DIFFERENCES IN STRUCTURAL CHANGES OF ORTHOPTERAN (Insecta: Orthoptera) ASSEMBLAGES DURING A VEGETATION PERIOD

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Abstract

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1. The seasonal changes in the structure of orthopteran assemblages in 4 grassland types influenced by different soil humidity were examined.
2. 648 orthopteran samples were collected by sweep netting on 54 sampling sites. Parallel to the insect sampling the microclimate (temperature and vapour content) was measured on 216 occasions.
3. Analyses revealed connections between the community structure parameters of orthopteran assemblages and the microclimatic temperature and vapour content of grasslands.
4. The orthopteran assemblages showed significant differences in their annual structure.
5. The microclimate (especially the vapour content) in the grassland patches showed significant seasonal changes in calcareous fens, drying fens, hayfields, semidry grasslands, which seems to be a determining factor in the adjustment of the spatial pattern and seasonal changes of orthopteran assemblages.

Key words: Orthopteran assemblages, grassland types, microclimate, community structure, seasonal changes

Introduction

Abiotic characteristics, species composition and structural differences between individual grassland types develop considerable differences in their microclimate and its annual dynamics (Précsényi, 1956; Kovács, 1958; Horvát, Papp, 1965; Cox, Moore, 1980; Bauer,

Kenyeres, 2006). Whole communities of grasslands are affected (to various degrees for each element) by these differences in microclimate and its seasonal changes. The community structure of the inhabiting invertebrates of the grasslands is changing along with the changing microclimate. It is important to know for managing grasslands how strong the relationship between the microclimate of the grasslands and the structure of the inhabiting invertebrates is. The taxa with a large density and species number in the grasslands could be the most suitable for revealing the above-mentioned connections. Furthermore, it is also an important requirement for the indicating taxa that their connection to the habitats is not based on specialized nutrition, reproduction or predation. Orthopteran assemblages seem to be suitable for the purposes of this examination. The climate, landscape and habitat structure dependence on species and community level of orthopteran species has been known for a long time, both on regional scale and local scale. On regional scale the landscape structure (Johnson, 1989; Kindwall, Ahlén, 1991; Hjerman, Ims, 1996; Kisbenedek, Báldi, 2000) or the dominant climate and weather (Claridge, Singhrao, 1978; Fielding, Brusven, 1990; Capinera, Thompson, 1987; Capinera, Horton, 1989; Köhler et al., 1999; Karpakakunjaram et al., 2002) might be important regulating factors. While on local scale, the habitat structure (Quinn et al., 1991; Craig et al., 1999; Joern, 1979), which usually means the vegetation structure (Wingerden et al., 1992; Kemp et al., 1990; Fielding, Brusven, 1995), has effects not only on the occurrence of a species but the structure of assemblages, too.

Beside the significant influence of vegetation structure, the determining role of microclimate (Franz, 1933; Isely, 1938; Nagy, 1944; Marchand, 1953; Dreux, 1962; Harz, 1957; Joern, 1982; Parragh, 1987; Samways, 1990; Kemp, 1992; Wingerden et al., 1992; Stoutjesdijk, Barkman, 1992; Rácz et al., 1994; Coxwell, Bock, 1995; Krausz et al., 1995; Varga, 1997; Ingrisch, Köhler, 1998; Báldi, Kisbenedek, 1999; Guido, Chemini, 2000; Krausz et al., 2000; Forsman, 2001; Rácz, 1998a, 2001, 2002; Gardiner et al., 2002; Nagy, Sólymos, 2002; Squitier, Capinera, 2002) also frequently emerges concerning orthopteran assemblages as 'imperfect repetitions' (McArthur, 1955). The indicator variables of this connection have not yet been adequately clarified (Rácz, 2001).

The phenological differences between individual species are based on various climatic needs (mainly thermotolerance) characterizing each stage (embryonic development, dormancy) of the life-cycle (Ingrisch, 1985, 1986a, b, c). In the habitat-choice, for example the post diapause egg development (PDD) – xerophytic species are characterized by long, hygrophytic and mesophytic species by short PDD (Wingerden et al., 1992) – of species laying their eggs in the soil is controlled by the grassland microclimate (mainly the temperature), which is a determining factor concerning the PDD (Hewitt, 1985; Johnson et al., 1986; Kemp, Sanchez, 1987). Studying the PDD factor of the species in the Carpathian basin is timely. Namely in the Carpathian basin the ecological circumstances considerably differ from the study area of the above-mentioned results. Apart from the vegetation cover, the physical characteristics of the soil are significant in this respect (Johnson, 1989). According to Choudhuri (1958), under oviposition – in the case of identical soil type –, *Chorthippus parallelus* (Zetterstedt, 1821) prefers wet while *Chorthippus brunneus* (Thunberg, 1815) dry surfaces.

Owing to the microclimate-sensitivity and the phenological differences between the grasshopper species, the effect of microclimate on the structure of orthopteran assemblages is not only a spatial but also a temporal factor at the same place. In terms of the annual structural changes of orthopteran assemblages, Nagy (1944) differentiates between the autumn and summer orthopteran assemblages (aspects) of saline associations and specifies microclimatic changes as one of the reasons for their structural change. Based on the quantitative analysis of open sandy grasslands, Balogh, Loksa (1948) separate three aspects with a characteristic species composition in this vegetation type (not in connection with the microclimate).

According to our hypothesis, the aspect change (density, species number, species composition, changes of the dominance-diversity) of orthopteran communities can also be detected in grassland types with striking marked annual microclimate change (Bauer, Kenyeres, 2006). The seasonal change of the Tettigonioidea/Acridoidea rate is also a typical feature of the communities. In order to prove these phenomena with quantitative examinations, parallel to the survey of orthopterans of various grassland associations (calcareous fens, drying fens, hayfields, semidry grasslands), microclimate measurements (temperature and vapour content) were carried out on 54 sampling sites. The botanical conclusions and a little part of the orthopterological results of our study were published (Bauer, Kenyeres, 2006, 2007). In this paper the detailed results and discussions are given about the differences in structural changes of orthopteran (Insecta: Orthoptera) assemblages during a vegetation period in calcareous fens, drying fens, hayfields, semidry grasslands.

