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Fine-scale spatial variability and pattern of grasslands' CO_2 gas exchange

The main points of the thesis

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THE ANTECEDENTS AND AIMS OF THE WORK

Coenological research of small, fragmented, sensitive and therefore mainly protected, natural or semi-natural grasslands, as well as description of their vertical and horizontal physiognomical structure has a long tradition in Hungary. The structure of vegetation and its change may be investigated at different time and space scales. The definition of a study scale determines the adequate methods and the questions to be answered for each community. Study scale for grasslands is traditionally the small- (micro-) scale, which expands from few cm-s to few m-s. Arbitrary chosen sample plot sizes and spatial sample series were applied in the last few decades.

Photosynthesis and respiration and therefore the role of grasslands in the global carbon cycle are of overriding importance from physiological processes. As non-forested vegetations cover 40 % of the terrestrial surface, this role is very important. CO_2 exchange of all kind of vegetation and its components has very large temporal and spatial variability, which is one of the main manifestations of the adaptation to changing environmental conditions.

Presumably, physiological properties of non-arborescent vegetations, including highly variable grasslands, change also along scales according to the changes of the coenological context. However, traditional ecophysiological studies hardly dealt with stand level functioning, partly because of methodological problems. Physiological performance of several species of natural grasslands were already investigated, although physiological performance of vegetation patches is not the sum of individual plants' functioning, and it is neither the average of horizontally uniform surfaces' functioning, but an issue of community level synphysiological processes.

Nowadays several international research project (Carboeurope IP, Nitroeurope IP, Carboocean IP etc.) is focusing on the effects of different ecosystems on greenhouse gas balances. However these studies are based on larger scale (several hectares) measurements and do not deal with community level processes.

Information about fine-scale functional spatial patterns (including CO_2 gas exchange) is important because of their hierarchical connections: momentary spatial pattern may refer to the photosynthetic performance of the individual species forming the community, to the sum of landscape-level sink-source activity, or to the structure of the stand. However, we do not know the dimension of the so-called functional characteristic areas..

Characteristic patch size of physiological processes and their constraining factors may be of different order of magnitude, detailed analyses are needed to reveal them.

The functioning of stands is also influenced by the environmental factors, disturbances and management practices of the studied spatial scale. The global climate change may modify the environmental factors of the given spatial scale, and therefore the functional pattern may also be modified. It seems that the biosphere's global changes touch primarily the processes at the grasslands' organization fine-scale, and ripple across to larger scales afterwards. Investigations on degraded stands have revealed increase of the scale of heterogeneity, and the "opening up" of the functioning and structure of the grasslands, although studies on the CO_2 gas exchange have not been conducted.before.

These questions are interrelated and reciprocal: change of the vegetation composition affects the pattern of the environmental factors, and their manipulation influence the vegetation.

The main aims of our work were therefore as follows:

- description and comparison of the average net ecosystem exchange and its seasonal and daily pattern from three Hungarian grasslands (sand, loess and oldfield communities),
- investigation of the correlation between some coenological characteristics (surface cover, number of species, diversity, ratio of monocots to dicots) and NEE,
- determination of the size of characteristic areas of synphenetical and synphysiological homogeneity and heterogeneity by spatial sample series, and look for correlations between them,
- investigatigation of the patch size of CO_2 gas exchange (mainly soil respiration) of several non-forested vegetations at phenological optimum,
- analysis of the effects of environmental factors, first of all the soil water content, on the spatial patterns under optimal and stress conditions,
- investigation of the presumable effects of the management practices (extensive, intensive management or abandonment) on the spatial patterns.

MATERIALS AND METHODS

Study sites

We conducted explorative studies at the following sites: Bíly Kríž (Czech Republic): wet mountain meadow, Bugac: sand pasture, Finse (Norway): alpine tundra, Gödöllő, Botanical Garden: bare soil, Isaszeg: loess grassland, Szurdokpüspöki: xeric mountain pasture and meadow, Vácrátót: sand grassland, Valkó: oldfield.

