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Variability of synphysiological processes in three non-arborescent temperate grasslands

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ABSTRACT Three plant communities, a loess, a sand and an old-field grassland showed considerable differences in synphysiological variability during an investigation at the same spatial scale in 2000. The two former are widely distributed in the Carpathian Basin and with the latter the Hungarian non-arborescent, herbaceous vegetation is well represented. To arrive at conclusions on the causes of variability of synphysiological characteristics can be difficult when allowing for both physiological and abiotic variability. On the other hand it was also obvious that stands' or vegetation types' physiological processes reflect changes of abiotic conditions in coefficients of variation which could not be demonstrated in parallel coenological investigations. Coenological responses are much slower than the synphysiological ones. When considering synphysiological data under conditions of good water supply and under severe drought stress a decrease of variability was found in all types in the latter case. This trait seems to be independent of any coenological characteristic. **Acta Biol Szeged 46(3-4):239-241 (2002)**

KEY WORDS

synphysiology
coefficient of variation
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The variability of temporally fluctuating populations and communities induced numerous theoretical and empirical studies. Theories like 1) increased variability can be an indicator of ecosystem stress (Odum et al. 1979) or 2) increased biodiversity leads to decreased variability (Schwartz et al. 2000) searched for support. Results are sometimes contradictory due to methodological and statistical causes. Further, the variability itself "may cloud our perceptions on how nature operates" (Cottingham et al. 2001). The related concept of "complexity-stability" has been an important research area for decades. Two ecologically relevant meanings of stability were found applicable to old-fields, the younger field being more resilient, the older one being more resistent to stress conditions (Leps et al. 1982). Furthermore, studies indicate that depauperated communities (*i.e.* the state after deletion of functional groups or from manipulations of species number) loose the ability to compensate for stochastic fluctuations in the microclimate (Chapin et al. 1998). The variability of bioclimatological characteristics is also dependent on communities' organization level. The amplitude of environmental fluctuations decrease during succession (Prach 1982).

Rewieving recent observations on traits of community level variability, the main purposes of this study were to:

1) attempt to reveal the trends of synphysiological variability at the same spatial scale along the degree of organization in three vegetation types representing different levels of organization,

2) reveal the averaging effect, the dampening of the variability while averaging different stands with fluctuating synphysiological characteristics through time.

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Materials and Methods

Description of study area

Three grassland types with different physiognomy, texture, spatial pattern, vegetation dynamical traits and physiological activity were selected to illustrate synphysiological variability. The loess steppe community on a loess soil type, *Salvio-Festucetum rupicolae* near Isaszeg, dominated by *Festuca rupicola, Chrysopogon gryllus, Stipa dasyphylla, Cytisus austriacus*, and *Carex humilis* was subdivided into three obviously different stand types (*Carex*, *Cytisus* and *Stipa* dominated types). The sandy steppe community, *Festucetum vaginatae danubiale* near Vácrátót grows on a shallow, immature soil. Vegetation is dominated by *Festuca vaginata, Botriochloa ischaemum* and *Stipa borysthenica,* smaller amounts of *F. domini, Fumana procumbens* and *Poa bulbosa* are present. Bryophytes and lichens are frequent mainly in the open type containing "black spots". Two obviously different other types, the closed one and the *Stipa* dominated have also been investigated. The ruderal vegetation type, *Convolvulo-Agropyretum repentis* was choosed as the third object, near Gödöllő on a sandy loess soil rich in nutrients. This old-field vegetation is very rich in species and can be subdivided into three patches dominated by *Artemisia vulgais, Daucus carota* and *Agropyron repens.* According to the microcoenological data, this old-field is in a rapidly changing state showing high (loess-like), low (sand-like) or medium level organization characteristics in different types (*i.e.* high number of species combinations, florula diversity and associatum in *Daucus* dominated patches, medium in *Agrpoyron* dominated ones and low in *Artemisia* dominated stands). These types were separated by analysing the coenological data with the SYN-TAX package (Podani 1993).

Table 1. CVs of sesonal aspects on grassland types.

		CV of A	CV of E	CV of WUE
Summer aspect	Sand	171.63%	71.78%	223.11%
	Loess	108.62%	94.37%	60.10%
	Old-field	60.19%	26.74%	51.74%
Autumn aspect	Sand	1242.00%	52.15%	1441.11%
	Loess	49.15%	29.12%	50.63%

A-CO_2-assimilation; E–transpiration

Synphysiological methods

We measured CO_2-exchange, transpiration, air temperature, relative humidity and vapour pressure, and calculated stomatal conductance by using a portable closed-loop IRGA gas exchange system (LI-COR 6200) sampling the air in a plexi-chamber of 60 cm diameter (ground area of the chamber is 2826 cm^2) and 70 cm height with three replicate measurements in each plot. water-use efficiency (WUE) is given as the ratio of net photosynthesis to transpiration, coefficient of variation of any investigated physiological respons as the ratio of standard deviation values to average values. photosynthetically active photon flux density (PPFD) values were recorded using sunfleck ceptometers (Decagon), and canopy-surface temperature was measured with an infrared thermometer (RayngerII.).

Our study was carried out from June till September 2000. During this period the loess type was investigated both under stressed (late June) and non-stressed conditions (early June and September) and obviously both in a fully developed (summer aspect) and in a senescent (autumn aspect) phase. Sand grassland was measured under conditions of severe (July, summer aspect) and not so harsh stress (September, autumn aspect). The data on the old-field vegetation were collected in August (summer aspect) under mild water stress conditions.