Materials and methods

The orthopteran assemblages were sampled by sweep netting in 54 sampling sites, 4 times per year (1999–2003, Table 1). The samplings were carried out three 10×10 m quadrats per sampling site, where the content of the net after 300 sweeps was considered one sample. Altogether 648 ortopteran samples were collected. In these quadrats microclimate measuring with TESTO 615 instrument was carried out 216 times. The temperature and the humidity (that is relative humidity: the rate of the real vapour press and the vapour press of the air saturated with steam on that temperature, in percentage) were measured on the ground surface and at heights of 10, 20, 30 and 120 cm in the grassland. At each sampling point (in heterogeneous stands) data were recorded in 3–5 patches on certain characteristic days from June to September (3–4 repetitions per sampling site; altogether 4320 measurements of air temperature and humidity). Since the effect of wind speed and evaporation related to it are strongly felt during measurements (Horváth, Papp, 1965) and make a distortion in the orthopteran samples, the samplings were carried out in clear and calm periods.

The structure of orthopteran assemblages was compared with ordination analysis (Standardized Principal Component Analysis, all orthopteran samples were taken into consideration per grassland type). The relative frequency values of individual species and density and species number of orthopteran species per sample were determined. The seasonal changes in the density and relative frequency values of dominant and subdominant species and established the average values for each level were figured (per sample). The correlation analysis (Pearson Product-Moment Correlation) was carried out (per grassland type) between the microclimate data (temperature and vapour content) of the levels and the above parameters of the orthopteran assemblages.

The statistical analyses were performed with Statistica 6.0 (StatSoft, 1995) and SYN-TAX 2000 (Podani, 2001) programme packages.

T a b l e 1. Sampling sites.

N	Code	Settlement	Locality	Height above sea-level	Plant association
1.	BF1	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Junco obtusiflori-Schoenetum nigricantis*
2.	BF2	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Junco obtusiflori-Schoenetum nigricantis*
3.	BF3	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Junco obtusiflori-Schoenetum nigricantis*
4.	BF4	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Junco obtusiflori-Schoenetum nigricantis*
5.	BF5	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Junco obtusiflori-Schoenetum nigricantis*
6.	BF6	Balatonszőlős	Sötét-rét meadow	~174 m	*Junco obtusiflori-Schoenetum nigricantis*
7.	BF7	Balatonszőlős	Sötét-rét meadow	~174 m	*Junco obtusiflori-Schoenetum nigricantis*
8.	BF8	Balatonszőlős	Sötét-rét meadow	~174 m	*Junco obtusiflori-Schoenetum nigricantis*
9.	BF9	Balatonszőlős	Sötét-rét meadow	~174 m	*Junco obtusiflori-Schoenetum nigricantis*
10.	BF10	Balatonszőlős	Sötét-rét meadow	~174 m	*Junco obtusiflori-Schoenetum nigricantis*
11.	BF11	Lesencetomaj	Lesencei-láprét marshy meadow	~120 m	*Junco obtusiflori-Schoenetum nigricantis*
12.	BF12	Lesencetomaj	Lesencei-láprét marshy meadow	~120 m	*Junco obtusiflori-Schoenetum nigricantis*
13.	BF13	Lesencetomaj	Lesencei-láprét marshy meadow	~120 m	*Junco obtusiflori-Schoenetum nigricantis*
14.	BF14	Lesencetomaj	Lesencei-láprét marshy meadow	~120 m	*Junco obtusiflori-Schoenetum nigricantis*
15.	BF15	Lesencetomaj	Lesencei-láprét marshy meadow	~120 m	*Junco obtusiflori-Schoenetum nigricantis*
16.	BF16	Szentbékkálla	Sásdi-rét meadow	~135 m	*Junco obtusiflori-Schoenetum nigricantis*
17.	BF17	Szentbékkálla	Sásdi-rét meadow	~135 m	*Junco obtusiflori-Schoenetum nigricantis*
18.	BF18	Szentbékkálla	Sásdi-rét meadow	~135 m	*Junco obtusiflori-Schoenetum nigricantis*
19.	BF19	Szentbékkálla	Sásdi-rét meadow	~135 m	*Junco obtusiflori-Schoenetum nigricantis*
20.	BF20	Szentbékkálla	Sásdi-rét meadow	~135 m	*Junco obtusiflori-Schoenetum nigricantis*
21.	DF1	Tapolcafő	Tapolcafői-láprét marshy meadow	~187 m	*Succiso-Molinietum*
22.	DF2	Tapolcafő	Tapolcafői-láprét marshy meadow	~187 m	*Succiso-Molinietum*
23.	DF3	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Succiso-Molinietum*
24.	DF4	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Succiso-Molinietum*
25.	DF5	Pápakovácsi	Attyai-láprét marshy meadow	~189 m	*Succiso-Molinietum*
26.	HF1	Hárskút	Gyöngyös-hegy hill	~480 m	*Anthyllido-Festucetum rubrae*

T a b l e 1. (Continued)

