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Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera)—a case study from the Elbe flood plains (northern Germany)

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Abstract

Diversity of insect communities in grasslands is often negatively correlated with management intensity. Targets of sustainable husbandry practices in agricultural systems should include the conservation of insects highly specific to certain types of grassland. In general, Auchenorrhyncha can be regarded as suitable indicators of biotic conditions in grasslands because (i) their response to management, like cutting, grazing and fertilizing, is strong and immediate, (ii) quantitative and semiquantitative sampling is relatively easy, (iii) their abundance and species numbers in grasslands are usually high, and (iv) they show different life strategies ranging from polyphagous pioneer species to strictly monophagous specialists.

This study was conducted in the floodplains of the middle course of the Elbe river (northern Germany). Its purpose was (i) a survey of local Auchenorrhyncha communities and their responses to different grassland management regimes, and (ii) a study of their suitability as indicators of habitat disturbance, particularly in comparison to plant communities. Samples were taken with the sweepnet in 1999, and with a suction apparatus in 2000. The plots included 25 sites in meadows, pastures and fallows. Altogether, 88 species were recorded. Regarding the distribution of generalist species, differences between plots being subject to high-intensity management and those being subject to low-intensity management were little pronounced. However, most plots of low-intensity pastures and fallows showed higher numbers and higher proportions of specialists. In late spring, suction sampling produced higher individual numbers in low-intensity sites. Moreover, diversity in high-intensity sites was reduced, with generalists dominating. We discuss different responses of plant and animal communities on grassland management and propose species numbers and proportion of both pioneer species and specialists as robust indicators of biotic conditions in grasslands. Furthermore, we make proposals for a future land use management of flood plain grasslands.
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Keywords: Auchenorrhyncha; Grasslands; Disturbance; Management; Indicator

1. Introduction

Grassland invertebrate communities are rather complex and diverse. Species and individual numbers are particularly high among Nematoda, Enchytraeidae, Lumbricidae, Acari and Insecta, with most above-ground studies focusing on the latter (Boness, 1953; Curry, 1994; Tscharntke and Greiler, 1995). Species numbers as well as proportions of specialists and threatened species are negatively affected by the intensity of management (Curry, 1987). Sustainable use of agricultural systems should include the conservation of communities adapted to the specific

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conditions in grasslands. However, arthropod responses to management can be group-specific, and the question arises which invertebrate taxa are most suitable for an indication of management effects. Morris and Rispin (1987) demonstrated that beetles in British calcareous grasslands show less clear responses to cutting than Auchenorrhyncha and Heteroptera, probably due to their less distinct niche separation in different layers of the vegetation. Important prerequisites of arthropod taxa used for monitoring biotic conditions in grasslands include both intrinsic characters, like diversity and niche separation, and extrinsic factors such as sampling and taxonomic practicability.

We chose the Auchenorrhyncha for the following reasons:

(i) They occur in high individual and species numbers. Abundances in grasslands are often high and may exceed 1000 ind./m^2 (Waloff, 1980; Curry, 1994). The total species number in German grassland ecosystems is almost 320 (see Nickel, 2003). Mown grasslands, i.e. meadows sensu stricto, altogether harbour only 120 species, with up to 40 occurring on one plot (Nickel and Achtziger, 1999).

(ii) Due to large population sizes and species numbers, Auchenorrhyncha form an important component of the grassland fauna, although functional aspects of their ecology are little studied. Most species live in the herbaceous layer. Nymphs and adults usually feed externally on the above-ground parts of plants, ingesting cell contents, phloem or xylem sap. As primary consumers, they assimilate plant biomass, damage plant tissue by oviposition and transmit plant diseases. Thus, they affect competitive relationships and species composition of plants and the direction of succession in agricultural systems (e.g. Brown, 1985; Jung et al., 2000). Moreover, they are an important prey for predators, particularly spiders (Araneae), ants (Hymenoptera, Formicidae) and songbirds (Aves, Passeres), and they are essential host organisms for parasitoids, notably the Dryinidae, Myrmaridae (both Hymenoptera), Pipunculidae (Diptera) and Strepsiptera (Waloff and Jervis, 1987).

(iii) They show specific life strategies and occupy specific spatial and temporal niches. Life strategies range from pioneers, which are usually polyphagous, macropterous and at least bivoltine, to stenotopic species, which are monophagous, usually brachypterous and monovoltine (Novotný, 1994a,b, 1995; Table 3). Depending on overwintering stage and generation numbers, maturity peaks may be reached in mid-spring, early or late summer. The species number of Auchenorrhyncha is positively correlated with species numbers of other important groups living in the herbaceous layer, like Heteroptera, Saltatoria and Rhopalocera (Achtziger et al., 1999) as well as of plants and their structural complexity (Denno, 1994; Denno and Roderick, 1991; Murdoch et al., 1972). Resource utilization is rather diverse regarding stratification and plant architecture (Andrzejewska, 1965) and, as a result, Auchenorrhyncha communities are richer in taller grasslands (Morris, 1971, 1973). Generally, host specialists are dominating, with many species being associated with grasses and sedges. Sedges (*Carex* spp.), fescue (*Festuca* spp.) and small-reed (*Calamagrostis* spp.) are among the most-favoured host plants of monophagous Auchenorrhyncha species in central Europe (Nickel, 2003). These include 1st degree monophages, being specific to a single plant species, and 2nd degree monophages, being specific to a single plant genus.

(iv) Their responses to management are immediate, with marked changes in dominance and community structure (Andrzejewska, 1991; Morris, 1981a,b; Morris and Plant, 1983). Eventually, communities become subject to selection of species tolerating the management regime (Nickel and Achtziger, 1999).

(v) Sampling of the whole species range can be done quickly on two or three dates a year. Suction samples, in particular, produce reliable estimates of abundance and dominance. Sweep-net samples can usually be compared within one study, although most epigeic species are under-represented. The effort for determination is reasonable. The knowledge of taxonomy and ecology of this group in grassland ecosystems is advanced (e.g. Waloff, 1980; Hildebrandt, 1995; Nickel and Achtziger, 1999; Nickel, 2003; see also Achtziger, 1999).

(vi) Suction samples of Auchenorrhyncha can produce a high spatial resolution due to high proportions of monophagous and oligophagous species closely associated with their hosts. Usually, reproduction on the plot can be inferred from the presence of nymphs and freshly emerged adults. In contrast, spatial resolution of pitfall and light trap catches is limited.

