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Seasonal and daily pattern, temporal and spatial variability of ecosystem CO_2-exchange in a temperate Pannonian loess grassland

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Abstract. In the photosynthetically most active spring, summer and autumn vegetation period the investigated grassland did maintain a relatively strong daytime carbon gain. During winter the grassland displayed a slight daytime carbon loss. These data suggest that the grassland was a weak sink for carbon in the investigated period. CO_2-exchange variability during the day seemed to be independent from that of the daily photosynthetic radiation. Thus other factors like soil respiration, soil moisture content and temperature and their interactions could be responsible for the high daily variability of grassland CO_2-exchange. The considerable temporal (daily and seasonal) variability of the grassland CO_2-exchange can be considered as a characteristic feature of the grassland CO_2-exchange. In the investigated loess grassland vegetation the variability of CO_2-exchange showed clear dependence on measuring area, which is obvious in the CV of NEE. We hypothetised that the spatial scale with the lowest variability is the characteristic area of the grassland ecosystem's CO_2-exchange (CO_2-exchange physiological unit). In general decreased variability indicates a more regulated state.

Keywords: carbon-balance, temperate grassland, chamber technique, net ecosystem CO_2-exchange, carbon gain

Abbreviations: Net Ecosystem Exchange (NEE), Photosynthetic Photon Flux Density (PPFD), air temperature (Ta), CO_2-concentration (Ca), Coefficient of Variation (CV), Net CO_2-uptake (A), leaf area index (LAI)

Introduction

Detailed leaf-, individual- and macroscale CO_2-exchange studies have long been conducted on grasslands (BREYMEYER ET AL. 1996). On the other hand there are relatively few information available on the micro-scale level, more specifically in temperate grasslands including loess grasslands.

Out of the physiological processes, the carbon cycle based on photosynthesis-respiration balances of ecosystems is of primary importance. Grasslands are characterised by the fact that large part of their organic matter (C-content) is contained in the belowground living plant parts and in the soil (RICE AND GARCIA 1994) and this feature is important also in terms of their C-cycle. The temporal pattern of the C-balance of a grassland is also influenced by soil respiration and microbial activity (DÖRR AND MÜNNICH 1987). Investigation of the CO_2-exchange rates of these grasslands is necessary to estimate their significance in the global carbon cycle and global climate change.

Temporal dynamics of the photosynthetical activity and its relation to climate have been intensively studied up to the present date. There are less information available on the relationships between the climate and phenology (leaf structure phenology) and the temporal variability of the CO_2-exchange. Phenology should definitely be considered in a study conducted on a yearly temporal scale. Net CO_2-exchange is primarily affected by senescence in the autumn period and not by the abrupt weather changes (HAM AND KNAPP 1998).

Moreover, patches of a grass stand are not alike. Considerable structural variability can be perceived even in intensively managed grasslands with profound consequences on their primary functioning. This also implies the necessity of carrying out scale-dependent stand level physiological studies when spatial variability is concerned. Closed chamber techniques are suitable tools for studying small-scale spatial variability and dynamics of CO_2 gas-exchange (ANGELL ET AL. 2001).

The temperate Salvio-Festucetum rupicolae loess grassland (steppe) has also been investigated in structural, dynamical and conservation terms for decades resulting in a considerable amount of information in these subject (ZÓLYOMI AND FEKETE 1994, VIRÁGH AND FEKETE 1984). At the same time, studies conducted on the spatial organization of these grasslands have revealed that the spatial scale of the most important processes (species exchanges, coexistence patterns, and diversity) is in the order of a few dm^2 to m^2 (MUCINA AND BARTHA 1999).

The aims of the present work are: i) to explore the daily and seasonal courses of CO_2 gas-exchange at a fixed spatial scale, ii) to describe the temporal (daily and seasonal) and spatial variability (heterogeneity) of the photosynthetical activity and iii) to study the spatial scale dependence of CO_2 gas-exchange in a Pannonian loess grassland (steppe) ecosystem.

