

# Short-term effects of extensive fertilization on community composition and carbon uptake in a Pannonian loess grassland

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## Abstract

Among the most extended ecosystems of the temperate zone, the seminatural, dry grasslands constitute a substantial proportion in the Carpathian Basin. The aim of our present study was to investigate the short-term effect of extensive fertilization on the species composition and CO<sub>2</sub> exchange of loess grassland at community level. The *in situ* investigation of the latter parameter have not been yet carried out in Pannonian loess grasslands. Most of the parameters studied showed a considerable interannual variation both in the fertilized and in the control stands. As a result of the treatment, the average species number of the fertilized stand decreased by 22%, which was more significant in the autumn (26%) than in the spring. Diversity values, including Shannon index and species richness, increased by nearly 1.5 times in the year with adequate rainfall compared with the initial values. In general, species richness and the ratio of dicots decreased, while the ratio of therophytes, alien competitors, and C<sub>4</sub> plants increased with the addition of fertilizers. Significant carbon sequestration potential was only detected during wet periods in the fertilized grass. The rate of CO<sub>2</sub> uptake was found to be nearly five times higher in the fertilized stand and nearly three times higher in the control stand during the wet year compared with the previous, extremely dry year. The CO<sub>2</sub> uptake potential of the fertilized grassland exceeded that of the control stand by 12% in the year with high rainfall, while the rate of CO<sub>2</sub> exchange dropped by 50% in the dry year in the fertilized stand. Our study reinforced the idea that the decline in species richness was not necessarily followed by the reduction of stand level carbon uptake in a short period due to an insignificant change in ecophysiological functional groups.

*Additional key words:* canopy chamber; *in situ* experiment; net ecosystem CO<sub>2</sub> exchange; nutrient treatment; species composition.

## Introduction

Grasslands constitute one of the largest ecosystems of the temperate zone covering about 20% of Europe (Soussana *et al.* 2007). In the Carpathian Basin, extended areas are covered by seminatural, grass communities (Czóbel *et al.* 2010) including dry grasslands. A recent country scale analysis of different habitat types showed that more than 175,000 ha of seminatural, dry grassland remained in Hungary (Molnár *et al.* 2008). The Central European loess grasslands are the representatives of the well structured, diversed dry grasslands, which are rich in

dicot species (Bölöni *et al.* 2011) being a reminescent of the tallgrass prairie. Only a few information is yet available on the stand level ecophysiological activity and carbon cycling of these loess grasslands.

Interactions between changing nutrient pools and different aspects of global climate change are likely to affect (semi)natural and managed terrestrial ecosystems (Frank 2007). Weather anomalies can have negative effects on grass functioning by decreasing their production and carbon uptake, especially, by summer drought

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**Abbreviations:** AC – alien competitors; ANOVA – analysis of variance; ANPP – annual net primary production; CO – competitors; Ch – Chamaephytes; DT – disturbance tolerants; G – generalists; H – Hemicryptophytes; H<sub>s</sub> – *Shannon's* diversity index; K – kryptophytes; MM – phanerophytes; N – nanophanerophytes; NEE – net ecosystem CO<sub>2</sub> exchange; NP – natural pioneers; PPFD – photosynthetically active photon flux density; RC – ruderal competitors; S – specialists; SWC – soil water content; T<sub>air</sub> – air temperature; Th – therophytes; TH – hemitherophytes; W – weeds.

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and heat (e.g. Ciais *et al.* 2005). Furthermore, it is also known that drought stress significantly decreases mycorrhizal colonization (e.g. Nilsen *et al.* 1998, Lutgen *et al.* 2003). The grass ecosystems of the Carpathian Basin can be particularly vulnerable to current and forecasted changes in land use including more intensive management regimes. Yet, the structural and functional responses of seminatural grasslands to the different management practices are not sufficiently understood (Czóbel *et al.* 2008).

A large number of publications deal with the carbon cycling in grasslands of temperate zone, but only a few studies (e.g. Haszpra 2011) are available for East-Central Europe, including the Pannonian Basin (Czóbel *et al.* 2010). Furthermore, the flux results are rarely linked to vegetation dynamic processes (Czóbel *et al.* 2008) despite the fact that responses of the ecosystem CO<sub>2</sub> exchange to climatic factors may vary according to phenological stages (Yuste *et al.* 2004). Managed grasslands can play an important role in the European carbon balance, although most of the grassland fertilization studies deal almost exclusively with their impact on soil respiration rate (e.g. Bouma and Bryla 2000).