Field sampling and coenological survey

990 stand physiological measurements were carried out in 210 plots in the loess steppe, 880 measurements in 192 plots in the sandy grassland and 369 measurements in 120 plots in the old-field vegetation, respectively. Percentage cover by the species was recorded in each plot.

Table 3. CVs at different water supply on grassland types and sub-types (* means dataset from 2001).

	CV of A	CV of E	CV of WUE
Better water supply			
Sand	1242.00%	52.15%	1441.11%
Loess	62.9%	51.3%	59.8%
Open type, sand	90.4%	26.0%	92.1%
Closed type, sand	92.4%	27.9%	98.7%
Carex type, loess	95.5%	76.3%	39.2%
Cytisus type, loess	47.1%	40.3%	56.5%
Agropyron type, ruderal*	40.8%	59.0%	189.2%
Stress conditions			
Sand	171.63%	71.78%	223.11%
Loess	50.3%	23.0%	54.5%
Open type, sand	56.6%	35.5%	96.0%
Closed type, sand	75.2%	34.7%	67.2%
Carex type, loess	60.5%	24.0%	45.7%
Cytisus type, loess	40.0%	21.3%	51.3%
Agropyron type, ruderal	36.9%	13.2%	34.2%

A-CO_2-assimilation; E–transpiration

Results and Discussion

Considering the variability of the three investigated grassland types we first examined the sesonal aspects (*i.e.* temporal variability) without decreasing the dataset by restricting the abiotic variability. Summer period measurements showed the highest coefficient of variation (CV) values of photosynthesis and WUE for the sand grassland, medium for the loess steppe and lowest for the old-field. As with transpiration, the order of the two former was found inverse. The autumn period dataset showed a surprisingly high variability in the photosynthesis and WUE values of the sand grassland type while the CV values of the loess steppe were lower. In general the variability of loess stands' physiological processes decreased in autumn probably caused by senescence while increased on sand stands (Table 1).

Table 2. CVs of sesonal aspects on grassland sub-types.

		CV of A	CV of E	CV of WUE			CV of A	CV of E	CV of WUE
Loess, summer aspect	Carex type	184.12%	152.39%	44.84%	Loess, autumn aspect	Carex type	56.39%	36.31%	62.46%
	Cytisus type	127.46%	97.50%	64.29%		Cytisus type	35.23%	18.90%	35.41%
	Stipa type	45.90%	19.58%	38.66%		Stipa type	47.90%	23.22%	55.24%
Sand, summer aspect	Open type	56.63%	35.53%	95.96%	Sand, autumn aspect	Open type	90.45%	26.00%	92.06%
	Closed type	75.22%	34.69%	67.20%		Closed type	92.44%	27.90%	98.66%
	Stipa type	60.41%	25.15%	72.92%		Stipa type	157.42%	57.24%	276.82%
Old-field, summer aspect	Agropyron type	36.89%	13.19%	34.24%					
	Artemisia type	51.89%	27.85%	42.25%					
	Daucus type	51.31%	33.19%	65.56%					

A-CO_2-assimilation; E–transpiration

Table 4. CVs of narrow PPFD-ranges on grassland types.

		CV of A	CV of E	CV of WUE
PPFD > 1400	Sand	101.69%	72.61%	100.83%
	Loess	53.85%	37.74%	39.97%
	Old-field	65.22%	28.67%	52.02%
PPFD > 2000	Sand	107.79%	58.22%	106.93%
	Loess	34.66%	24.67%	29.64%
	Old-field	35.07%	24.07%	14.25%

A-CO_2-assimilation; E–transpiration

The three types of each community were also examined. These CV values show that searching a sesonally characteristic value of variability and averaging the physiological responses may mask the vegetation's ability to give a prompt answer to the changing abiotic conditions. Clear conclusions can not be drawn on stands' variability when considering measurements in periods of severe drought stress and under favorable water conditions together (for example *Carex* or *Cytisus* dominated loess steppes). So CV values of photosynthesis on different types of loess steppe were found to be the highest, medium on sand grassland types and lowest on different old-field types. The trend was found the same for CV values of transpiration while those of WUE on loess steppe and old-field were similar and smaller than on sand. The trends observed sesonally on the two grassland types were the same for the three sub-types: the CV decreased on loess types and increased on sand types (with two exceptions in the case of transpiration values in open and closed types) from summer to autumn (Table 2).

These results highlight the importance of studying these trends after removing the variance due to the abiotic environmental factors. Comparing measurements performed under conditions of good water supply and under severe drought stress the responses were similar by the three vegetation types: a decrease of variability in the main as well as in the sub-types. This trait seems to be independent of any coenological characteristic Nearly the only exception was again the variability of transpiration by the sand grassland. This feature can be seen as a consequence of differential stomatal closure of sandy plant species (resulting a more mosaic-like activity) in high temperature stress on an open site (Table 3).

After all we thinned our summer dataset to the saturated PPFD range, examined only measurements performed at PPFD values higher than 1400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and higher than 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Decrease of CV values was found (Table 4) as compared to the whole dataset, except for the old-field vegetation. (It's important to note that the number of replicates was small in some cases in this operation.) This led to similarity in CVs of the physiological responses by the loess and the old-field, different prior to data reduction. Averaging the sub-types masks differences in micro-coenological organization levels.

Values of the coenological variability show considerable differences between the loess and sand grasslands. The CV values of plant cover (the main type-defining feature), species diversity (high ratio of summer efemerals) and ratio of monocots to dicots were much higher in the sand grassland, while CV of the cover of dominant species was smaller on sand steppe, than on loess steppe.

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