Materials and Methods

Study site

The measurements were conducted in the years 2000-2001 on the loess grassland situated at the village Kerepes (Gödöllő-Monor-Irsa Hills, 170 m a.s.l., 25 km south-east from Budapest). The climate is a temperate continental with hot dry summers and cold winters; mean annual precipitation 550-600 mm or less; annual mean temperature of 11 °C; and large annual amplitude of temperature changes (22 °C).

The investigated loess grassland

The vegetation is a xeric temperate loess steppe (*Salvio-Festucetum rupicolae pannonicum* Zólyomi). The community is dominated by *Festuca rupicola, Chrysopogon gryllus, Stipa dasyphylla, Cytisus austriacus,* and *Carex humilis.*

The parent rock is sandy loess with thick humus- and nutrient-rich A layer. The original grassland is made up of more than 90 species. It is a perennial and overwintering, vertically well-structured (60-80 cm height) grassland, with many broad-leaved dicotyledonous species. The loess grassland can be considered as the representative of the European temperate xeric grassland (steppe) vegetation.

Measurements of the net ecosystem CO_2-exchange rates

Net ecosystem CO_2-exchange rates (parallel with transpiration, air temperature, relative humidity, vapour pressure and stomatal conductance) were measured by using a portable closed-loop IRGA (LI-COR 6200, operated in absolute mode) sampling the air in a cylinder-shaped plexi-chamber of 60 cm diameter and 70 cm height, with three replicates in five plots. Mixing of the air in the chamber was achieved by operation of mixing fans. Ambient conditions (Ta and Ca) at the beginning of each measurement have been re-established by lifting the chamber while the fans were running. The duration of a measurement was 10 to 25 seconds, therefore the changes in the Ta and Ca in the chamber were small. PPFD values and canopy surface temperatures were recorded using ceptometers (Decagon) and an infra red thermometer (Raytek MX4). CO_2 gas-exchange values from five plots were used to calculate average net photosynthesis values and daytime C-balances. Coefficient of variation was also calculated for each average. Daily courses of gas-exchange have been measured from sunrise to sunset (1.5-2 hours intervals) seasonally, (04/10/2000, 20/03/2001, 23/05/2001, 03/07/2001) to consider phenological effects, too.

Set-up for measuring spatial scale-dependence of the ecosystem CO_2-exchange

The set-up for estimating spatial dependence of CO_2 gas-exchange on measuring area consisted of six chambers with different diameters. Ground areas of the six gas exchange chambers follow a logarithmic scale with the diameter of the chambers doubling from 7.5 cm to 240 cm. The height of each chamber is 70 cm. The cylinder-jacket of the chambers has been arched from UV-B resistant water clean plexiglass. The air motion within the chambers is supplied by outer fan except for the two largest chambers, where the ventilation systems are within the chamber. The chambers are suited for measurements in closed system. The measurements have been carried out on 13th June 2001, in nine patches with three replications at each chamber size.

Results and Discussion

Daily courses of net CO_2-exchange in the four seasons

Daily courses of net ecosystem CO_2-exchange in the four seasons (including soil and root respiration in addition to photosynthesis), air temperature and PPFD average values from the five measured patches are presented (Fig. 1.). The aim was to describe the seasonal features of NEE, as based on these measurements.

Autumn (04/10/2000)

Air temperature was higher than expected at this date and ranged between 16.2-32.9 °C. Cloudiness caused 20-30 % CV considering PPFD. There was a strong correlation between NEE and PPFD until midday. After midday, stomatal limitation of photosynthesis due to water shortage caused this correlation to become weaker at high Ta values. NEE reached its maximum (5.37 $\mu mol\ CO_2 m^{-2} s^{-1}$) in the early morning hours, this value was far below those measured in spring or summer, which is the consequence of the decreased photosynthetically active LAI due to the autumn senescence of many species.