Numerous studies focused on the effects of different management treatments on the community composition of temperate grasslands. Many investigations showed that artificial nitrogen supply of grasslands has negative, often dramatic effects on species number and diversity (e.g. Tilman 1987, Turner and Knapp 1996, Gough *et al.* 2000, Piper *et al.* 2005), although grazing could eliminate these effects (Jacquemyn *et al.* 2003). In drier prairie vegetation, mineral fertilization decreased the species number and the percentage cover of legumes and numerous species were found to be intolerant to increased nitrogen concentration. In a comparative tallgrass and shortgrass steppe study (Piper *et al.* 2005), the addition of nitrogen

increased the annual net primary production (ANPP) by 9% in unburned and by more than two thirds in burned tallgrass prairie (Knapp *et al.* 1998) due to the different nitrogen pool.

Fertilization (and other resource manipulations) resulted in increased invasibility of the grassland community and resource enrichment increased generally productivity. These responses were contingent upon species availability and tended to be more pronounced in the presence of an expanded propagule pool (Foster and Dickson 2004). Net primary production and nutrient dynamics of grasslands are regulated by different biotic and abiotic factors, which may differentially affect the biomass of the plant functional groups (e.g. Semmarin *et al.* 2007). For example, simultaneous addition of water and nitrogen led to increased dominance of two the most abundant grass species, *Bromus carinatus* and *Elymus glaucus* (Harpole *et al.* 2007). Production is controlled by the nutrient level of a soil, especially, by its phosphorus and nitrogen concentration (Thiel-Egenter *et al.* 2007). The latter one is reported to be the most important limiting factor of ANPP (Knapp *et al.* 1998).

The aim of our study was to investigate the short-term effect of extensive fertilization on the community composition and CO<sub>2</sub> exchange of a loess grasslands at vegetation level during a three-year study.

Some specific question areas addressed here included: (1) Effects of extensive nitrogen, phosphorous, and potassium (NPK) fertilization on community composition determined by *Shannon's* diversity index (H<sub>s</sub>), species richness, plant functional groups, and net ecosystem CO<sub>2</sub> exchange (NEE) values; (2) Significance of the inter-annual and seasonal dynamics of the parameters studied; (3) Relationship between botanical and CO<sub>2</sub>-flux data in the studied loess grassland.

## Materials and methods

**Study site and experimental plots:** The extensively fertilized site (mineral fertilizers applied once a year) was located in the Gödöllő Hills between Isaszeg and Nagytarcsa (47°42'N, 19°24'E, 255 m a.s.l.). The climate of the region is temperate continental (mean annual precipitation is 560 mm, mean annual temperature is 9.1°C), and the soil is a moderately eroded, lime-impregnated chernozem. During our three-year study, the annual precipitation ranged from 432 mm in 2003 to 627 mm in 2004. The climatic zonal loess grassland vegetation is a vertically well stratified and rich in broadleaf dicotyledons (Bölöni *et al.* 2011). The fertilization experiment was carried out on 10 assigned small, loess grassland plots (1 m × 1 m) in order to study the structural and synphysiological responses of vegetation as the function of fertilization. The plots were selected along two types of transects (5 treated, 5 control). The transects were 5 m apart, whilst the plots within the transects were at a distance of 1.5 m

one from another. A total of 10 plots (1 m<sup>2</sup>) were designated on a flat plateau, therefore the results were not influenced by the inclination and exposure of the land. The analysis of the soil samples taken prior to the application of fertilizers showed no statistically significant difference between the soil parameters in the designated stands. The fertilized plots were not randomly designated, because lateral flows could influence the nutrient supply of the control plots. Due to the surrounding vegetation, the designation of more and larger plots was not possible. Mineral fertilizer (*Compacted GENEZIS NPK*, *BiGe Holding Ltd.*, Szolnok, Hungary) was applied once a year at the beginning of the growing season (June 13 in 2002, April 23 in 2003, April 29 in 2004) in form of NH<sub>4</sub>NO<sub>3</sub>, P<sub>2</sub>O<sub>5</sub>, and K<sub>2</sub>O [10 g(N) m<sup>-2</sup>, 5 g(P) m<sup>-2</sup>, and 5 g(K) m<sup>-2</sup>]. The delayed application of fertilizer in 2002 was due to rescheduling measurement protocols of Greengrass EU R & D projects (EVK2-CT2001-00105).

**Plants:** The nomenclature of plants followed Simon (2000). The studied vegetation was a xeric, species rich, tall loess grassland, *Salvio nemorosae-Festucetum rupicolae*, (Czóbel *et al.* 2008, Bölöni *et al.* 2011). The fertilized plots were initially dominated by *Festuca rupicola* (78%), *Dorycnium herbaceum* (12%), and *Salvia nemorosa* (5.6%). Other characteristic taxa of the community, such as *Seseli osseum* and *Galium verum*, were commonly encountered in the plots. The total species number of the initial vegetation varied between 23 (fertilized plots) and 25 (control plots).