All of these sites are in different dynamical states and they are or were recently managed altough with varying intensity and frequency.. Long managing tradition has an important role in the maintenance and stabilization of grasslands, and abandonment or change in management practice is a stress factor, which is being followed usually by degradation. Depending on the research aims synphysiological (for the study of temporal variability, of the dependence of spatial variability on the measuring area, and of the spatial pattern) and microcoenological, coenological sampling was applied.

Measuring equipment

CO_2 gas exchange was measured by gas exchange chambers of different size, depending on the aims of the study: (1) to measure the net ecosystem exchange a series of cylinder-shaped plexi-chambers was used where the diameter ranged (it had been doubled) from 7.5 to 480 cm, while the height was constantly 70 cm, (2) the soil respiration was measured with a plexi hemisphere chamber with a 20 cm diameter, with a cylinder-shaped chamber (15 cm in diameter and 18 cm in height) or with the soil respiration chamber of the LICOR 6400 gas analyser.

CO_2 gas exchange was measured with portable IRGAs (LICOR 6200, LICOR 6400 (Li-Cor, Lincoln, NE, USA) and CIRAS-2 (PP Systems, Hitchin, UK).)

Photosynthetically active radiation (PAR) was measured by a ceptometer (Decagon Devices, Pullmann, WA, USA). Transmittance of PAR was occasionally used for analysis of the closing of the vegetation and for calculating LAI.

Surface temperature of the stand and of the soil was measured by an infrared thermometer (Raytek MX4, Raytek, Santa Cruz, CA, USA), while soil temperature was measured by mercury thermometer.

Time domain reflectometry (TDR) was used for soil water content measurements (ML-2, Delta-T Devices Co, Cambridge, UK).

Above-ground biomass was cut, owen-dried and weighed.

NDVI pictures were taken by an ADC-2 (Dycam, Woodland Hills, CA) digital camera, and processed by Vegan software.

Statistical methods

Basic statistics for comparison of the data were as follows: calculation of average, median, standard deviation, CV, Kolmogorov-Smirov test, f- and t-tests, ANOVA, Pearson test, Mann-Whitney test, Kruskal-Wallis test, Spearman rankcorrelation test.

Florula diversity, number of realized species combinations, associatum and interassociatum were used from the information statistical functions.

Semivariance and cross-semivariance were applied from the tools of geostatistics. Exponential, Gaussian and spherical variogram models were fitted to the data. To interpret the spatial patterns random shift of parallel data series was applied in the case of cross-semivariance analysis.

In some cases, allocation of measured data was used to improve the graphic quality of the results.

RESULTS

Temporal variability of CO_2 gas exchange of several Hungarian grasslands

Our results demonstrated the temporal variability of CO_2 exchange of several Hungarian grasslands. Effect of soil water content on gas exchange, mainly its limitation under water stress conditions became obvious. Different stands of loess steppe could perform similarly despite of their compositional differences, while that was not true for the sandy grassland, which was originally more patchy at the same scale. Peak biomass was usually accompanied by peak physiological activity at early summer, and the longest constant periods of environmental conditions could have been at this time of the year too.

Variability of functioning is characteristic for every period. We supposed, that the most characteristic pattern of a stand might be detected at the phenological optimum, that is, under optimal circumstances. Due to the transformation of patterns caused by different effects different types of patches may be shown similar, that is these effects may mask the specialities.

Correlation between structure and gas exchange of some Hungarian xeric grasslands

Basic architectural, compositional and LAI differences of the investigated entities were reflected in net ecosystem exchange, statistically significant correlation was found between it and surface cover. However, increasing species number along with increasing cover did not show acceptable correlation with gas exchange.

Micro-coenological differences related to the scale of dominant species' coexistence resulted in different sized characteristic areas in grasslands. Spatial association of species determines their coexistence and dynamical processes, and we demonstrated overriding importance of dominant species in gas exchange as well. After all, we concluded that characteristic areas of CO_2 gas exchange are also different in each vegetation types, and synphenetical and synphysiological scales may correlate.