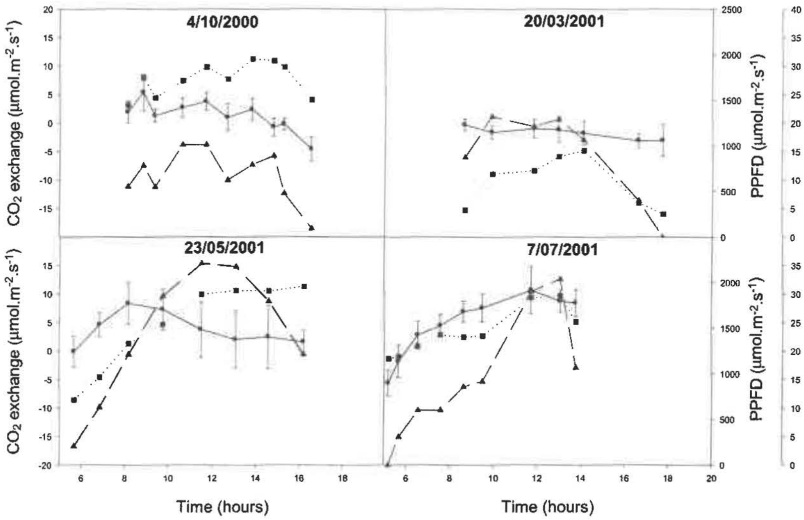

Figure 1.: Daily course of loess grassland CO_2 exchange (dots with error bars, solid line) measured on 60 cm diameter stand plots, of the photosynthetic photon flux density (PPFD, triangles, dashed line) and of air temperature (Tair, squares, dotted line) on four seasonally different days. One symbol represents the average value of five stand plots.

Late Winter – Early spring (20/03/2001)

Soil respiration increased at Ta values above 15°C, balancing the CO_2-uptake. As a result NEE was negative throughout the day caused also by dawn frosts, small LAI values and below optimal Ta values for photosynthesis while PPFD was high.

Spring (23/05/2001)

Growth is most intensive in loess grasslands in this period of the year. NEE followed the rapidly increasing Ta and PPFD values during the morning with the maximum of 9.51 μmol $CO_2m^{-2}s^{-1}$. From midday Ta was above 30°C and NEE declined with low soil water content (12% by volume) and high vapor pressure deficit of the air.

Summer (03/07/2001)

NEE followed the rapidly increasing Ta and PPFD values during the morning with the maximum of 10.68 μmol $CO_2m^{-2}s^{-1}$. Ta range was narrower than that measured in May. Increasing cloud cover from early afternoon caused decreasing PPFD and hence NEE values, with the break of the measurements due to afternoon rains.

The observed large seasonal fluctuation of the daily CO_2-exchange rates also indicates that this pattern is subjected to large variation season by season and year by year due to the fluctuation of the climatic factors. Among others this inter-seasonal variability underlines the necessity of the continuous long-term measurements.

Temporal variability of grassland CO_2-exchange

Daily course of variability of NEE in representative, still rather variable, randomly selected patches of the loess grassland was investigated. PPFD data (average of the three replicates) and CV of NEE (of the three replicates) are presented for each patch (Fig. 2.). Large CV values in the early morning hours in May and July can be explained by the light intensity values around the compensation point (large part of the canopy is self-shaded), resulting in either positive or negative NEE values and therefore high standard deviation. CV values decreased later in the morning with the majority of values between 10-30%. Increase of CV (NEE) in the afternoon suggest water shortage induced, species and leaf specific, variable stomatal closure as the cause of high variation in NEE.