**Applied methods:** The botanical sampling of the designated stands was carried out twice a year during the growing period, at the end of the spring, by mid June, and in the autumn, by late October. The spring data of 2003 were not used due to the incomplete dataset. Percentage of the cover for each species was estimated using the relevé method (Mueller-Dombois and Ellenberg 1974, Van Der Maarel 1979) by  $1 \times 1$  m quadrats, out of which species richness ( $H_s$ ), mean cover, number of  $C_4$  species, and the relative distribution of plant functional groups (including Social Behaviour Types based on Borhidi 1993) were calculated. Stand level  $CO_2$ -flux measurements (NEE = net ecosystem  $CO_2$  exchange) were carried out episodically at monthly or bimonthly intervals during the vegetation period using chamber technique and a portable infrared gas analyser (*CIRAS-2, PP Systems*, Hitchin, UK) operating in the open system mode. The photosynthetic system was connected to a water clean, portable, nondestructive, self-developed chamber (diameter = 60 cm, made from plexiglass) taking air

samples from the connecting (inner and outer) tubes (Czóbel *et al.* 2004).  $CO_2$ -exchange rate was calculated from the differences or changes in  $CO_2$  concentrations (Czóbel *et al.* 2004, 2005). Stand level chamber (NEE) measurements were carried out on clear and sunny days between 10:00 and 16:00 h in order to avoid the unsteady meteorological parameters. On a typical NEE measurement day, the carbon fluxes of 3 control and 3 treated plots were measured alternately for an average of 60 min per plot. Photosynthetic photon flux density (PPFD) and air temperature ( $T_{air}$ ) were measured by *CIRAS-2* sensors parallelly with the carbon flux data, and a time-domain reflectometer (*ML2, Delta-T Devices Co.*, Cambridge, UK) was used to detect the volumetric soil water content (SWC). The aboveground biomass was removed (at 5 cm) twice a year at biomass peak after the 1<sup>st</sup> and the 2<sup>nd</sup> growing period in early June and November. Study area was extensively grazed by sheep earlier and as a result, the vegetation was adapted to being occasionally removed and therefore the removal of the biomass did not affect subsequent measurements.

**Statistical analysis:** All measured and calculated data were analyzed by the *R-statistical program* (R Development Core Team 2009). The botanical and synphysiological responses as the effects of fertilization were tested using *ANOVA* and the *post hoc* test of *Tukey's* honestly significant difference (HSD) with corrections (adjusted  $P$ -values for the multiple tests). For *Shannon's* diversity and cover of  $C_4$  species, the variability was assessed using the standard deviation calculated from five spatial replicates.

## Results

**Community composition:** The 2<sup>nd</sup> year was much drier, while the 3<sup>rd</sup> year was more humid than usual, based on the comparison of annual and long-term meteorological data (Czóbel *et al.* 2008). The variance analysis showed no significant differences between the fertilized and control stands neither for  $H_s$  (*ANOVA*  $F = 1.741$ ,  $P = 0.2351$ ,  $Df = 1$ ) nor for the sum of or the total species richness (*ANOVA*  $F = 1.639$ ,  $P = 0.2477$ ,  $Df = 1$ ). As a result of the treatment, the average number of species of the fertilized stand decreased by 22%, more in the autumn (26%) than in the spring.  $H_s$  increased by nearly 1.5 times in the year with favourable precipitation level compared with the initial ones at both stands (Fig. 1). Vegetation in the fertilized plots was dominated initially by the monocot, *F. rupicola* Heuff., while in the third year a dicot taxa, *S. nemorosa* L., became the dominant species. In addition, some graminoid species (*Dactylis glomerata* L., *Koeleria cristata* L./Pers.) and dicot (*Astragalus onobrychis* L., *Medicago falcata* L., *S. osseum* Cr. em. Simk.) showed a positive response to additional nitrogen supply. In contrast, inhibiting effect of

fertilization was found in *e.g.* *Chrysopogon gryllus* /Torn./Trin. and *F. rupicola*, out of which the former disappeared from the treated plots. The relative proportion of monocot species increased, whilst that of the legumes decreased in the fertilized grassland (Fig. 2). However, the total cover of monocots decreased. Concerning life forms, hemicryptophytes dominated the fertilized plots (Fig. 3) in general; this represents a typical life form of the Hungarian grasses. The number of hemicryptophytes (H) and therophytes (Th) increased, whereas that of cryptophytes (K), chamaephytes (Ch), and nanophanerophytes (N) dropped as a result of fertilization. In the treated stand, alien competitors (AC) appeared, ruderal competitors (RC) disappeared, while the number of specialists (S), competitors (CO), and generalists (G) slightly decreased, presumably due to the effect of management (Fig. 4). In autumn, the mean percentage cover of  $C_4$  taxa increased in all stands due to the expected temporal variation of  $C_4$  species, although fertilization elevated the mean cover of this functional group. In each sampling time, only one  $C_4$  species,