In this paper, we present a case study on flood plain grasslands in the middle Elbe valley (Lower Saxony, Germany). Unlike most studies focusing on direct and short-term effects of treatments (e.g. Morris, 1981a,b; Southwood and van Emden, 1967), we concentrate on long-term changes of the species composition under different management regimes in meadows, pastures and fallows. For demonstrating differences between treatments, we apply a classification scheme based upon Auchenorrhyncha life strategies, which allows an indication of habitat disturbance.

2. Sites, methods and material

The study sites are located in the lower part of the middle Elbe valley (northern Germany) (Fig. 1). In this section of the river, anthropogenic influences on river morphology and dynamics have been less severe than in most other central European river valleys, with vast areas of sandy and muddy river banks, willow scrub and grassland being subject to periodical flooding. Due to these floodings, much of the outer dike area is used as meadows and pastures, whereas most inland areas are used as fields. We studied 25 sites covering the most widespread management regimes, moisture conditions and vegetation types (Table 1):

1. Five sites of high-intensity grassland (HIG) being subject to at least two cuts per year, occasional cattle grazing and frequent mineral fertilizing. Dominating plant communities include the Lolio-Cynosuretum and the *Alopecurus pratensis* community. Moisture conditions during summer

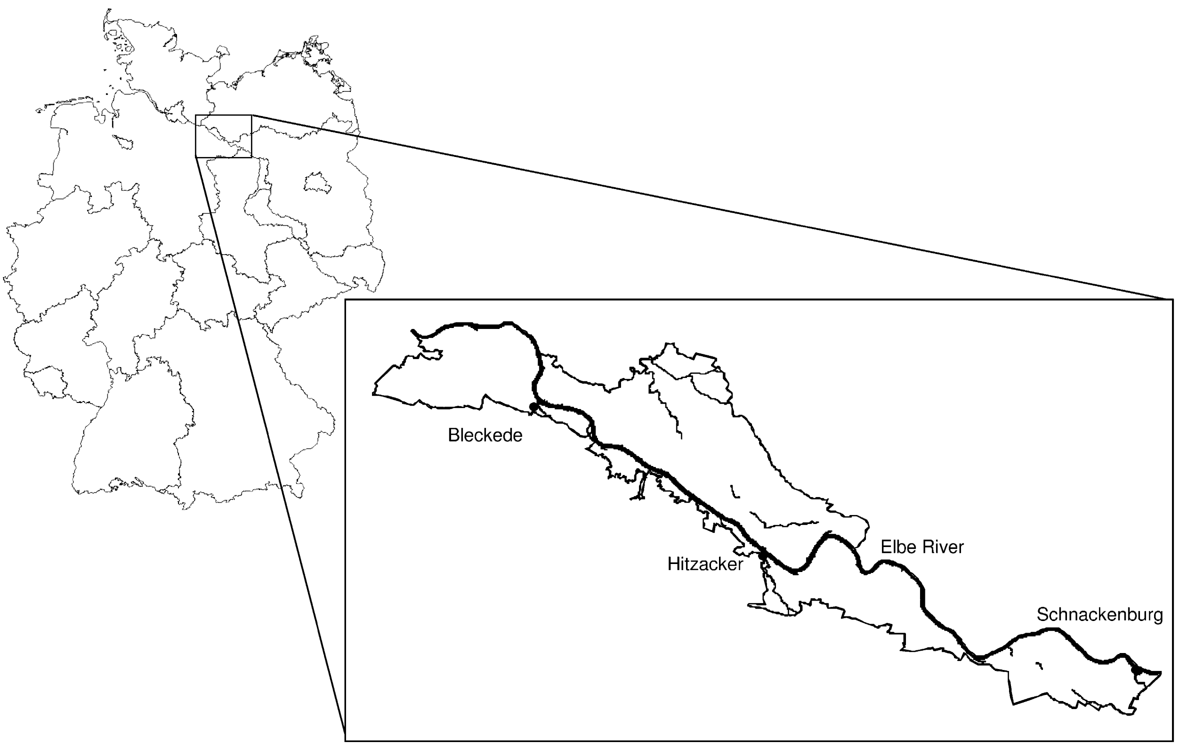

Fig. 1. Location of the study area.

Table 1
Overview of the study plots

Plot no.	Plant community/dominating plants	Moisture condition	Management regime[a]
1	Lolio-Cynosuretum	Damp	HIG
2	*Alopecurus pratensis* community	Damp	HIG
3	*Festuca rubra, Holcus lanatus, Deschampsia cespitosa*	Damp	F
4	Chrysanthemo-Rumicetum thyrsiflori	Damp	LIM
5	Cnidio-Deschampsietum (depression)	Moist	LIM
6	Cnidio-Deschampsietum	Moist	LIM
7	*Phalaris arundinacea, Alopecurus pratensis, Symphytum officinale*	Moist	F
8	*Silaum silaus* community	Moderately moist	LIM
9	Lolio-Cynosuretum	Damp	HIG
10	Lolio-Cynosuretum/Chrysanthemo-Rumicetum thyrsiflori	Damp	HIG
11	Ranunculo-Alopecuretum geniculati	Moderately wet	LIP
12	Diantho-Armerietum	Moderately dry	LIM
13	*Carex arenaria, Festuca ovina, Artemisia campestris*	Moderately dry	LIP
14	*Festuca ovina, Anthoxanthum odoratum, Agrostis capillaris*	Moderately dry	LIP
15	*Elymus repens, Carex hirta*	Moist	LIP
16	*Corynephorus canescens, Holcus lanatus, Agrostis capillaris*	Moderately dry	F
17	*Calamagrostis epigejos, Elymus repens*	Moderately dry	LIP
18	Caricetum vulpinae/Ranunculo-Alopecuretum geniculati	Moist	LIP
19	*Corynephorus canescens, Carex arenaria, Festuca ovina*	Moderately dry	LIP
20	*Alopecurus pratensis* community	Damp	LIP
21	Lolio-Cynosuretum	Damp	HIG
22	*Carex gracilis* community	Wet	F
23	*Lolium perenne, Elymus repens, Apera spica-venti*	Damp	F
24	Cnidio-Deschampsietum	Moist	LIM
25	Cnidio-Deschampsietum (depression)	Moderately wet	LIM

[a] HIG: high-intensity grassland, LIM: low-intensity meadow, LIP: low-intensity pasture, F: fallow. Plant communities after Redecker (unpublished).

range from moist to damp, occasionally moderately dry. In most years, during winter and early spring these sites become flooded, except sites no. 1 and 2.