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27.	HF2	Porva	Csárda-tető peak	~382 m	*Anthyllido-Festucetum rubrae*
28.	HF3	Zirc	Pintér-hegy hill	~380 m	*Pastinaco-Arrhenatheretum*
29.	HF4	Úrkút	Dozmat-rét meadow	~440 m	*Pastinaco-Arrhenatheretum*
30.	HF5	Nagyvázsony	7. nyiladék 7th glade	~480 m	*Pastinaco-Arrhenatheretum*
31.	HF6	Ajka - Padragkút	Segg-berek meadow	~244 m	*Pastinaco-Arrhenatheretum*
32.	HF7	Káptalantóti	Tóti-rét meadow	~116 m	*Cirsio cani-Festucetum pratensis*
33.	HF8	Bakonybél	Som-hegy hill	~410 m	*Anthyllido-Festucetum rubrae*
34.	HF9	Lókút	Óbányapuszta	~422 m	*Pastinaco-Arrhenatheretum*
35.	SD1	Várpalota	Barbély-völgy valley	~260 m	*Brachypodium pinnatum* semidry grassland
36.	SD2	Várpalota	Barbély-völgy valley	~260 m	*Brachypodium pinnatum* semidry grassland
37.	SD3	Balatonalmádi	Vödör-völgy valley	~230 m	*Bromus erectus* grassland
38.	SD4	Balatonalmádi	Vödör-völgy valley	~235 m	*Brachypodium pinnatum* semidry grassland
39.	SD5	Balatonalmádi	Vödör-völgy valley	~235 m	*Brachypodium pinnatum* semidry grassland
40.	SD6	Berhida	Koldustelek valley	~150 m	*Brachypodium pinnatum* semidry grassland
41.	SD7	Berhida	Koldustelek valley	~150 m	*Brachypodium pinnatum* semidry grassland
42.	SD8	Berhida	Koldustelek valley	~150 m	*Brachypodium pinnatum* semidry grassland
43.	SD9	Berhida	Koldustelek valley	~150 m	*Brachypodium pinnatum* semidry grassland
44.	SD10	Pápakovácsi	Attyai-láprét marshy meadow	~190 m	*Brachypodium pinnatum* semidry grassland
45.	SD11	Pápakovácsi	Attyai-láprét marshy meadow	~190 m	*Brachypodium pinnatum* semidry grassland
46.	SD12	Esztergom	Strázsa-hegy hill	~220 m	*Brachypodium pinnatum* semidry grassland
47.	SD13	Esztergom	Tábla-hegy hill	~240 m	*Brachypodium pinnatum* semidry grassland
48.	SD14	Esztergom	Tábla-hegy hill	~245 m	*Brachypodium pinnatum* semidry grassland
49.	SD15	Esztergom	Tábla-hegy hill	~245 m	*Brachypodium pinnatum* semidry grassland
50.	SD16	Esztergom	Tábla-hegy hill	~230 m	*Brachypodium pinnatum* semidry grassland
51.	SD17	Esztergom	Tábla-hegy hill	~230 m	*Brachypodium pinnatum* semidry grassland
52.	SD18	Aggtelek	Szőlő-hegy hill	~400 m	*Brachypodium pinnatum* semidry grassland
53.	SD19	Aggtelek	Szőlő-hegy hill	~400 m	*Brachypodium pinnatum* semidry grassland
54.	SD20	Aggtelek	Szőlő-hegy hill	~400 m	*Brachypodium pinnatum* semidry grassland
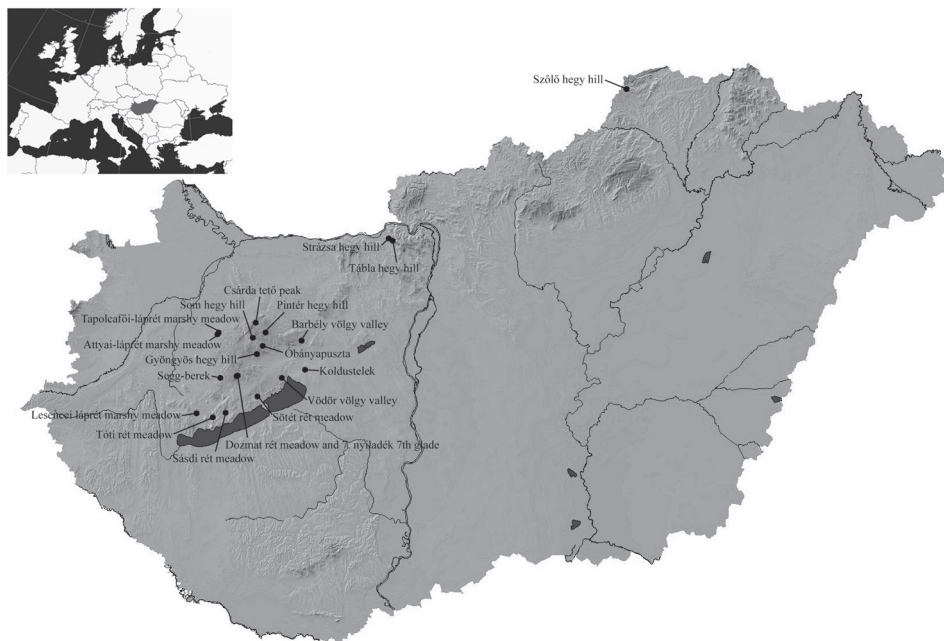
Fig. 1. Map of the localities (scale 1 : 2 000 000).

Study area

The examinations were performed in the following grassland types and associations frequently found in the Transdanubian Mountains in Hungary. Fig. 1 and Tables 1, 2 give information about the localization and basic circumstances of the sampling sites:

– calcareous fens (*Caracion davallianae* K l i k a 1934): *Junco obtusiflori-Schoenetum nigricantis* A l l o r g e 1921; *Caricetum davallianae* D u t o i t 1924.

– drying fens (*Molinion coeruleae* K o c h 1926): *Succiso-Molinietum hungaricae* (K o m l ó d i 1958) S o ó 1969; *Agrostio-Deschampsietum caespitosae* (S o ó 1928) Ú j v á r o s i 1947.

– hayfields (*Arrhenatherion* K o c h 1926): *Pastinaco-Arrhenetheretum* (K n a p p 1954) P a s s a r g e 1964; *Anthyllido-Festucetum rubrae* (M á t h é e t K o v á c s 1960) S o ó 1971; *Cirsio cani-Festucetum pratensis* M á j o v s k y e t R u ž i č k o v á 1975.

– semidry grasslands (*Cirsio pannonicae-Brachypodion pinnati* H a d a č e t K l i k a 1944): *Bromus erectus* or *Brachypodium pinnatum* dominated semi-dry grasslands, partly with unclarified coenological status.

Nomenclature of the plant association was used after Borhidi (1996, 2003), nomenclature of the grasshopper species was used after Nagy (2003).

T a b l e 2. Vegetation characteristics of the sampling sites.

Grassland type	Plant association	Dominant/subdominant grass and sedge species	Vegetation cover
Calcareous fen (*Caricion daval-lianae*)	*Junco obtusiflori-Schoenetum nigricantis, Juncetum subn-odulosi* *Caricetum davallianae* (in the above association with little mosaic patches)	*Schoenus nigricans* *Juncus subnodulosus* *Potentilla erecta* *Mentha aquatica* *Carex panicea* *Allium suaveolens*	40–100%
Drying fen (*Molinion coer-uleae*)	*Succiso-Molinietum hungaricae*	*Molinia hungarica* *Deschampsia caespitosa* *Succisa pratensis* *Serratula tinctoria* *Sanguisorba officinalis*	80–100%
Hayfield (*Arrhenatherion*)	*Pastinaco-Arrhenatheretum*	*Arrhenatherum elatius* *Avenula pubescens* *Dactylis glomerata* *Galium verum* *Pastinaca sativa*	80–90%
	Anthyllido-Festucetum rubrae	*Festuca rubra* *Avenula pubescens* *Trisetum flavescens* *Anthyllis vulnearia* *Cynosurus cristatus* *Campanula patula*	70–90%
	Cirsio cani-Festucetum pratensis	*Festuca pratensis* *Avenula pubescens* *Cirsium canum* *Ranunculus acris* *Angelica sylvestris*	90–100%
Semidry grassland (*Cirsio pannoni-cae-Brachypodion pinnati*)	*Brometum erecti* s.l. *	*Bromus erectus* s.l. *Dianthus pontederae* *Festuca rupicola* *Teucrium chamaedrys* *Salvia pratensis*	90–100%
	Brachypodietum pinnati s.l. *	*Brachypodium pinnatum* *Festuca rupicola* *Stachys recta* *Adonis vernalis* *Filipendula vulgaris* *Trifolium montanum*	95–100%

Notes: * – *Bromus erectus* sl. or *Brachypodium pinnatum* dominated semidry grasslands, partly with unclarified coenological status

Results

4733 specimens of 41 grasshopper species (N-Tettigonioidea = 805; N-Acridoidea = 3928 were detected in the four grassland types (calcareous fens, drying fens, hayfields, semidry grasslands). The results are presented to vegetation types.