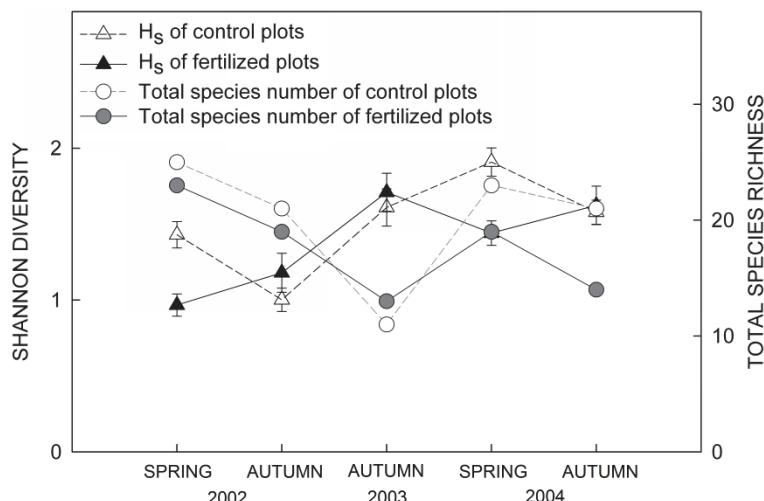


Fig. 1. Seasonal and interannual variation of mean Shannon diversity and species richness due to fertilization treatment (2002-2004; Isaszeg, Hungary). Error bars show SD,  $n = 5$ .  $H_s$  – Shannon's diversity index.

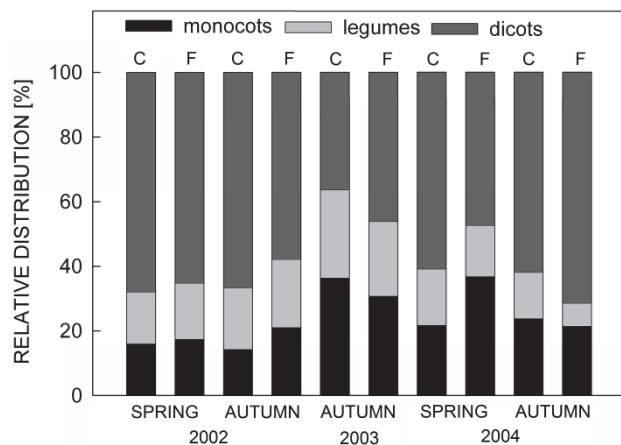


Fig. 2. Relative distribution of monocots, legumes and dicots (excluding Fabaceae) in nontreated (A) and treated (B) plots in 2002 and 2004.  $n = 5$ . C – control; F – fertilized.

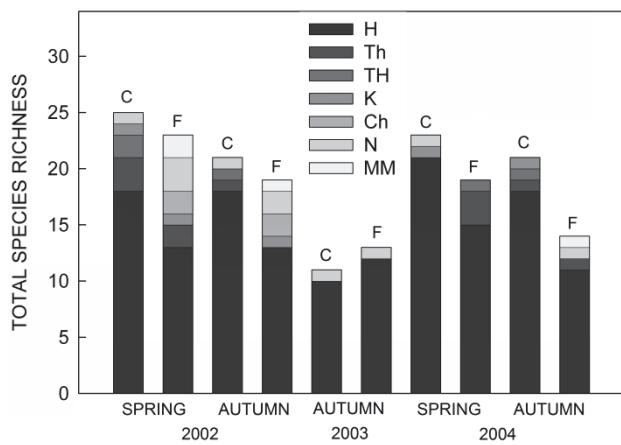


Fig. 3. Temporal variation in the frequency of Raunkier's life forms in fertilized and nontreated loess plots.  $n = 5$ . C – control; F – fertilized. H – hemicryptophytes; Th – therophytes; TH – hemitherophytes; K – kryptophytes; Ch – chamaephytes; N – nanophanerophytes; MM – phanerophytes.

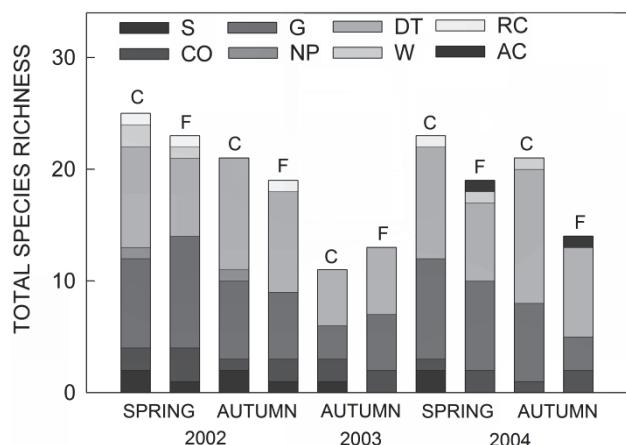


Fig. 4. Temporal variation in the frequency of social behaviour types due to fertilization.  $n = 5$ . S – specialists; CO – competitors; G – generalists; NP – natural pioneers; DT – disturbance tolerants; W – weeds; RC – ruderal competitors; AC – alien competitors.