2. Seven sites of low-intensity meadows (LIMs), harbouring endangered plant communities specific to lowland river basins (‘Cnidion meadows’). This type of grassland only thrives in sites inundated for 40–100 days a year, being of major concern for conservation due to the occurrence of *Cnidium dubium* (Schkuhr) Thell., *Silaum silaus* (L.) Schinz and Thell., *Lathyrus palustris* L. and other endangered plants (Redecker, unpublished). The management regime includes two cuts a year after mid-June without use of fertilizers.
3. Eight sites of low-intensity pastures (LIPs), ranging from wet and regularly flooded to moderately dry sites, grazed by cattle over large areas. Cattle density is low and ranges from 0.9 to 1.2 livestock units per hectare. Floodings occur more or less frequently during winter and early spring.
4. Five fallow sites (F), including fallow fields, abandoned meadows and a tall sedge swamp formerly used for straw production. These sites may be mown after several years to prevent growing of shrubs. In summer, moisture conditions range from moderately wet to moderately dry. Sites no. 7 and 22, but not the remaining sites, are frequently flooded in winter and spring.

Sweepnet samples, taken on 9, 10 and 11 June, and 29 and 30 August 1999, comprised 50 sweeps per plot, respectively, done by a 32 cm × 26 cm linen net. Suction samples, taken on 30 and 31 May, and 6 and 7 August 2000, were done by an ‘Eco-Vac’ (made by Eco-Tech, Bonn, Germany), which is essentially a converted leaf blow apparatus. The nozzle area measured $0.015\,m^2$, the maximum air velocity was $76\,ms^{-1}$. Each sample involved placing the nozzle onto the surface for ca. 5 s, which was repeated 10 times per plot. The sample was then removed by inverting the collection bag into a linen funnel, the outlet meeting into a screw-cap glass filled with alcohol.

In order to standardize the different numbers of plots per treatment type we calculated an index value, dividing the number of threatened species by the number of replicates.

A statistical analysis of sweepnet samples in 1999 was performed using detrended canonical analysis (DCA) (Kovach, 1999). We applied a $\log_e$-transformation to the data and downweighted rare species (Jongman et al., 1995). In 1999, sites no. 24 and 25 could be sampled only on the 30 August 1999. Thus, these data were excluded from the DCA. Likewise, sites no. 3 and 19 could be sampled only in 1999.

3. Results

3.1. Ecological characteristics of the Auchenorrhyncha communities

In both years, altogether 16.613 individuals belonging to 88 species were sampled. The leafhoppers *Psammotettix confinis* (Dhlb.), *Errastunus ocellaris* (Fall.), *Deltocephalus pulicaris* (Fall.), *Arthaldeus pascuellus* (Fall.), *Notus flavipennis* (Zett.) and *Cicadula quadrinotata* (F.) were most abundant, the last two with clear preference of wet sites. Eight species occurred as single individuals only and were treated as non-resident. Eighteen species are listed in the Red Data Book of Germany, 14 of which are considered as threatened, mainly comprising specialists restricted to dry or wet habitats (Remane et al., 1998; Nickel et al., 1999).

The degree of food plant specialization appears to be high. Host specialists associated with a single plant species or genus (i.e. 1st or 2nd degree monophagous—see Table 2 for explanation) comprise more than one-third of the species total. The majority of species is 1st degree oligophagous, comprising 42%, while the remaining species are 2nd degree oligophagous or polyphagous. We compiled the information on the regional species pool, defined as the sum of species living in herbaceous vegetation known from Lower Saxony and the adjacent federal states of Schleswig–Holstein and Mecklenburg–Vorpommern (after Schiemenz, 1987, 1988, 1990; Schiemenz et al., 1996; Wagner, 1935; Nickel, 2003). A comparison reveals that the proportion of host specialists is considerably lower in the study sites than in the regional pool (Fig. 2).

Suction samples in 2000 revealed highest population densities in late spring on plot no. 7, in a fallow dominated by *Phalaris arundinacea* L., and on plot no. 15, in an LIP with dominating *Carex hirta* L. (Fig. 3). All high-intensity sites showed relatively low abundances on this date, which was reflected, in particular, by densities of eurytopic and epigeic species, e.g. *E. ocellaris* (Fall.) and *Anoscopus flavostriatus* (Don.). In August, differences to low-intensity sites were less pronounced.

Seven species were found exclusively in the suction samples, namely *Paraliburnia adela* (Fl.), *Criomorphus albomarginatus* Curt., *Agallia brachyptera* (Boh.), *Dikraneura variata* Hardy, *Rhytistylus proceps* (Kbm.), *Cicadula persimilis* (Edw.) and *Cosmotettix costalis* (Fall.). Most of these are more or less epigeic and more specific regarding habitat requirements. *D. variata* Hardy is probably an immigrant from neighbouring pine forests. Thus, in sweepnet samples, generalist species tend to be over-represented, particularly in stands of taller vegetation.

3.2. Differences between treatments

Differences in species composition are only slight between HIGs and LIMs, both treatments showing a dominance of eurytopic grass-dwelling species and only low individual numbers of a few specialists, like *Euconomelus lepidus* (Boh.) and *Mocuellus metrius* (Fl.). The two latter are mainly restricted to small patches of depressions with dominating *Eleocharis* spp. or *P. arundinacea* L., which may, for technical reasons, be difficult to reach for mowing machines. Moreover, some of these species were not recorded as nymphs, and hence, there was no breeding evidence.

Species numbers and proportion of specialists are much higher in LIPs. This increase in diversity is often caused by the patchy occurrence of additional host species, like *Festuca ovina* L., *Calamagrostis epigejos* (L.) Roth, *Hypericum perforatum* L. and others, which are absent from most mown sites. Communities

Table 2
Auchenorrhyncha catches in the study sites[a]