Calcareous fens

25 orthopteran species were detected in calcareous fens. Among them the characteristic orthopteran species of the wetland sites whose dominance exceeding 5% in the total assemblage: *Conocephalus discolor* T h u n b e r g, 1815, *Metrioptera roeselii* (H a g e n b a c h, 1822), *Chrysochraon dispar* (G e r m a r, 1834), *Euthystira brachyptera* (O c s k a y, 1826), *Chorthippus parallelus* and *Chorthippus montanus* (C h a r p e n t i e r, 1825).

From June to August both the total-density and the density of the dominant species showed a declining tendency. The total-density in August and September was closely identical.

In the calcareous fens three orthopteran aspects could be separated: one early summer and two autumn assemblages. All of the early summer samples (June, July) can be separated in a group on the diagram of Fig. 2. The separation is based on the next species: *Euthystira brachyptera, Chrysochraon dispar* and *Chorthippus parallelus* as well as *Metrioptera roeselii* and *Chorthippus montanus* species. In Fig. 2 two different autumn aspect-types of the orthopteran assemblages can be differentiated in calcareous fens. (1) In calcareous fens, whose water supply is quite good samples from August and September are characterized by the frequently highly dominant *Conocephalus discolor*. (2) The separation of the samples from Sásdi-rét meadow in Szentbékkálla is caused by the dominance in the cut grass of xerophytic species (e.g. *Chorthippus brunneus, Chorthippus biguttulus* (L., 1758), *Chorthippus mollis* (C h a r p e n t i e r, 1825)) in August and September – owing to the droughts. The experiences suggest that if there is adequate rainfall and no cutting these xerophytic species cannot dominate in the autumn aspect in this sampling site either (for example in 2005).

The Pearson correlation analyses showed a significant positive correlation between the density of orthopteran assemblages and the vapour content in the grass on the soil surface (r_{1ss} = 0.644, p_{1ss} = 0.007); at a height of 10 cm (r_{1a} = 0.633, p_{1a} = 0.008); and 20 cm (r_{1b} = 0.600, p_{1b} = 0.014) in the grassland and as well as with the average value (r_{1av} = 0.591, p_{1av} = 0.016). A significant positive correlation was found between the density of the species, *Metrioptera roeselii* (soil surface: r_{2ss} = 0.540, p_{2ss} = 0.031; 10 cm: r_{2a} = 0.585, p_{2a} = 0.017) and *Euthystira brachyptera* (soil surface: r_{3ss} = 0.545, p_{3ss} = 0.029; 20 cm: r_{3b} = 0.607, p_{3b} = 0.013; 30 cm: r_{3c} = 0.513, p_{3c} = 0.042; average: r_{3av} = 0.556, p_{3av} = 0.025) and the vapour content.

No significant relationship was found between the structural indices of orthopteran assemblages and the temperature of the grass.
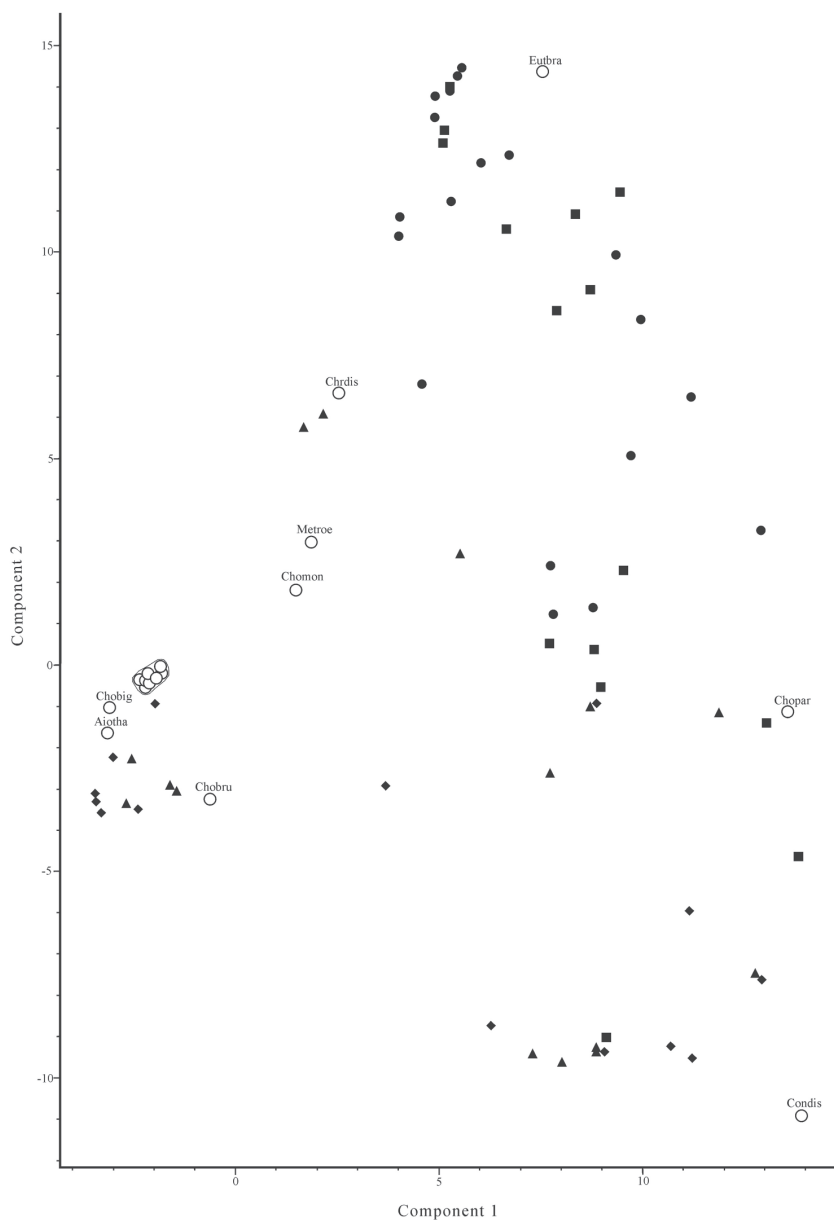
Fig. 2. In the calcareous fens three orthopteran assemblages could be separated: one early summer and two autumn assemblages (Standardized Principal Component Analysis) Legends: empty circle: orthopteran species, black circle: samples of June, black sqare: samples of July, black triangle: samples of August, black diamond: samples of September.