*Chrysopogon gryllus* (2002 spring) or *Bothriochloa ischaemum* /L./Keng (all the other time), represented this functional group, except the spring in 2004, when *Bothriochloa* occurred only in the fertilized plots (Fig. 5).

**Stand level CO<sub>2</sub> exchange:** Compared with the previous, extremely dry year, the rate of CO<sub>2</sub> uptake was nearly five times higher in the fertilized grasslands and three times higher in the control stand in the year with higher rainfall (2004) (Fig. 6). The carbon exchange potential of fertilized grassland exceeded that of the control stand by 12% in the year with high precipitation, whilst the CO<sub>2</sub> exchange was lower by 50% in the treated stand in the dry year. Repeated ANOVA measures of NEE did not demonstrate significant differences between treated and nontreated stands ( $F = 0.902$ ,  $P = 0.355$ ,  $Df = 1$ ) during 3 years. However, statistical analysis showed a significant interannual variation of NEE both in the fertilized

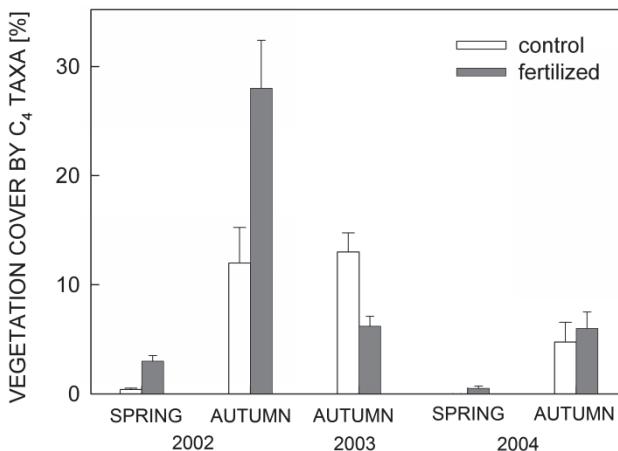


Fig. 5. Seasonal and interannual changes in mean percentage cover in fertilized and control loess plots.  $n = 5$ .

(ANOVA  $F = 169.88$ ,  $P < 0.001$ ) and the control (ANOVA  $F = 131.27$ ,  $P < 0.001$ ) plots. Related to the temporal changes of NEE, in each year and both stand, the highest carbon uptake were found in June, while the lowest sequestration rate or even carbon release occurred in

## Discussion

**Community composition:** The most rapid changes were observed in the species composition, especially at the fertilized plots. It was rather due to climatic anomalies than to the treatment, because the decline was similar in both the fertilized and nontreated plots (Fig. 1).  $H_s$  values were similar at the end of the experiment, because the taxa, which disappeared and reduced in number, were particularly replaced by perennial graminoids (e.g. *Dactylis glomerata*, *Koeleria cristata*) and weeds (e.g. *Conyza canadensis* /L./Cronq.) in the treated stands. An artificial nitrogen supply had negative effects on species richness and diversity in dry grasslands (e.g. Tilman 1987, Turner and Knapp 1996, Huberty *et al.* 1998) causing dramatic shifts (e.g. Tilman 1987, Gough *et al.* 2000) in a relatively short period of time in many cases, although our experiment did not support these findings. In our study, the treated plots did not display such negative trends compared with the controls. The quick recovery of species richness and  $H_s$  after the extremely dry year could show that the Pannonian loess grassland has a significant regeneration potential on short term scale. As a result of increased grazing, the structure, total cover, and species number of the Pannonian loess grasslands showed similar decline, which led to the dominance of net ecosystem CO<sub>2</sub> exchange a few grass species and to further decline in the proportion of dicots (Bölöni *et al.* 2011). Changes in the species pool was followed by shifts in the dominant structure of fertilized plots. The latter was probably due to the increasing dominance of net ecosystem CO<sub>2</sub> exchange a disturbance-