Treatment site no.	HIGs					LIMs							LIPs								F					Total	Host specificity	Voltinism	Status
	1	2	9	10	21	4	5	6	8	12	24	25	11	13	14	15	17	18	19	20	16	3	23	7	22				
Pioneer species																													
Empoasca pteridis (Dhlb.)	**3**	**1**		X		1	**4**	**2**	X	**1**	**1**		**1**								**1**		2			17	po	2?	
Javesella pellucida (F.)	**5**	**9**	X	**12**	**26**	**26**	**7**	**4**	**15**	**16**	**3**	X	**1**	**2**	1	**2**	X	X		**11**	X	**10**	X	**6**		156	po	2	
Laodelphax striatella (Fall.)		X	1																			1				2	o1	2	
Macrosteles cristatus (Rib.)					1																		2			3	po	2	
Macrosteles laevis (Rib.)	19	20		15	8		3		4	7	8	8	7							**4**					1	104	po	2	
Macrosteles quadripunctulatus (Kbm.)																	1									1	po?	2	3
Macrosteles sexnotatus (Fall.)	22	23		1	**54**	1	22	13	3	7	7	22	1				10			2					15	203	po	2	
Macrosteles viridigriseus (Edw.)		4					22	X	X			1	**168**	2										2		197	o1?	2	
Psammotettix alienus (Dhlb.)	2	8		2	3	X	5				3	9		1	X		X	1			3	2	1			40	o1	2	
Psammotettix confinis (Dhlb.)	5	50	**32**	**44**	**14**	**28**		**4**	58	**40**	**4**		**24**	**282**	**143**	2	32	**67**	**70**	**136**	**839**	12	**5**			1591	o1	2	
Eurytopic species																													
Anoscopus serratulae (F.)	X	X	X	X	X	**1**	X	X	X	X				X	2	2	X						X	X		5	o1	1	
Arthaldeus pascuellus (Fall.)	52	10	**29**	**28**	**17**	**3**	**3**	**11**	21	**4**	**21**	**5**	**66**	**20**	**39**	**34**	**2**	**234**	**11**	**5**	**1**	**18**	**5**	**6**	X	645	o1	2	
Deltocephalus pulicaris (Fall.)	4	11	**31**	**16**	**11**	**26**	**3**	**2**	192	**38**	2	X	**30**	6	**15**	X	X	**334**	**33**	143	**19**			**2**		918	o1	2	
Dicranotropis hamata (Boh.)																1										1	o1	2	
Errastunus ocellaris (Fall.)	**47**	1	**20**	**19**	**48**	**87**	**17**	**18**	85	**8**	**34**	**3**	**23**	**148**	**178**	**11**	**90**	**83**	**212**	**90**	**21**	**8**	**61**	**50**	X	1362	o1	2	
Euscelis incisus (Kbm.)	**4**	7	1	1	X			X	2	12	3			18	20				40	1	1		**48**	3		161	o2	2	
Javesella dubia (Kbm.)												2					1									3	o1	2	
Philaenus spumarius (L.)									1	1			1										3	**18**		24	po	1	
Streptanus aemulans (Kbm.)	X	X		X	1		X				X	X		X		1	**1**	2		2	2	**1**	**4**	**3**		17	o1	2?	
Oligotopic species																													
Agallia brachyptera (Boh.)						X	X	X																X		X	o2?	1	
Aphrodes bicincta (Schrk.)														**3**	**3**						2					8	o1?	1	
Aphrodes makarovi Zachv.				1									X			**3**							X	1		5	po	1	
Anaceratagallia ribauti (Oss.)		X		X			1			X										X			**4**			5	o2?	1	
Anoscopus albifrons (L.)																	1				6					7	o1	1	
Anoscopus flavostriatus (Don.)					X	X	X	2	X	X		X	X			**1**		X			X	**1**		**4**	X	8	o1	1	
Artianus interstitialis (Germ.)	**1**		X	1		**2**		1	1					**6**	**2**		2	1	**4**		16	1	**1**			39	o1	1	
Athysanus argentarius Metc.														1		X	1				1	1				4	o1	1	
Balclutha punctata (F.)				1		2															4	2				9	o1	1	
Chlorita paolii (Oss.)					3									**46**	1				36		1		1			88	o1	2	
Cicadella viridis (L.)								1																		1	po	1	
Cicadula quadrinotata (F.)					1		5	X			1	X		2	7	**429**	**20**	29	2		1			**9**	4	510	o1?	2	
Criomorphus albomarginatus Curt.															X											X	o2?	1	
Dikraneura variata Hardy															X											X	o1	2?	
Doratura homophyla (Fl.)		**1**			1					**3**				**52**	**20**	X	**26**		**111**	**65**	87					366	o1	2	
Doratura stylata (Boh.)														7	**9**			2	**48**			1				67	o1?	1	
Elymana sulphurella (Zett.)																							**2**			2	o1	1	
Eupteryx atropunctata (Goeze)	1	1											8										1			11	po	2	
Eupteryx notata Curt.											1			**3**	X				1							5	o2	2	
Eupteryx vittata (L.)							1	X			X	X												**4**	**1**	6	o2	2	
Eurybregma nigrolineata Scott														X		1							X			1	o1	1	
Graphocraerus ventralis (Fall.)														X	1	**3**					5		**4**			13	o1	1	
Jassargus pseudocellaris (Fl.)								1		2			1	**6**	**59**	**3**			1				**10**			83	o1	2	
Javesella obscurella (Boh.)		X					1					X	13					**9**								23	o1?	2	
Limotettix striola (Fall.)							1	1					**1**					1								4	o1	2	
Mocuellus collinus (Boh.)		4															4	1			95		9			113	o1	2	
Neophilaenus lineatus (L.)									1							4	3									8	po	1	
Neophilaenus minor (Kbm.)					1														4		9					14	o1	1	V
Notus flavipennis (Zett.)					1	1	11					**52**					7						1	7	**523**	603	o1?	2	
Psammotettix helvolus (Kbm.)										10				2					5							17	o1	2	
Psammotettix kolosvarensis (Mats.)	1	**4**	**25**	**9**		6		X	1	1				**6**	**1**	X	**69**	**45**		139	9	**1**		1		318	o1	2	3

Table 2 (*Continued*)

