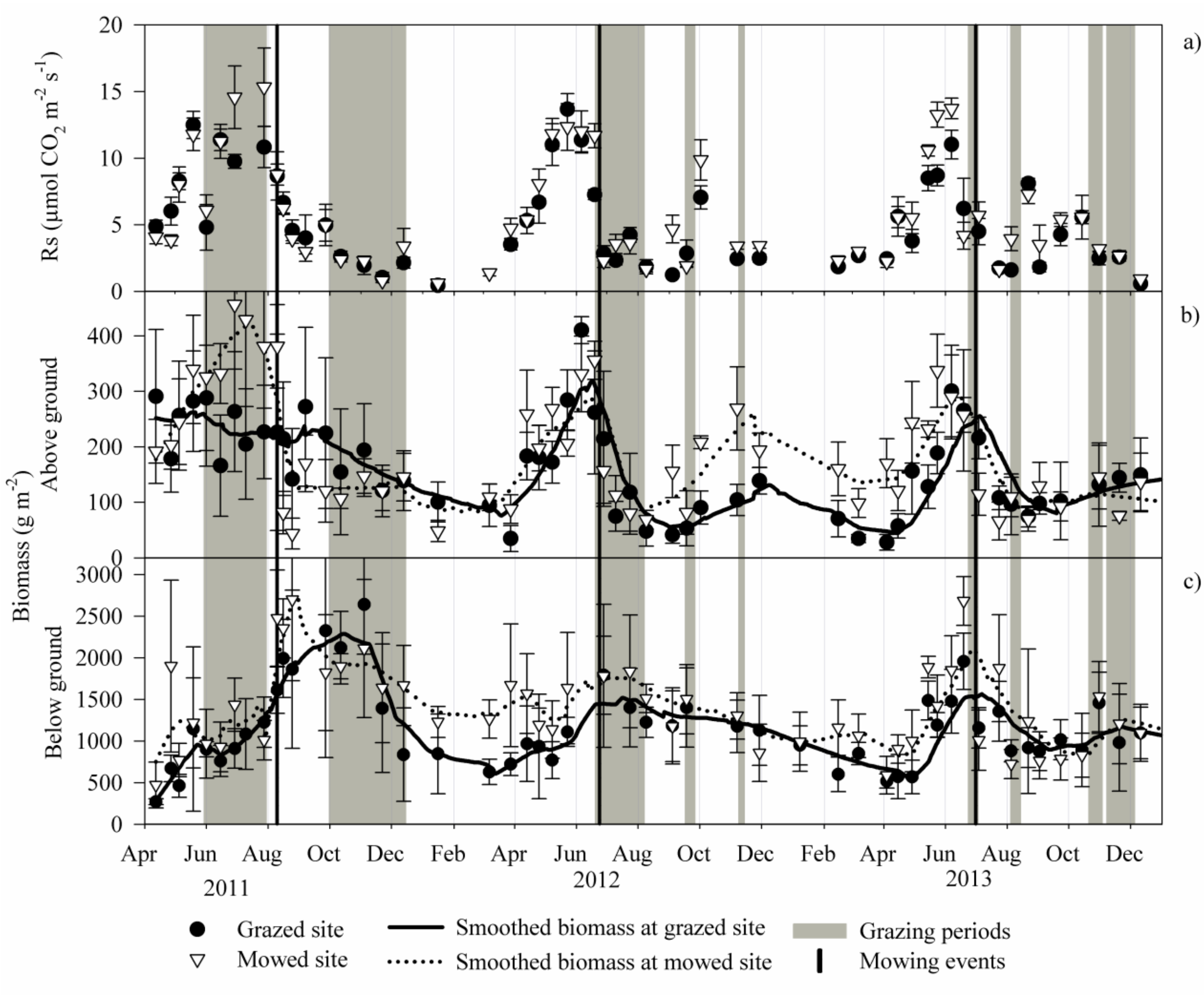

Fig. 3 Average soil respiration [Rs, μmol CO_2 m^{-2} s^{-1}] (a) and above (b) and below (c) ground biomass [g m^{-2}] dynamics at grazed and mowed sites (2011-2013), error bars show standard deviation.