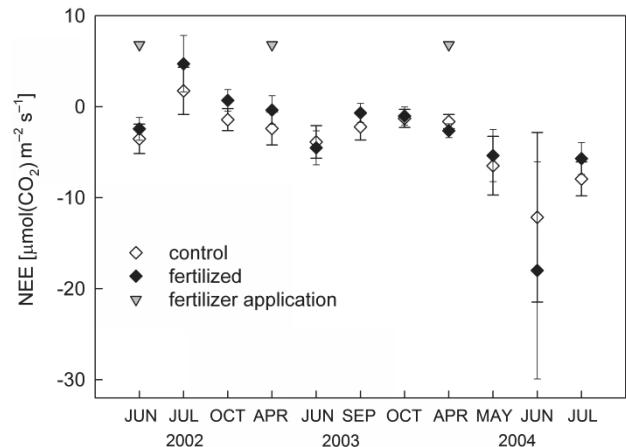


Fig. 6. Seasonal and year-to-year dynamics of CO<sub>2</sub> flux of fertilized and control loess grassland plots at Isaszeg site (Hungary) during 2002–2004 period. Error bars show SD.  $n = 3$ . NEE – net ecosystem CO<sub>2</sub> exchange.

April (2003: fertilized, 2004: both stand), July (2002: carbon release in both stand), and October (2003: control).

tolerant *Salvia nemorosa*, which could assist in the observed decline in species richness. This observation was in accordance with other studies, which highlight the positive effect of more intensive management on strong competitors (e.g. Jacquemyn *et al.* 2003, Harpole *et al.* 2007, Czóbel *et al.* 2008). The positive responses to nitrogen supplementation observed in certain species were in agreement with the findings of Piper *et al.* (2005). It was the fact that mineral fertilization decreased the species number and percentage cover of legumes (Fig. 2) in drier prairie vegetation. The taxa, which disappeared and reduced in number as well as the plant functional groups, were chiefly replaced by perennial hemicryptophytes, competitors, disturbance-tolerant plants, and alien competitors (Figs. 3,4). It seemed that fertilization slightly increased the colonization of invasive species and it was favourable to alien competitors, which appeared in this stand (Fig. 5).

**Stand level CO<sub>2</sub> exchange:** The magnitude of other chamber flux measurements in tallgrass prairie (e.g. Dugas *et al.* 1999, Suyker *et al.* 2003) with similar physiognomy to loess grassland were, on average, of the same order to those observed in our study (Fig. 6). The differences in the amount and distribution of precipitation during the years under investigation affected the physiological activity of vegetation and influenced the NEE results of the manipulation experiment. In general, significant capacity of carbon sequestration was only apparent in the fertilized grasslands during periods of

high precipitation. In grasslands, much of the variation in NEE is constrained by the amount of precipitation (Flanagan *et al.* 2002). In the wet year, nutrient manipulation increased stand C-fixation considerably, but not statistically significantly compared with the control. However, enhanced nitrogen utilization of additionally fertilized plants accompanied by intensive growing assumably caused a negative feedback on NEE in the fertilized plots in the middle of the growing season. It was probably due to the increased nitrogen consumption by the vegetation. During the spring 2003, an extremely dry period (Ciais *et al.* 2005) induced moisture stress and could be responsible for the significantly lower NEE in the fertilized plots. In the studied dry grassland, seasonal and interannual variation of NEE could be mainly explained by unbalanced nutrition uptake under drought stress, causing significantly lower NEE values. The negative NEE values observed in the fertilized plots in the first year could be linked to the partly burned out vegetation due to the late fertilization and a lack of precipitation. The very low, sometimes positive, NEE averages were probably caused by the fact that the rate of soil respiration was higher than the CO<sub>2</sub> uptake of the grassland due to drought and the accompanying high temperature in the growing season (Ciais *et al.* 2005). In addition, respiration exhibits an exponential temperature dependence at subcellular and individual levels, but at the ecosystem level, respiration can be modified by several variables including community abundance and biomass (Yvon-Durocher *et al.* 2012). Under water-limited conditions, most of the daily carbon exchange activity is linked to the short wet periods (Xu *et al.* 2004, Hastings *et al.* 2005), and significant source activity may also occur during drought (Li *et al.* 2005, Ciais *et al.* 2005). In our research, there was no significant correlation between the cumulative species richness and the average NEE, although higher H<sub>s</sub> values and the periods of dominant dicot cover could be characterized by higher rate of CO<sub>2</sub> exchange.