Treatment site no.	HIGs					LIMs							LIPs								F					Total	Host specificity	Voltinism	Status
	1	2	9	10	21	4	5	6	8	12	24	25	11	13	14	15	17	18	19	20	16	3	23	7	22				
Psammotettix nodosus (Rib.)										3																3	o1	2	
Psammotettix sabulicola (Curt.)																			8							8	o1?	2	2
Streptanus marginatus (Kbm.)																			1							1	o1	1	
Streptanus sordidus (Zett.)			1	X		X	1	X	X		4	X	**5**					**11**								22	o1	2	
Turrutus socialis (Fl.)					1					3			1						71				1			77	o1	2	
Stenotopic species																													
Acanthodelphax denticauda (Boh.)																								1		1	m1	2	3
Acanthodelphax spinosa (Fieb.)															8											8	m2	2	
Arocephalus punctum (Fl.)															X				26							26	m2?	2	
Balclutha rhenana W.Wg.												X					2							X		2	m1	1	
Cicadula flori (J. Shlb.)																									**65**	65	m2	2	V
Cicadula persimilis (Edw.)																										X	m1	2	
Cosmotettix costalis (Fall.)																							X			X	m2	1	2
Delphacinus mesomelas (Boh.)														**3**	**5**	1										9	m2	1?	
Euconomelus lepidus (Boh.)							X			1								1								2	m2?	1	3
Eupelix cuspidata (F.)														1	X						X					1	m1?	0.5	
Eupteryx calcarata Oss.	7																									7	m1?	2	
Kelisia sabulicola W.Wg.														**17**	**1**				**41**		8					67	m1	1	3
Kosswigianella exigua (Boh.)														40	**24**				**77**							141	m1	2	
Megamelus notula (Germ.)	1																								**14**	15	m2	1?	
Metalimnus formosus (Boh.)																									**26**	26	m2	1	2
Mocuellus metrius (Fl.)			X	1			2	2	X		8	1	**2**				**9**	11	1					**5**	**1**	43	m1	2?	
Mocydiopsis parvicauda Rib.														3	**9**											12	m1	1	
Muellerianella brevipennis (Boh.)	1		1	1					2														1	**3**		9	m1	1	
Muellerianella fairmairei (Perr.)																						7				7	m2	2?	D
Paluda flaveola (Boh.)																2	1							**4**		7	m2?	1	
Paraliburnia adela (Fl.)																		X								X	m1	1	3
Psammotettix excisus (Mats.)					1														17		18					36	m1?	2	3
Rhopalopyx preyssleri (H.-S.)						X								X	X	**15**										15	m1	1	
Rhopalopyx vitripennis (Fl.)					9					**8**				8	3				44		1	6	7			86	m1	2	3
Rhytistylus proceps (Kbm.)																					X					X	m1?	1	3
Ribautodelphax albostriata (Fieb.)					1	X									2					1						4	m1	2	
Ribautodelphax angulosa (Rib.)															4				8							12	m1	2	1
Ribautodelphax collina (Boh.)										1				3	**11**			2			26	11				54	m1	2	
Stenocranus major (Kbm.)											1						2	4	1							8	m1	1	
Stenocranus minutus (F.)		1																								1	m2	1	
Stroggylocephalus agrestis (Fall.)							2					1													**4**	7	m2?	1	V
Xanthodelphax straminea (Stal)									1	1				**6**	**9**			3								20	m2	1	3
Zygina hyperici (H.-S.)															3						2		3			8	m1	2	
Not determinated to species level																													
Deltocephalinae—juveniles	1		2		6	5	50		2	6	17	34	3	2	7		28	7	113	65		1	6			355			
Delphacidae—juveniles							3	1					12	1		1	1	1	8							28			
Ribautodelphax—females			1												7											8			
Ribautodelphax—juveniles															20											20			
Macrosteles—females			3	19	36	4			10	8	16	15	94					3	1		1				6	216			
Macrosteles—juveniles	7	4		13	13		1		6	7	6	2	50					2								111			
Psammotettix—females										38									29							67			
Psammotettix—juveniles	6	7	6							8									37							64			
Number of individuals	24	14	22	44	87	13	63	9	29	90	72	78	172	97	127	34	60	52	422	86	72	28	40	20	138	1893			
Number of recorded species	18	21	13	20	22	18	23	21	20	23	17	19	19	32	34	21	24	22	25	13	29	16	27	21	13	88			
Number of resident species	13	16	9	13	13	14	18	17	15	17	13	16	12	29	29	16	18	17	20	11	22	9	20	18	10	80			

[a] Numbers are given for sweep net samples in 1999 only. X: recorded in suction samples in 2000 only, bold: recorded both in sweepnet and suction samples. Host plant specificity: m1: 1st degree monophagous (on one plant species), m2: 2nd degree monophagous (on one plant genus), o1: 1st degree oligophagous (on one plant family), o2: 2nd degree oligophagous (on two plant families or up to four plant genera belonging to up to four families), po: polyphagous. Red Data Book of Germany (after Remane et al., 1998)—1: critical, 2: endangered, 3: vulnerable, V: near threatened, D: data deficient (categories adapted to the IUCN criteria). HIGs: high-intensity grassland; LIMs: low-intensity meadows; LIPs: low-intensity pastures; F: fallows; status: conservation status.

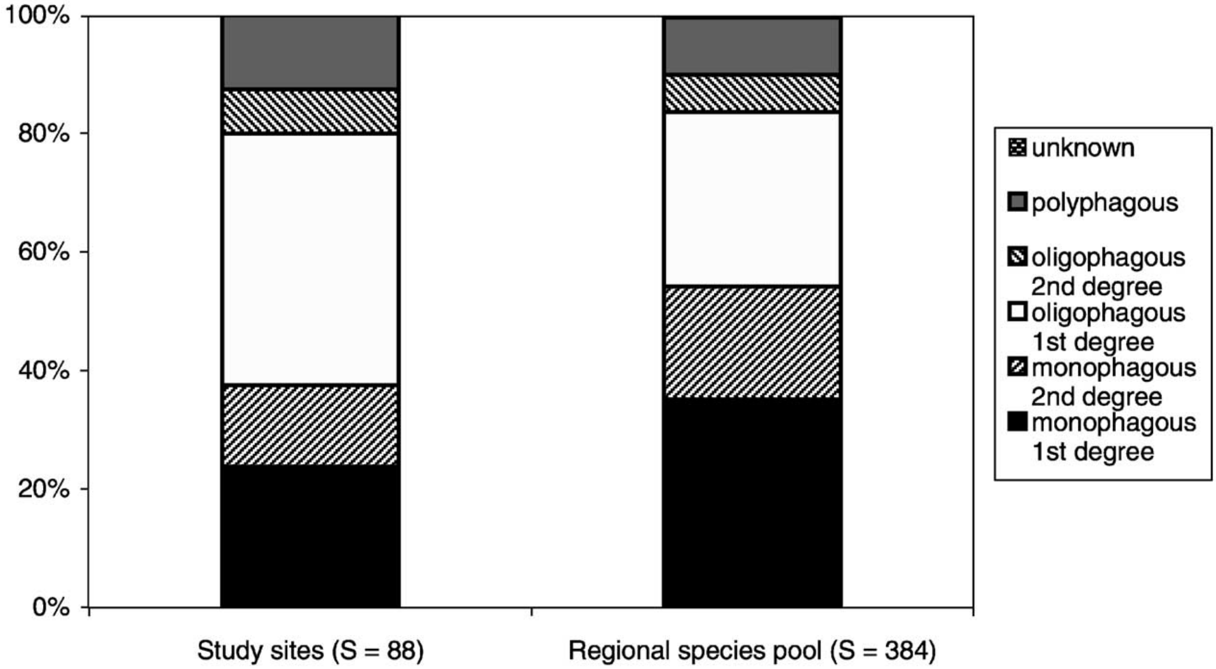

Fig. 2. Diet width of the Auchenorrhyncha species of the study sites and the regional pool.