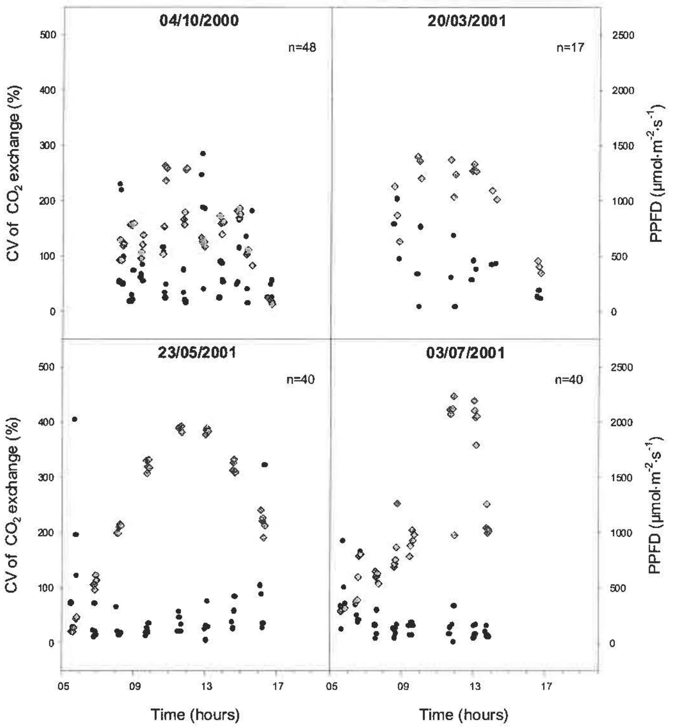

Figure 2.: Daily courses of the coefficient of variation of loess grassland CO_2 exchange measured on 60 cm diameter single stand plots (CV, dots) and of the photosynthetic photon flux density (PPFD, diamonds) on four seasonally different various days. (One symbol represents the CV value of three independent measurements on the same plots, n=number of measurements.)

Spatial variability of the litter decomposition and soil respiration rates are the probable causes of the highly varying NEE at the time of the spring measurement. High CVs of NEE in October are most probably caused by highly varying PPFD during the day as opposed to the situation experienced in May, when CV(NEE) was much smaller due to the steadily changing light conditions. Temporal variabilities of NEE in the patches and the average variability considering all the patches are presented in Tab. 1.

Concerning the daily temporal variability of grassland CO_2-exchange, one of the most remarkable observation was that after sunrise the CO_2-exchange variability during the day seems to be rather independent from the considerable changes of the daily photosynthetic radiation. Thus other factors like soil respiration, soil moisture content and temperature and their interactions can be responsible for the high daily variability of grassland CO_2-exchange. The considerable temporal (daily and seasonal) variability of the grassland CO_2-exchange can be considered as the characteristic feature of the grassland CO_2-exchange. This reflects the necessity of the high number and continuous measurements during the days and as much possible during the seasons.

Table1: Daily temporal and spatial variability of CO_2 exchance rates on five different plots with 60 cm diameter (plot 1- plot 5) of temperate loess grassland (04/10/2001). Variability is expressed as % value of variation coefficient (CV%).

Periods of measurements	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Period's average
08:07 - 08:24	54,0	229,0	219,0	49,0	98,0	98,1
08:44 - 08:58	18,0	16,0	29,0	21,0	73,0	58,5
09:17 - 09:30	991,0	330,0	66,0	84,0	54,0	92,5
10:34 - 10:49	115,0	108,0	34,0	24,0	48,0	61,9
11:43 - 11:55	34,2	74,6	21,3	18,5	14,2	41,0
12:43 - 12:56	245,8	187,9	283,9	39,5	185,4	246,9
13:46 - 13:59	23,9	89,8	85,9	56,7	52,8	80,9
14:43 - 14:56	48,7	52,5	114,6	164,0	167,3	212,5
15:15 - 15:36	135,0	39,7	15,4	513,3	180,8	568,9
16:27 - 16:43	24,4	22,5	47,6	55,6	24,9	46,0

Spatial variability/spatial heterogeneity of grassland CO_2-exchange

The spatial variability of grassland CO_2-exchange rate can be seen as the sign of the spatial heterogeneity of the ecosystem CO_2-exchange. CVs of NEE (Tab. 1.) also demonstrate the spatially different behaviour of the five measured patches.

Coenological studies have proved that a few dm^2 to m^2 sampling unit size is suitable for finding the highest variability in species composition and combinations in this grassland (MUCINA AND BARTHA 1999, BARTHA ET AL.1997). Consequently, variability of LAI is also high at micro-scale (CV over 30% at 60cm) explaining in part the background of the spatial variability of CO_2-exchange.

From this one can conclude that parallel measurements of many unevenly distributed grassland plots with the same diameter are required.