**Conclusions:** This study presented results of the short-term effect of extensive NPK fertilization on the structure and CO<sub>2</sub> gas exchange of a dry, continental loess grassland community. The exceptionally high interannual variation, including the unprecedented drought in 2003

and the above average rainfall in the succeeding year, masked strongly the effect of the fertilization treatment. This made the effects of the treatments relatively small and led to statistically less markedly supported differences. The comprehensive statistical analysis showed that the interaction between the studied variables (season and treatment) was not significant in the treated and nontreated plots, which presumably meant that the different NPK levels in the fertilized and control plots produced similar responses due to the interannual variation under current meteorological factors. Most of the parameters studied showed considerable interannual variations both in the fertilized and the control stands. It seemed that the ratio of hemicryptophytes, therophytes, disturbance-tolerant plants, alien competitors, monocots, and C<sub>4</sub> plants increased immediately after the fertilization, while species richness and the ratio of legumes decreased in response to the addition of fertilizers in the loess grassland. The latter one were probably due to the increasing dominance of a disturbance-tolerant species, *S. nemorosa*. The gaps created by the application of fertilizers and periods of extreme drought were occupied by perennial grass species, native and alien competitors.

Based on chamber measurements, the NEE flux values of the fertilized stands only exceeded the averages of the control stand in periods of higher rainfall, but no significant differences between the two stands were found in any of the seasonal periods studied. Enhanced production of fertilized plants supposedly caused a negative feedback on NEE at fertilized plots due to the increasing nitrogen consumption towards the peak of the growing seasons in the wet year. Presumably, in the extremely dry year, total ecosystem respiration was suppressed to a lesser extent by drought stress than the carbon uptake of the community. NEE measurements showed a significant interannual variation between the dry and wet year both in the fertilized and nontreated plots. Production and NEE data reinforced our previous suggestion (Czóbel *et al.* 2008) that the studied *Salvio nemorosae-Festucetum rupicolae* loess grassland could be regarded as a carbon sequester on a yearly horizon in case of extensive nutrition treatment. The results might be of potential benefit for grassland conservation and planned grassland intensification practices.

## References

Borhidi, A.: [Social behaviour types of the Hungarian Flora, its naturalness and relative ecological indicator values.] – Janus Pannonius Univ. Publ., Pécs 1993. [In Hungarian]

Bouma, T.J., Bryla, D.R.: On the assessment of root and soil respiration for soils of different textures: interactions with soil moisture contents and soil CO<sub>2</sub> concentration. – *Plant Soil* **227**: 215-221, 2000.

Bölöni, J., Molnár, Zs., Kun, A. (ed.): [Habitat of Hungary. Description and guidebook of the Hungarian vegetation types.] – MTA ÖBK Plubl., Vácrátót 2011. [In Hungarian]

Ciais, Ph., Reichstein, M., Viovy, N. *et al.*: Europe-wide reduction in primary productivity caused by the heat and drought in 2003. – *Nature* **437**: 529-533, 2005.

Czóbel, Sz., Balogh, J., Fóti, Sz. *et al.*: Long-term effects of irrigation and fertilization on stand CO<sub>2</sub> fluxes and soil biochemical processes in a Hungarian loess grassland. – In: Proceedings of the III. Alps-Adria Scientific Workshop (Dubrovnik, Croatia). Pp. 130-134, Dubrovnik 2004.

Czóbel, Sz., Fóti, Sz., Balogh, J. *et al.*: Chamber series and space-scale analysis of CO<sub>2</sub> gas-exchange in grassland

vegetation. A novel approach. – *Photosynthetica* **43**: 267-272, 2005.

Czóbel, Sz., Horváth, L., Szirmai, O. *et al.*: Comparison of  $\text{N}_2\text{O}$  and  $\text{CH}_4$  fluxes from Pannonian natural ecosystems. – *Eur. J. Soil Sci.* **61**: 671-682, 2010.

Czóbel, Sz., Szirmai, O., Nagy, J. *et al.*: Effects of irrigation on the community composition, and carbon uptake in Pannonian loess grassland monoliths. – *Commun. Ecol.* **9**: 91-96, 2008.

Dugas, W.A., Heuer, M.L., Mayeux, H.S.: Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum. – *Agr. Forest Meteorol.* **93**: 121-139, 1999.

Flanagan, L.B., Wever, L.A., Carlson, P.J.: Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. – *Global Change Biol.* **7**: 599-615, 2002.

Foster, B.L., Dickson, T.L.: Grassland diversity and productivity: The interplay of resource availability and propagule pools. – *Ecology* **85**: 1541-1547, 2004.

Frank, D.A.: Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. – *Oecologia* **152**: 131-139, 2007.

Gough, L., Osenberg, C.W., Gross, K.L. *et al.*: Fertilization effects on species density and primary productivity in herbaceous plant communities. – *Oikos* **89**: 428-439, 2000.

Harpole, W.S., Potts, D.L., Suding, K.N.: Ecosystem responses to water and nitrogen amendment in a California grassland. – *Global Change Biol.* **13**: 2341-2348, 2007.

Hastings, S.J., Oechel, W.C., Muhlia-Melo, A.: Diurnal, seasonal and annual variation in the net ecosystem  $\text{CO}_2$  exchange of a desert shrub community (*Sarcocaulus*) in Baja California, Mexico. – *Global Change Biol.* **11**: 927-939, 2005.