Spatial variability of CO_2 gas exchange of several Hungarian grasslands

Variability investigations at Hungarian natural, semi-natural grasslands showed contrasting, more or less different characteristic areas in the case of sandy and loess grasslands and their size was similar to the size of the synphenetic ones. Standard deviation of the mountain meadow's CO_2 exchange did not show spatial scale dependence. In the case of the oldfield vegetation we found high uncertainties in the results because of the sub-optimal environmental conditions.

Spatial pattern of CO_2 gas exchange of non-forested vegetation types

Our results returned high variability of patterns of the investigated communities. Functional characteristics of homogenous grassland patches were diverse at fine scale, but did not necessarily show spatial autocorrelation, and different variables of the same vegetation type did not show similar patch sizes. Our studies proved that soil water content had overriding importance in determining functional patterns. Patterns from periods with good water supply were characterised by smaller patch sizes than those of water stressed periods. Several times, high water content homogenized the pattern to such a degree that we found pure nugget effect. However, good and poor water supply should be determined only with knowledge of the soil conditions, composition, structure and phenological state of the vegetation. Variety of patterns, mainly those of the same site but from different environmental conditions proved that patterns may change, may have different characteristics depending on seasons, and may show signs of water or heat stress as well as degradation and other dynamical processes.

NEW SCIENTIFIC RESULTS

According to our work on the Hungarian loess steppe we concluded that photosynthetic performance of different stands of the grassland could be similar under well-watered conditions despite of their compositional differences, while functioning becomes more patchy under water stress or senescence. The micro scale spatial heterogeneity, mainly the mosaic appearance of covered and bare soil surfaces in the case of the sandy grassland is more pronounced at any time, than on the loess grassland, so the relative spatial variability of the CO_2 exchange is also greater.

We demonstrated the spatial scale dependence of the variability of CO_2 gas exchange in the case of the majority of investigated Hungarian grasslands.

We quantified the sizes of synphysiological characteristic areas, that is the maximum and minimum scales of the variability of CO_2 exchange of several Hungarian xeric grasslands

We found correlation between synphenetical and synphysiological characteristic patch sizes:

- in the case of the sandy grassland maximum of variabilities,
- in the case of the loess grassland the maximum of associatum of dominant species, the calm down of the synphysiological variability, and also the patch size of soil respiration had very similar spatial scales.

We described the patch pattern of the gas exchange, mainly the soil respiration, and the soil water content of several Hungarian grasslands and other investigated communities. We pointed out the close determination of the gas exchange pattern by the latter: patch size of soil respiration was smaller under well-watered conditions, than under water stress, and the effect of management's abandonment, that is shrub-effect on the loess grassland was also more pronounced in the latter case.

We applied geostatistical analysis for the first time in the case of net ecosystem exchange and soil respiration of physiognomically homogenous stands. Our work was different from many others with similar aims and approach that we described the inner variability of stands' gas exchange and not the visually striking heterogeneity of them.

We developed sampling methodology for the investigation of spatial pattern of synphysiological processes.

CONCLUSIONS AND PROPOSITIONS

Our results proved that the applied coenological-microcoenological based methods were adequate for the realization of the research purposes. We were able to know the spatial variability of CO_2 exchange of several Hungarian grasslands, to describe the spatial characteristics of the variability and, in some cases, we found synphysiological characteristic units by the blocked quadrate method.

We also concluded that measurements along transects (that is with relatively small disturbance) and data processing by geostatistics (semivariance and cross-semivariance analysis) were adequate for the analysis of the spatial pattern of CO_2 exchange. The sample size applied was enough for the mentioned statistical methods, and the stationarity was not injured along measurements (quick data collection in time, isotropic sampling in space).

After our results, patterns have different parameters under phenological optimum circumstances and under stress and we suppose that they differ in grasslands with similar texture and structure but different dynamical state. These characteristics should allow us to follow the state of some potentially sensitive, disturbed stands.

With our pattern and variability parameters we plan a spatio-temporal gas exchange model in the future for predict the long-term activity, photosynthetic performance of just our sensitive, critical state non-forested vegetations, and also for estimate the effects of the planned intervention for conserve or sustain the grassland.

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