Drying fens

14 orthopteran species were detected in drying fens, species dominance exceeding 5% were the following: *Leptophyes albovittata* (K o l l a r, 1833), *Conocephalus discolor, Metrioptera roeselii, Pholidoptera fallax* (F i s c h e r, 1853)*, Stethophyma grossum* (L., 1758)*, Chrysochraon dispar, Euthystira brachyptera* and *Chorthippus parallelus.*

In the habitat *Metrioptera roeselii, Euthystira brachyptera, Stethophyma grossum, Chrysochraon dispar* and *Chorthippus parallelus* species are dominant in the early summer aspect, the above-mentioned species disappear at late summer and the new aspect dominated by *Conocephalus discolor* develops. Similarly to calcareous fens this grassland has also good water supply. The similarity between the structures of the orthopteran assemblages in the two fen-types can also be caused by the geographical site of the grasslands. Microgeomorphological differences in the ground surface or fluctuations of the ground water by some decimetres can result in the transformation of these fen types. However, in accordance with the field experiences this orthopteran assemblage-type may also develop in drying fens not adjoining calcareous fens.

The correlation analyses show a significant positive correlation between the species number of orthopteran assemblages and average vapour content in the grass ($r_1 = 0.620$, $p_1 = 0.014$), furthermore diversity of orthopteran assemblages and average vapour content in the grass ($r_2 = 0.6613$, $p_2 = 0.007$), too. A significant positive correlation was also shown between the species number of orthopteran assemblages and the average temperature in the grass ($r_3 = -0.607$, $p_3 = 0.016$) as well as between the diversity of orthopteran assemblages and the average temperature in the grass ($r_4 = -0.6492$, $p_4 = 0.009$).

No significant correlation was found between the data measured at different levels of the grasslands and the structural parameters of the orthopteran assemblages.

Hayfields

25 orthopteran species were caught in hayfields. Species with dominance exceeding 5%: *Stenobothrus lineatus* (P a n z e r, 1796), *Chorthippus parallelus*, *Ch. montanus* and *Euchorthippus declivus* (B r i s o u t, 1848). Grass cutting (mowing) in late June and early July has a drastic effect on the density of orthopteran species especially the density of chortobiont species (for example *Chorthippus parallelus, Ch. montanus, Metrioptera roeselii*). Grass cutting also results in a sharp decline in the density of the subxerophytic *Euchorthippus declivus*. Samples taken from grasslands, where the microclimate in the growing grasses is becoming more and more humid with the growth of the phytomass after the early summer cutting (Bauer, Kenyeres, 2006), were characterized by a higher density in September. The ordination analysis showed the separation annual aspects of the orthopteran assemblages and the importance of the incremental species causing these. The dominant species of the early summer orthopteran aspect are *Chorthippus parallelus* and *Ch. montanus,* while *Ch. brunneus* and *Ch. biguttulus* characterize the autumn aspect of hayfields that have xerophytic orthopteran assemblages. Since no significant difference was found between the structures

of the late summer/early autumn (August, September) and early summer orthopteran aspects of the orthopteran assemblages on grasslands with good water supply, in the ordination analysis these samples were ranked with that group.

The vapour content of hayfields showed a large deviation every month, presumably caused by the differences in their naturalness and treatment (Bauer, Kenyeres, 2006). The correlation analyses did not reveal significant correlations between the density of the orthopteran assemblages of hayfields and the vapour content and temperature of the grassland. But a significant positive correlation was found between the densities of some hygrophytic species and the vapour content in the grass: *Conocephalus discolor*: 10 cm: $r_{cda} = 0.501$, $p_{cda} = 0.034$; 20 cm: $r_{cdb} = 0.539$, $p_{cdb} = 0.021$; *Ruspolia nitidula* (S c o p o l i, 1786): 10 cm: $r_{rna} = 0.507$, $p_{rna} = 0.032$; 20 cm: $r_{rnb} = 0.552$, $p_{rnb} = 0.018$. A significant negative correlation was found between density of *Leptophyes albovittata* and the vapour content in the grass (soil surface: $r_{lass} = -0.587$, $p_{lass} = 0.010$; 10 cm: $r_{laa} = -0.541$, $p_{laa} = 0.021$; 20 cm: $r_{lab} = -0.543$, $p_{lab} = 0.020$; 30 cm: $r_{lac} = -0.563$, $p_{lac} = 0.015$; average: $r_{laav} = -0.513$, $p_{laav} = 0.030$).

Brachypodium pinnatum dominated semidry grasslands

28 orthopteran species were found in *Brachypodium pinnatum* dominated semi-dry grasslands. Species with dominance exceeding 5%: *Leptophyes albovittata*, *Metrioptera bicolor* (P h i l i p p i, 1830), *Euthystira brachyptera*, *Chorthippus parallelus*, *Ch. montanus* and *Gomphocerippus rufus* (L., 1758).
Fig. 3 shows that the total density of orthopteran assemblages as well as the density of the most abundant species (*Euthystira brachyptera, Metrioptera bicolor, Chorthippus parallelus, Leptophyes albovittata*) decreased from June till to September. The early summer samples could be separated by the ordination analysis of Fig 4. Based on the differential species two other types of the early summer aspect could be separated: (1) *Euthystira brachyptera* dominated aspect, and (2) *Chorthippus parallelus* and *Metrioptera bicolor* dominated aspect. The above-mentioned groups derived mainly from samplings in June and July but, owing to the different origin, situation and water supply of the analysed *Brachypodium pinnatum* dominated semidry grasslands, some samples in August and September could be presumably also classified into the same group. The same applies to the early summer assemblages, developed in dry habitats, of certain sampling sites, the structure of which assemblages was close to the grasslands normally drying out till the beginning of autumn. No typical autumn aspect could be seen in this grassland-type. In this period significantly differing assemblages of small density, mainly dependent on the neighbouring habitats can be observed. At this time, for example, in stands adjoining steppe grasslands and xerophytic oak forests the *Gomphocerippus rufus* is present (SD14 and SD15 in September), while the subhygrophytic *Conocephalus discolor* or the mesophytic *Euthystira brachyptera* are present in patches adjoining hygrophytic grasslands (SD11 in September).