Daily maximum values of grassland CO_2-exchange and daytime carbon gains

Daily maximum values of NEE (Fig. 3.) are in good agreement with both the daytime carbon gain values (528, -864, 2624 and 2171 $mgCm^{-2}$ on the four representative days, respectively) and with the phenological stages of the vegetation. The maximum of NEE and hence the carbon balance are negative in March, the autumn NEE values are considerably lower than the ones in the summer. Consequently, in the photosynthetically most active spring, summer and autumn vegetation period the investigated grassland did presumably maintain a relatively strong daytime carbon gain, while during winter the grassland displayed a slight daytime carbon loss. The above data indicate that in the year of 2000-2001 the investigated overwintering grassland vegetation was very probably acting as a carbon sink.

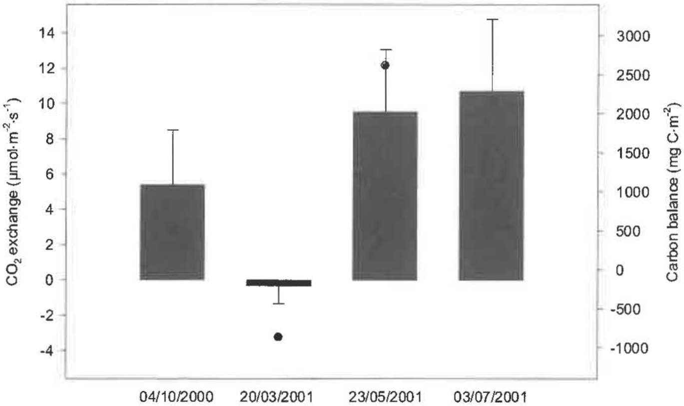

Figure 3.: Daily maximum values of CO_2 exchange rates (bars) and the carbon balance values of the investigated days (dots) in the temperate loess grassland.

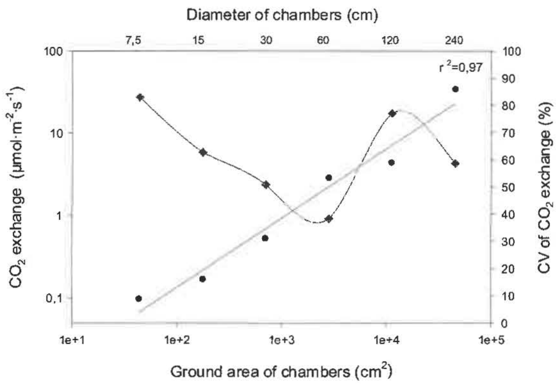

Figure 4.: Spatial scale dependence of CO_2 exchange (dots) and its coefficient of variation (CV, diamonds) in temperate loess grassland. (One symbol refers to nine plots measured in three separate replicates on 13/06/2001, the CO_2 exchange and the ground area values are plotted on a logarithmic scale.)

Spatial scale-dependence of grassland CO_2-exchange

Spatial scale-dependence of NEE was investigated with different chamber sizes (different diameters, 70cm height). Logarithmic values are shown in Fig. 4. The regression CO_2-uptake values vs. chamber size shows good fit ($p<<0.01$). However CV of NEE shows scale-dependence with minimum of variability at 60 cm patch diameter, suggesting this scale to be characteristic unit of this grassland, where the suparindividual regulation is the most pronounced.

In the investigated loess grassland vegetation the variability of CO_2-exchange showed clear spatial scale-dependence. The most probable factors which are candidates for causes of variability pattern along the investigated space series are: the ratio of covered and uncovered soil surfaces, the spatial heterogeneity of soil moisture, soil temperature and litter deposition, the changes of species composition (e.g. dicots/monocots ratio, plant density), the height and the physiognomical and micrometeorological structure of the canopy in the relation to the changes of the botanical composition. Presumably the spatial scale with the lowest variability can be considered as the characteristic scale of the CO_2-exchange (CO_2-exchange physiological unit) of the grassland ecosystem. But this aspect and relationship between coenological (botanical composition) and physiological scale-dependence should be a matter of future detailed analysis. In general decreased variability indicates a more regulated state. Thus it is probably that the spatial scale with the lowest variability represents the supraindividually most regulated physiological – CO_2–exchange- units of the grassland.

Acknowledgements

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