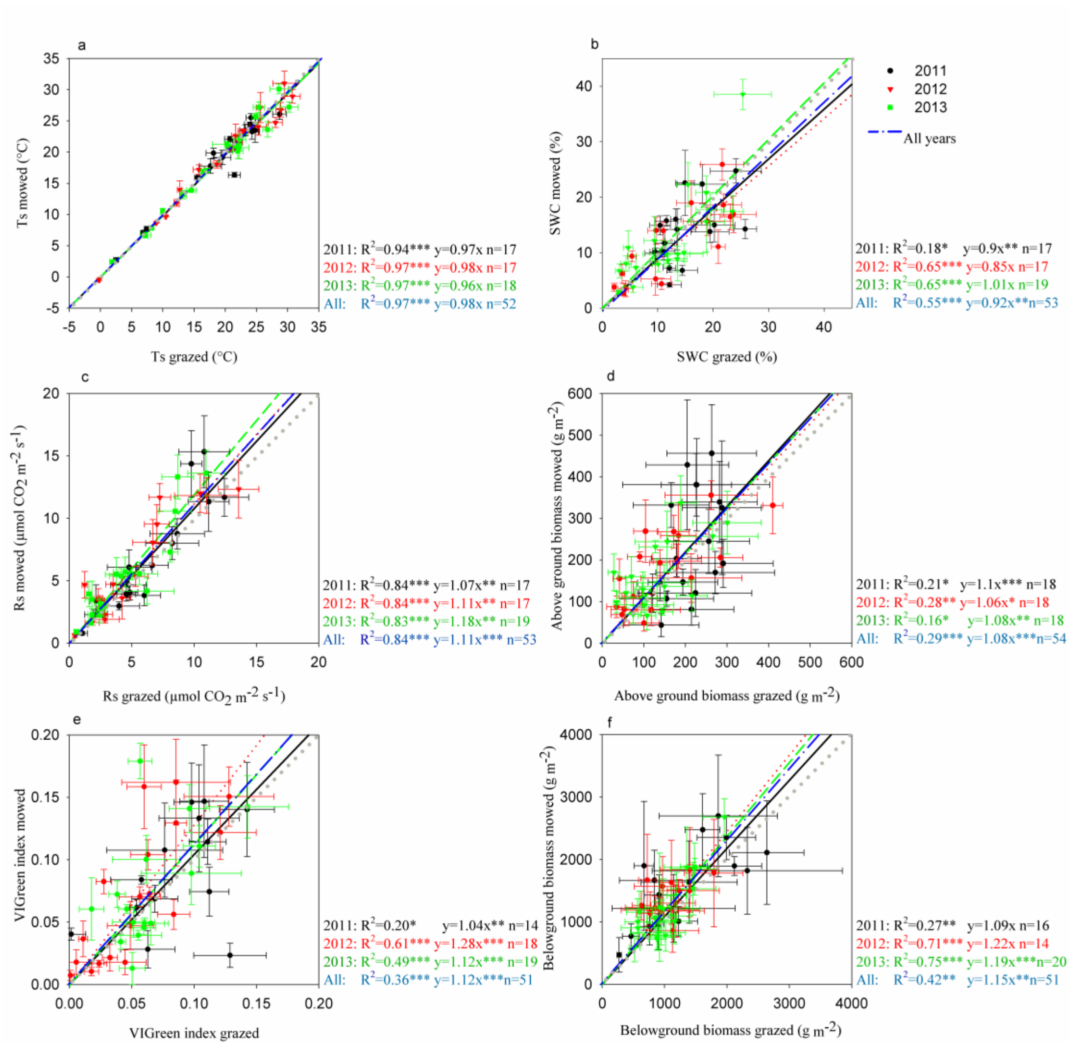

Figure 4 Correlation between (a) soil temperature [Ts, °C], (b) soil water content [SWC, %], (c) soil respiration [Rs, μmol CO_2 m^{-2} s^{-1}], (d) above ground biomass [g m^{-2}], (e) VIGreen index and (f) below ground biomass [g m^{-2}] at the grazed vs. mowed sites by years (2011-2013). One data point represents the average of one measurement campaign, which consisted of 15 measurements for Ts, SWC and Rs, and 5 measurements for biomass and VIGreen index (error bars are standard deviations). R^2 values are the determination coefficients for linear regression (at p<0.001***, p<0.05** and p<0.1* significance levels). Significant deviation of the 1:1 slope (dotted, grey line) from linear regression (y=x) is represented by stars after the linear regression equation (at p<0.001***, p<0.05** and p<0.1* significant levels). The symbol of the regression lines by years is a continuous black line for 2011, red dots for 2012, green dashes for 2013 and blue dash-dot-dash line for all years.

Table 1 Annual average soil respiration (Rs), soil temperature (Ts) and soil water content (SWC) at grazed and mowed sites (April-December for all years, 2011-2013), standard deviations are shown in brackets.