With the correlation analyses a significant positive correlation was shown between (1) the species number of the orthopteran assemblages and the temperature of the soil surface; (2) the density of the orthopteran assemblages and the vapour content of the grassland (soil
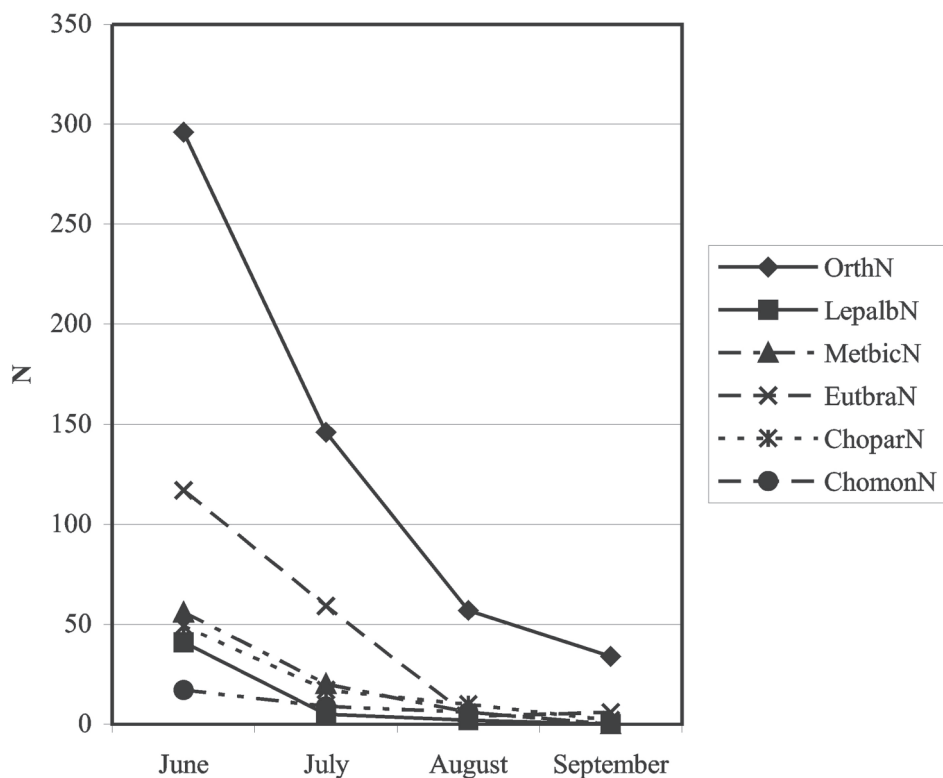
Fig. 3. The total density of orthopteran assemblages of the *Brachypodium pinnatum* dominated grasslands as well as the density of the most abundant species (*Euthystira brachyptera, Metrioptera bicolor, Chorthippus parallelus, Leptophyes albovittata*) decreased from June till to September.

surface, at a height of 10, 20 cm in the grassland and average); (3) density of the dominant species (*Leptophyes albovitatta*, *Metrioptera bicolor*, *Chorthippus parallelus*, *Ch. montanus*) and the measured vapour content of every grassland level (Table 3). The correlation analyses showed a significant negative correlation between (1) the density of the orthopteran assemblages and the temperature of the grassland (soil surface, at a height of 10, 20 cm in the grassland and average temperature); (2) the density of *Leptophyes albovittata* and the temperature in the grassland (soil surface, at a height of 10, 20 cm in the grassland and average temperature); (3) the density of *Metrioptera bicolor* and the temperature of the soil surface; (4) the density of *Euthystira brachyptera* and the temperature of the grassland at a height of 10, 20 cm and the average temperature; (5) the density of *Chorthippus parallelus* and the temperature of the grassland at the soil surface and a height of 10 cm (Table 4).
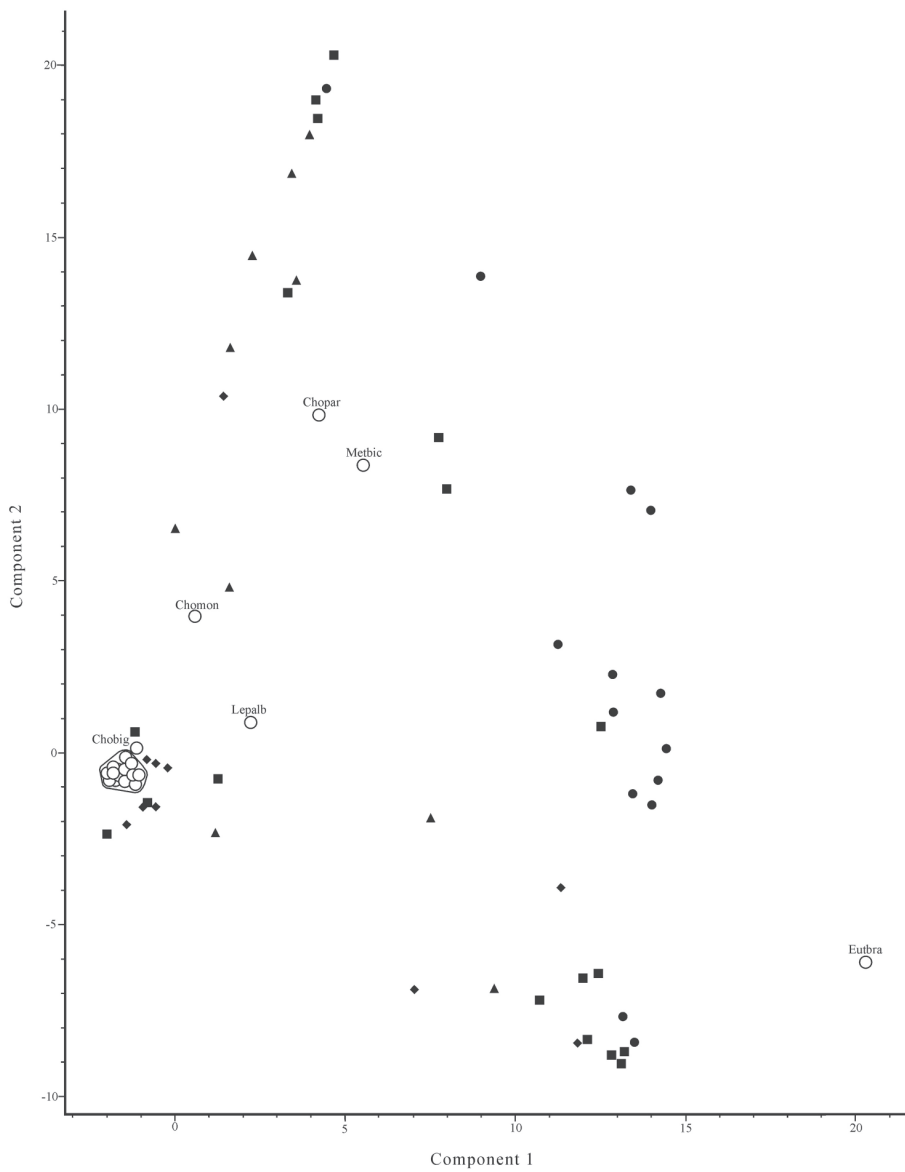
Fig. 4. The early summer samples could be separated by the ordination analyses (Standardized Principal Component Analysis) of *Brachypodium pinnatum* dominated grasslands. Based on the differential species two other types of the early summer aspect could be separated: (1) *Euthystira brachyptera* dominated aspect, and (2) *Chorthippus parallelus* and *Metrioptera bicolor* dominated aspect. Legends: empty circle: orthopteran species, black circle: samples of June, black sqare: samples of July, black triangle: samples of August, black diamond: samples of September.