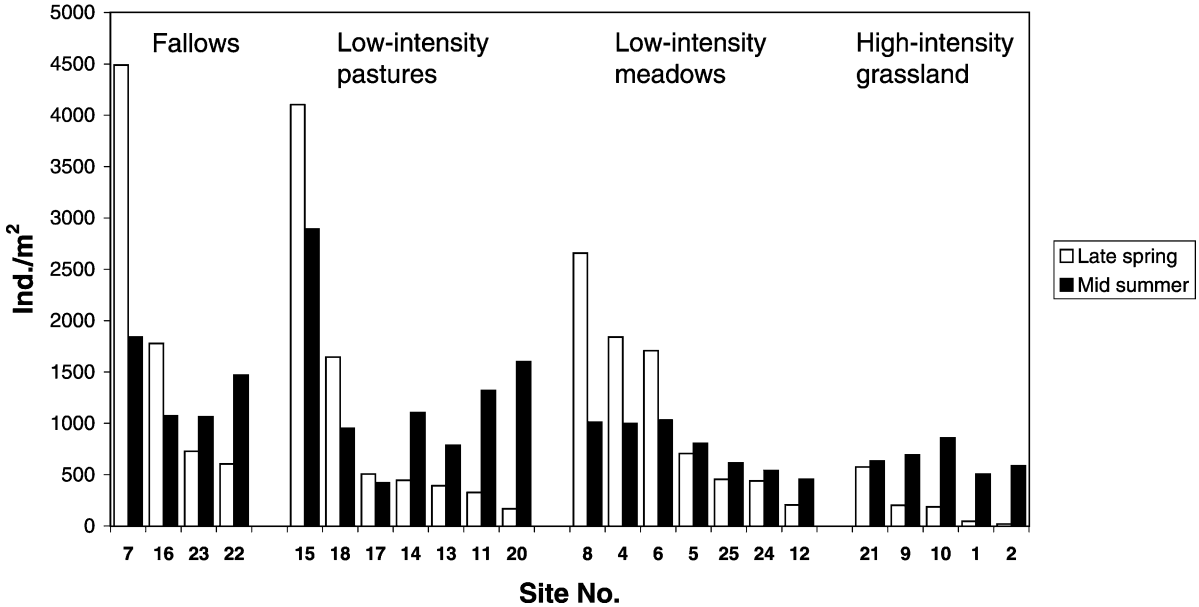

Fig. 3. Total suction sample catches of Auchenorrhyncha in study sites of the Elbe flood plains in 2000.

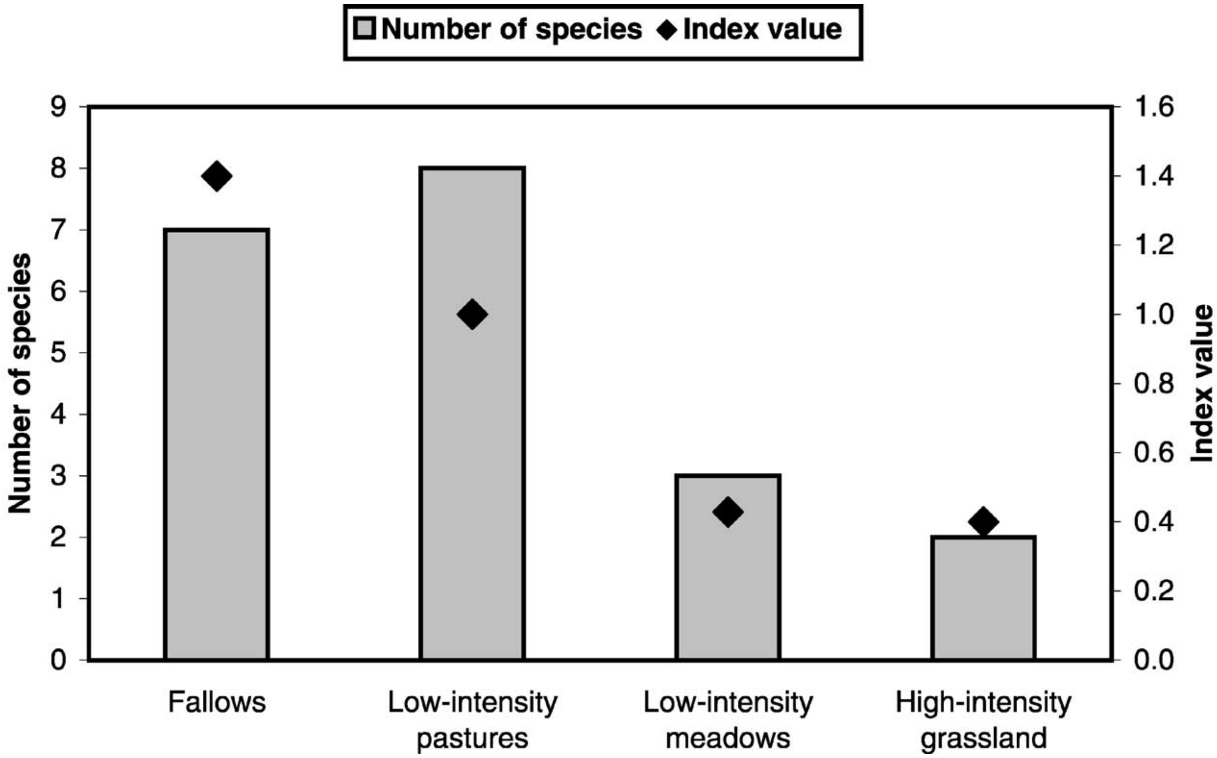

Fig. 4. Distribution of threatened species (categories 1, 2, 3, R, after Remane et al., 1998). Index value = number of species divided by the number of sites.

in fallow sites (F) show marked differences in moisture requirements. Moderately dry sites are dominated by xerophilous species, e.g. *Ribautodelphax collina* (Boh.), whereas sedge-dwelling species, like *N. flavipennis* (Zett.), *Cicadula* spp. and *Metalimnus formosus* (Boh.) are common on wet sites.