Haszpra, L. (ed.): Atmospheric greenhouse Gases: the Hungarian Perspective. – Springer Books, Dordrecht – Heidelberg – London – New York 2011.

Huberty, L.E., Gross, K.L., Miller, C.J.: Effects of nitrogen addition on successional dynamics and species diversity in Michigan old-fields. – *J. Ecol.* **86**: 794-803, 1998.

Jacquemyn, H., Brys, R., Hermy, M.: Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. – *Biol. Conserv.* **111**: 137-147, 2003.

Knapp, A.K., Briggs, J.M., Blair, J.M., Turner, C.L.: Patterns and controls of aboveground net primary production in tallgrass prairie. – In: Knapp A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (ed.): *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. Pp. 193-221. Oxford Univ. Press, New York 1998.

Li, S.-G., Asanuma, J., Eugster, W. *et al.*: Net ecosystem carbon dioxide exchange over grazed steppe in central Mongolia. – *Global Change Biol.* **11**: 1941-1955, 2005.

Lutgen, E.R., Muir-Clairmont, D., Graham, J.J., Rillig, M.C.: Seasonality of arbuscular mycorrhizal hyphae and glomalin in a western Montana grassland. – *Plant Soil* **257**: 71-83, 2003.

Molnár, Zs., Biró, M., Bölöni, J., Horváth, F.: Distribution of the (semi-)natural habitats in Hungary I. Marshes and grasslands. – *Acta Bot. Hung.* **50**: 59-105, 2008.

Mueller-Dombois, D., Ellenberg, H.: *Aims and Methods of Vegetation Ecology*. – John Wiley & Sons, Pp. 45-66. New York – Chichester – Toronto – Brisbane – Toronto 1974.

Nilsen, P., Børja, I., Knutson, H., Brean, R.: Nitrogen and drought effects on ectomycorrhizae of Norway spruce [*Picea abies* L.(Karst.)]. – *Plant Soil* **198**: 179-184, 1998.

Piper, J.K., Billings, D.N., Leite, V.J.: Effects of nitrogen fertilizer on the composition of two prairie plant communities. – *Commun. Ecol.* **6**: 93-100, 2005.

*R Development Core Team*: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. – URL <http://www.R-project.org>, 2009.

Semmarin, M., Oyarzabal, M., Loret, J., Oesterheld, M.: Controls of primary productivity and nutrient cycling in a temperate grassland with year-round production. – *Austral. Ecol.* **32**: 416-428, 2007.

Simon, T.: [Identification Guide to the Hungarian vascular Flora.] – Nemzeti Tankönyvkiadó Publish., Budapest 2000. [In Hungarian]

Soussana, J.F., Allard, V., Pilegaard, K. *et al.*: Full accounting of the greenhouse gas ( $\text{CO}_2$ ,  $\text{N}_2\text{O}$ ,  $\text{CH}_4$ ) budget of nine European grassland sites. – *Agr. Ecosyst. Environ.* **121**: 121-134, 2007.

Suyker, A.E., Verma, S.B., Burba, G.G.: Interannual variability in net  $\text{CO}_2$  exchange of a native tallgrass prairie. – *Global Change Biol.* **9**: 255-265, 2003.

Thiel-Egenter, C., Risch, A.C., Jurgensen, M.F. *et al.*: Response of a subalpine grassland to simulated grazing: aboveground productivity along soil phosphorus gradients. – *Community Ecol.* **8**: 111-117, 2007.

Tilman, D.: Secondary succession and pattern of plant dominance along experimental nitrogen gradients. – *Ecol. Monogr.* **57**: 189-214, 1987.

Turner, C.L., Knapp, A.K.: Responses of a  $\text{C}_4$  grass and three  $\text{C}_3$  forbs to variation in nitrogen and light in a tallgrass prairie. – *Ecology* **77**: 1738-1749, 1996.

Van Der Maarel, E.: Transformation of cover-abundance values in phytosociology and its effects on community similarity. – *Vegetatio* **39**: 97-114, 1979.

Xu, L.K., Baldocchi, D.D., Tang, J.W.: How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. – *Global Biogeochem. Cy.* **18**: GB 4002, 2004.

Yuste, J.C., Janssens, I.A., Carrara, A. *et al.*: Annual  $\text{Q}_{10}$  of soil respiration reflects plant phenological patterns as well as temperature sensitivity. – *Global Change Biol.* **10**: 161-169, 2004.

Yvon-Durocher, G., Caffrey, J.M., Cescatti, A. *et al.*: Reconciling the temperature dependence of respiration across timescales and ecosystem types. – *Nature* **487**: 472-476, 2012.