T a b l e 3. With the correlation analyses many significant positive correlation (*) were shown between the parameters of the orthopteran assemblages' structure and the measured vapour content values in *Brachypodium pinnatum* dominated semidry grasslands.

Taxon/ Microclimate	Vapour content in the grass				
	soil surface	10 cm	20 cm	30 cm	average
OrthS	*0.331	0.194	0.199	0.039	0.212
OrthN	*0.406	*0.357	*0.441	0.224	*0.384
LepalbN	*0.297	*0.327	*0.472	*0.319	*0.372
MetbicN	*0.574	*0.561	*0.583	*0.407	*0.569
EutbraN	0.117	-0.005	0,068	-0.067	0.035
ChoparN	*0.451	*0.474	*0.566	*0.358	*0.493
ChomonN	*0.434	*0.403	*0.388	*0.315	*0.413

Marked correlations are significant at $p < 0.05$

T a b l e 4. With the correlation analyses many significant negative correlation (*) were shown between the parameters of the orthopteran assemblages' structure and the measured temperature values in *Brachypodium pinnatum* dominated semidry grasslands.

Taxon/ Microclimate	Temperature in the grass				
	soil surface	10 cm	20 cm	30 cm	average
OrthS	-0.176	-0.149	-0.097	-0.052	-0.123
OrthN	*-0.400	*-0.370	*-0.308	-0.215	*-0.336
LepalbN	*-0.418	*-0.352	*-0.295	-0.239	*-0.339
MetbicN	*-0.310	-0.278	-0.204	-0.097	-0.231
EutbraN	-0.288	*-0.307	*-0.322	-0.277	*-0.310
ChoparN	*-0.348	*-0.315	-0.219	-0.107	-0.257
ChomonN	-0.154	-0.128	-0.063	0.046	-0.078

Marked correlations are significant at $p < 0.05$

Discussion

Earlier studies have revealed that grassland-types with different habitat-structure could be characterized by orthopteran assemblages with different community structure (species composition, life form-spectra etc.). One of the possible reasons for this could be the microclimate in the habitat, which might be of significantly influence on density of species with different habitat-preferences. Our results in grasslands with significant seasonal microclimatic changes (calcareous fens, drying fens, hayfields, semidry grasslands) indicated that the microclimate of grasslands (mainly the vapour content) is not only a spatial but

also a temporal factor (within a year) in the seasonal changes of orthopteran assemblages, that are partly based on phenological facts. Concerning the influence of microclimatic differences of grasslands with various succession stages on the structure of orthopteran assemblages Rácz (1998b) suggests that strongly hygrophytic species are suppressed parallel to the decrease in vapour content. Our results indicate that, in grasslands that show marked seasonal changes (desiccation), this structural change can be recognized within a year. The numerous significant correlations observed suggest that the seasonal structural changes in Orthopteran assemblages are caused by the microclimatic changes (mainly the decrease of vapour content) of the grasslands. This can be described in the following phenomena: (1) the large-scale early summer presence and subsequent disappearance of hygrophytic and mesophytic species; (2) in the case of good water supply (high ground water level in the observer wells), the late summer aspect is organized with low species number, based on some hygrophytic and mesophytic species or rather delay in the decline of these species; (3) in the case of bad water supply, the high abundance of xerophytic species in the late summer aspect is typical.

Our results confirmed that the seasonal change of the Tettigonioidea/Acridoidea rate is one of the typical assemblage-features. From June to September the percentage of Tettigonioidea density decreased in *Brachypodium pinnatum* dominated grasslands, increased in drying fens (because of high density of *Conocephalus* spp. in late summer and autumn) and stagnated in hayfields and calcareous fens. Significant positive correlation was found between the density of Tettigonioidea species and the vapour content in the grass in *Brachypodium pinnatum* dominated grasslands. Also significant positive correlation was found between the density of Acridoidea species and the vapour content in these grasslands. It caused by the dominancy of the hygrophilous Tettigonioidea and Acridoidea species in June and July. The sensitivity to humidity of hygrophilous and mesophilous Acridoidea species was affirmed by the result which revealed significant positive correlation between the density of Acridoidea species and the vapour content in calcareous fens. The correlation analyses did not reveal significant correlations between the density of Tettigonioidea or Acridoidea species and the vapour content and temperature of the grassland in hayfields and drying fens.

Owing to the complicated habitat-dependence of orthopteran species as well as assemblages it can be suggested that the correlations leading to these conclusions might be mere statistical products. The fact that aspect change could only be the consequence of the coexistence of species with characteristic phenology cannot be supported since PDD and the pace of later development probably are determined by climatic factors (mainly the temperature) (Ingrisch, 1986a).