A comparison of the distribution of threatened species shows marked differences between the treatments (Fig. 4). Highest index values were found in F (=1.4) and LIP sites (=1.0); index values were lower in LIM and HIG sites (=0.4, respectively). Highest species numbers were found in LIP (eight species) and F sites (seven species). LIM and HIG sites harboured only three and two species, respectively.

The DCA (Fig. 5) reveals a dense cluster of both HIGs and LIMs. This indicates a strong and equalizing effect of a mowing regime comprising two cuts or more a year. However, there are a few exceptions: sites no. 11 and 20 are both LIP. The former is a deep depression close to the river bank being subject to most inundations among all sites, the latter was subject to heavy trampling by cattle. Site no. 3, situated in close vicinity to HIG and LIM sites, is a young fallow on a former field on highly fertile soil. Site no. 5, which is the only LIM outside the cluster, is situated in a meadow depression, where mowing depth was reduced for technical reasons. All other sites are widely scattered, suggesting that low-intensity grazing and fallowing offers a high potential for sustaining local biodiversity.

3.3. Life strategies

Achtziger and Nickel (1997) proposed a classification scheme of grassland Auchenorrhyncha species based upon their life strategies (Table 3). Accordingly, there are four groups showing distinct combinations of ecological traits and differential response to treatments.

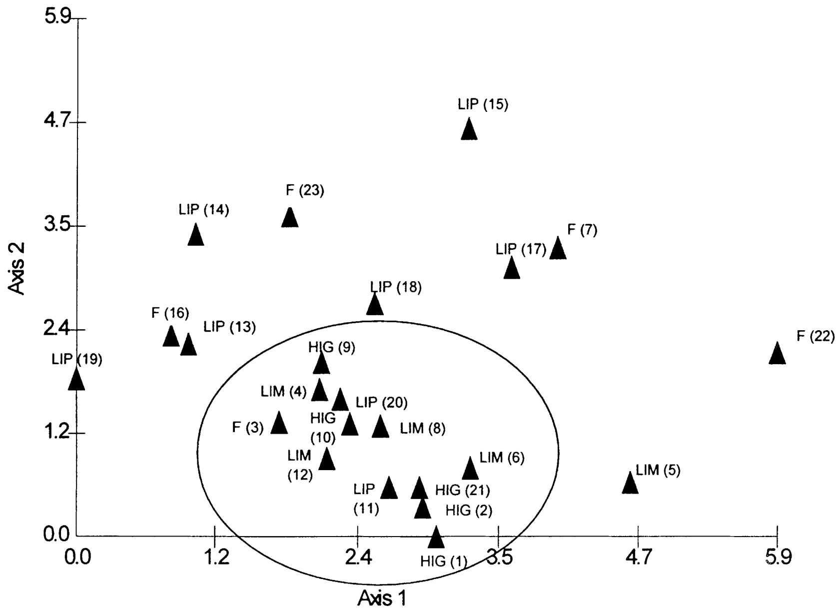

Fig. 5. DCA of Auchenorrhyncha communities (sweepnet samples 1999) (explained variance of the ordination = 38.2; axis 1 = 18.3, eigenvalue = 0.67; axis 2 = 9.1, eigenvalue = 0.3).

(i) Pioneer species are macropterous and highly mobile, often dominating in aerial catches (see della Giustina and Balasse, 1999; Waloff, 1973) although populations of *Laodelphax striatella* (Fall.) and *Javesella pellucida* (F.) in more stable habitats may occasionally comprise some brachypterous individuals. Early successional stages are usually colonized within one season, but influx of individuals is noted in all terrestrial habitats, although breeding may not be successful. All species are bivoltine in central Europe, perhaps locally even trivoltine. Most species are polyphagous; those which are oligophagus usually feed on a broad range of grasses.

(ii) Eurytopic species are widespread and common in various types of grass-dominated habitats. They occupy a wide range of moisture conditions and tolerate disturbance by mowing and grazing. Most species are bivoltine and oligophagous, feeding on grasses. Flight ability tends to be reduced, but new habitats are colonized within some years due to large population sizes along

Table 3
Auchenorrhyncha life strategies in central European grasslands

Life strategy trait	Generalists		Specialists	
	Pioneer species	Eurytopic species	Oligotopic species	Stenotopic species
Habitat preference	Mainly in early successional stages	Eurytopic in various types of grasslands	Associated with specific abiotic conditions	Associated with specific abiotic conditions
Wing length and dispersal	Always long-winged; permanent influx into most terrestrial habitats	Long- or short-winged, flight activity moderate	Long- or short-winged, flight activity moderate	Mostly short-winged; low flight activity
Host plant specialization	Usually polyphagous	Usually oligophagous on Poaceae	Usually oligophagous	1st or 2nd degree monophagous
Voltinism	At least bivoltine	Mostly bivoltine	Uni- or bivoltine	Uni- or bivoltine