Years	Management	Rs [µmol CO_2 m^{-2} s^{-1}]	Ts [°C]	SWC [%]
2011	Grazed	6.05 (3.62)[a]	18.80 (6.98)[a]	14.80 (5.50)[a]
	Mowed	6.34 (4.44)[a]	18.60 (6.72)[a]	13.71 (6.05)[a]
2012	Grazed	5.08 (3.70)[b]	21.90 (6.75)[b]	11.98 (8.48)[b]
	Mowed	6.06 (3.98)[a]	21.66 (6.37)[b]	11.75 (7.49)[b]
2013	Grazed	4.73 (3.17)[b]	20.10 (7.34)[a]	11.06 (7.79)[b]
	Mowed	5.69 (3.78)[a]	19.66 (7.06)[a]	10.92 (6.17)[b]

[a,b] Different letters indicate significant differences among years and managements within columns at $p<0.05$ (Mann-Whitney test)

Table 2 Yearly management and biomass production of grazed and mowed sites (2011-2013), standard deviations are shown in brackets. Biomass is given as dry weights. Different letters indicates significant differences between managements within years and amongst years within managements at $p<0.05$ (n=14 per year per management, Mann-Whitney test), LSU is livestock unit.

	Grazed site			Mowed site		
	2011	2012	2013	2011	2012	2013
Grazing period [days year^{-1}]	138	65	62	-	-	-
Stocking density [LSU ha^{-1} year^{-1}]	0.78	1.50	1.34	-	-	-
Harvest days	-	-	-	Aug-10	Jun-24	Jul-01
Grazed forage/harvested hay [g m^{-2} year^{-1}]	102.1	87.05	73.9	293.3	145.9	229.2
Above ground peak biomass [g m^{-2}]	258.9 (3.14)^{a}	306.8 (9.15)^{b}	248.1 (6.7)^{c}	436.6 (18.8)^{d}	281.28 (4.1)^{e}	301.8 (4.9)^{f}
Below ground peak biomass [g m^{-2}]	2270.3 (14.2)^{a}	1492.8 (22.8)^{b}	1537.4 (17.2)^{c}	2620.6 (107)^{d}	1748.1 (12.6)^{e}	2050.0 (45.4)^{f}
Above ground average biomass [g m^{-2}]	213.5 (107.83)^{a}	144.7 (107.99)^{b}	129.9 (87.15)^{b}	234.3 (145.9)^{a}	177.07 (98.7)^{b}	158.6 (88.7)^{b}
Below ground average biomass [g m^{-2}]	1306.0 (479.1)^{a}	1091.5 (359.7) ^{a}	1040.0 (269.0) ^{a,b}	1585.1 (502.6) ^{a}	1404.5 (430.0) ^{a}	1230.0 (347.7)^{a,b}
Harvest index [%]	39.4	28.83	29.8	67.2	51.5	83.6

Models	Drivers included	Management	R_{10}	E_0	SWC_{opt}	d	r^2	n
1	Ts	Grazed	2.4***	124.8***			0.2***	256
		Mowed	2.8***	129.4***			0.21***	262
2	Ts, SWC	Grazed	3.2***	325.1***	26.4***		0.75***	253
		Mowed	3.8***	298.0***	26.3***		0.59***	258
3	Ts, SWC, B	Grazed	3.8***	289.8***	25.9***	-0.05	0.6***	224
		Mowed	4.3***	301.1***	24.6***	-0.1*	0.61***	233
4	Ts, SWC, A	Grazed	3***	331.2***	26.5***	0.1***	0.76***	248
		Mowed	2.5***	252.1***	19.8***	2.0***	0.7***	254
5	Ts, SWC, LAI	Grazed	2.9***	310.9***	25.2***	0.1**	0.77***	249
		Mowed	2.9***	251.2***	20.9***	0.1***	0.65***	253
6	Ts, SWC, G	Grazed	3.0***	323.2***	26.1***	0.2***	0.78***	247
		Mowed	3.4***	291.7***	25.2***	0.3***	0.64***	251
7	Ts, SWC, VIGreen	Grazed	2.4***	311.9***	21.2***	3.4***	0.8***	236
		Mowed	2.5***	266.1***	17.2***	3.9***	0.75***	235

Table 3 Results of soil respiration Models 1-7. Coefficients; R_{10} (respiration rate at 10 °C [µmol CO_2 m^{-2} s^{-1}], E_0 (parameter related to the activation energy in [K]), SWC_{opt} (optimal soil water content [%]), *d* (model parameter related to below ground biomass (*B*), above ground biomass (*A*), leaf area index (*LAI*), above ground green biomass (*G*) and *VIGreen* index, respectively), R^2 (determination coefficient) values and number of data points (N). Statistical significance levels of coefficients after fitting the different models to Rs data of all three years are *** $p<0.0001$, ** $p<0.001$ and * $p<0.05$. *Ts* is soil temperature, *SWC* is soil water content.