Parallel to the change in the grassland microclimate, the food sources also change to a certain degree, therefore it can be concluded that the seasonal structure of assemblages of oligophagous insects is determined by this change. Owing to the interactions of plant structure and microclimate (Jakucs, 1961, 1968; Jakucs et al., 1968; Matlack, 1993; Chen et al., 1995; Gehlhausen et al., 2000; Bauer, Kenyeres, 2006) and the complex relationship between orthopterans and their habitats, the categorical separation of the two habitat characteristics can only be supported by local scale, autoecological analyses of adjoining

habitats (for example Adamović, 1969; Kenyeres et al., 2004; Kenyeres, Bauer, 2005). These statements (the determining influence of microclimate on assemblage-structure) are confirmed by numerous analyses.

Basically the air temperature ensures the needed temperature for the activity of orthopterans (Anderson et al., 1979). Individual species differ in their thermoregulatory ability, fundamentally determining their choice of habitat. In his analyses Willott (1997) confirmed that the connection of *Myrmeleotettix maculatus* (T h u n b e r g, 1815) to short swards, of *Omocestus viridulus* (L., 1758) to tall swards and of *Chorthippus brunneus* and *Stenobothrus lineatus* to swards of intermediate height can be related to their thermoregulatory ability. The vegetation-dependence of phytophytic and geophytic orthopterans is closely connected with the insect energy budgets and is a determining factor in their behaviour, too (Uvarov, 1977; Hochkirch, 1996). Phytophytic species (the acridids also) spend most of their active period on leaves (mainly dicotyledonous plants). The time spent on leaves usually highly exceeds that of nutrition. It is known that in the case of high air temperatures, in order to accelerate egg production, females spend more time on these surfaces than males (Hochkirch, 2000).

El-Shazly, Shahpa (2004) pointed out that the locust species density is fundamentally determined by the temperature of their habitat. In the case of several species, a negative correlation was found between various vapour data and the size of locust populations. Dry, warm microclimatic conditions – aiding nutrition and oviposition and reducing the effect of natural enemies and parasites – generally result in a high orthopteran density. The phenomenon, however, cannot be applied to all orthopteran assemblages (Dempster, 1963; Capinera, 1987; Capinera, Thompson, 1987; Capinera, Horton, 1989).

Johnson (1989) also indirectly supports the outstanding significance of microclimate when – by discarding the 'intrinsic hypothesis' (Isely, 1937) – he states that the abundance of orthopteran assemblages shows a significant relationship to the soil-type of the habitat determined by climate, vegetation and land use rather than the physical characteristics of the ground surface.

In order to confirm the hypothesis that the seasonal structural changes outlined above are not caused by the relationship between the oligophagous nutrition of orthopterans and the change in host-plant cover, the results concerning host-plant preferences of orthopterans have to be analysed, too. In the plant preference of grasshoppers Smith, Capinera (2005) defined – confirmed by laboratory analyses – some of the correlations between the density of some orthopteran species and the plant cover of certain plants as host plant-dependence. However, several plant species showed significant correlation with the density of some orthopteran species for reasons other than oligophagous nutrition. Smith, Capinera (2005) consider the latter as 'indicator species' of preferred habitat(s). The dicotyledonous preference of several phytophagous grasshopper species has long been known, but a more or less specialized nutrition can be observed in locust species, too (Clarke, 1948; Richards, Waloff, 1954; Mulkern, 1967; Bernays, Chapman, 1970). Earlier (Joern, 1983) the nutrition of locust species was thought to have an identical frequency of some plant taxa in the field and the gut of orthopterans. According to the results of El-Shazly, Shahpa (2004), however, there are

significant differences in the case of certain plant families. The frequency in the acridids' gut of Gramineae, Cyperaceae or Cruciferae species is far behind their frequency in the field while that of the Leguminosae family exceeds it by far. The preference for mesophytic monocotyledonous species (for example *Dactylis glomerata*) has been confirmed in the case of several mesophytic species such as *Chorthippus parallelus*, which is dominant in many of our samples. Nevertheless, no exclusiveness can be observed, consequently, host-plant changes are not problematic for insects (Bernays, Chapman, 1970; Gardiner, Hill, 2004). Laboratory experiments confirm that *Brachypodium pinnatum*, the dominant species in one of the analysed grassland types, has an outstanding significance in the nutrition of orthopterans (Corcket et al., 2003) (mainly in early- and mid-summer, because later the leaves are usually desiccated). Our results indicate that, within the year, gradual drying can be observed in *Brachypodium pinnatum* dominated semidry grasslands. This phenomenon is presumably caused by the decrease of the dominant grass species' (*Brachypodium pinnatum*, *Bromus erectus* sl.) and accompanying species' transpiration (Bauer, Kenyeres, 2006). The change in the structure of *Brachypodium pinnatum* dominated semidry grasslands in the second half of summer does not only result in drier microclimate but also in the growth of dry leaves of the same species – less preferred by orthopterans (Gardiner, Hill, 2004). Owing to the correlation between vegetation structure and microclimate, it can be ascertained that, in this grass type, the condition of host-plants is also related to the change in microclimatic conditions (which naturally is not independent from the phenological changes in the plant species of the grassland) (Bauer, Kenyeres, 2006), therefore the effect of the two variables is simultaneous and cannot be separated.

Based on the above-mentioned papers and our own results it can be stated that the significant correlations between the structural parameters of the orthopteran assemblages and the measured microclimate values can reveal real relationships.

Some preferences can be established in the nutrition of the orthopteran species and their assemblages but no exclusive nutrition relationships of these species are known. In spite of the fact that the species composition of plants shows no or minimal changes within such a period, the quick changes (for example calcareous fens in droughty years) in an unusual direction of the microclimatic conditions of grasslands can also be shown in the composition of orthopteran assemblages (aspect with xerophytic species). Based on earlier studies, the failure to bloom of some more sensitive species and the slightly smaller biomass of the dominant plant species are – on their own – unlikely to result in such marked changes in the sampled insect assemblages. Our results indicate that, in the case of similar plant structure, the aspect change of orthopteran assemblages is influenced by the microclimatic conditions of the habitat. Keeping the complicated nature of synbiological phenomena, the listed arguments and counter-arguments in mind, it can be concluded that the microclimatic conditions of grasslands play a significant role in the dynamics of orthopteran assemblages but, naturally, they are not fully independent from purely abiotic factors, the phenological characteristics of the community and different anthropogenic influences.

Translated by the authors

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