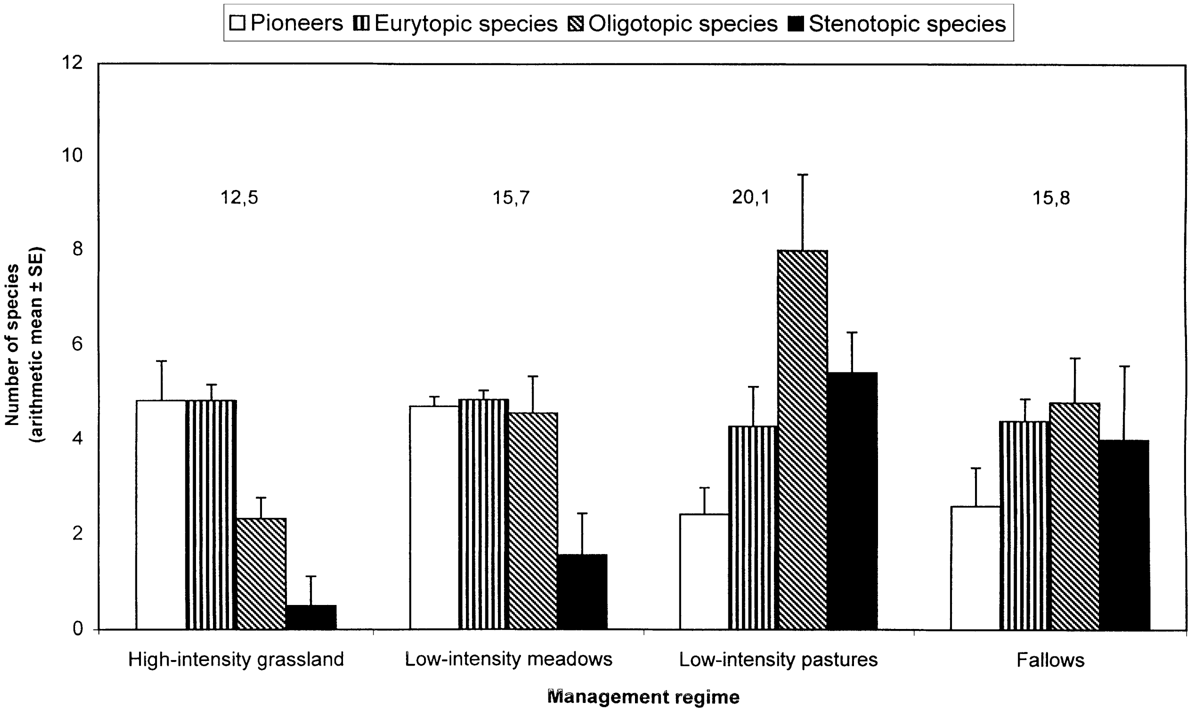

Fig. 6. Numbers of Auchenorrhyncha species under different management regimes. Numbers above grouped columns indicate the total sums of columns.

roadsides, field margins and ditches all over central European lowlands.

(iii) Oligotopic species are also widespread and show similar traits of life history, but they are restricted to a narrower range of abiotic conditions, like moisture, nutrient contents or vegetation height. Their tolerance towards disturbance by mowing, grazing and fertilizing is reduced. Flight ability is also reduced, but new habitats may be colonized within some years, depending on location and densities of the nearest resident populations. Univoltine species prevail.

(iv) Stenotopic species also occupy a narrow range of abiotic conditions, but in addition, they show a close association with certain host species or genera, i.e. they are 1st or 2nd degree monophagous. Due to specific requirements of their host plants, their distribution may be rather localized and confined to certain geological, hydrological or microclimatic features, e.g. limestone regions, valley bottoms or forest margins.

The two former groups are referred to here as generalists, the two latter as specialists. We used this scheme for characterizing the communities found in the Elbe valley. Considering the number of generalist species, differences between the four treatments are slight. However, specialists clearly favoured LIPs and fallows, with only small numbers in high-intensity sites and LIMs (Fig. 6). Interestingly, a further reduction of disturbance on the fallow sites, which are mown at most after several years, did not lead to a further increase of numbers of species and specialists. Instead, numbers declined compared to LIPs.

4. Discussion

4.1. Time scale

There is a general need for distinction between short-term and long-term effects of grassland management. Removal of plant biomass by mowing and grazing is usually followed by an immediate decrease of individual numbers of most taxa living above-ground (Curry, 1994). On the other hand, the management regime has long-termed effects on the structure and composition of the vegetation by excluding some plant species and promoting others, thus strongly affecting host availability and habitat conditions of phytophagous insects. Furthermore, management prevents immigration of shrubs and trees which would eventually lead to succession and tree cover. It should also be noted that most studies on grassland management were run over a period of a few years only. Thus, long-term developments were out of their scope.

4.2. Management intensity

Conventional grassland management aims at increasing the net primary production, which can only be achieved by a combination of increased use of fertilizers and removal of plant biomass by mowing or grazing. In turn, this is usually correlated with a decrease of diversity of plant species and architecture, and consequently, with a reduction of faunal diversity (see Curry, 1994). Responses of Auchenorrhyncha species numbers to an increased management intensity are also negative, although the effects of fertilizing and removal of plant material could not be disentangled (e.g. Andrzejewska, 1991; Remane, 1958). Considering species groups favouring different life strategies in Bavarian grasslands, Achtziger and Nickel (1997) and Achtziger et al. (1999) found that effects on generalist species numbers were insignificant. Specialists, however, were almost absent from high-intensity sites, but common and diverse in unfertilized meadows mown only once a year. Pioneer species, like *J. pellucida* (F.) and *Macrosteles laevis* (Rib.), have been repeatedly reported to show a strong increase of population densities in HIGs and other disturbed habitats (Andrzejewska, 1979; Novotný, 1994b).

Our data show differences in species numbers and proportions of specialists between high-intensity sites (HIG) on the one hand and low-intensity pastures (LIPs) and fallows (F) on the other hand. However, these differences were less pronounced between high-intensity treatments (HIGs) and low-intensity meadows (LIMs). These results indicate a rather severe impact of the mowing regime, even in unfertilized sites, which may lead to a long-term exclusion of a number of stenotopic Auchenorrhyncha species. Moreover, such grasslands may constitute sinks for large numbers of ovipositing individuals on dispersal flight, the offspring of which will die after the next cut. It is also noteworthy, that the proportion of stenotopic species in the study sites is lower than among the total regional fauna of grassland Auchenorrhyncha (see Fig. 2), providing further evidence for the selection of generalists by disturbance in managed flood plain grassland.

4.3. Effects of fertilizing

Short-term effects of mineral fertilizers on Auchenorrhyncha were studied in a Polish meadow dominated by *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl and C. Presl, *Dactylis glomerata* L., *Poa pratensis* L., and *Festuca rubra* L. (Andrzejewska, 1976). After 3 years, differences between treated and control plots were only slight in Auchenorrhyncha biomass, but marked in community structure. In the fertilized plots, generalists, like *J. pellucida* (F.), *M. laevis* (Rib.), and *Streptanus aemulans* (Kbm.), had increased. Most specialists, however, e.g. *Acanthodelphax spinosa* (Fieb.), *Ribautodelphax albostriata* (Fieb.), *Rhopalopyx preyssleri* (H.-S.), and *Athysanus argentarius* Metc. remained confined to the untreated plots or had a much higher emergence rate there.

Other short-term field experiments were made by Sedlacek et al. (1988) and Prestidge (1982), both revealing higher population densities after a few years of fertilizing, but without discussing the life strategies of species and the composition of communities. From a study of Auchenorrhyncha communities on the grass *Holcus lanatus* L., the latter author concluded that both increased food quality and plant architecture were the main factors. However, all species found by him (see also Prestidge and McNeill, 1983) were generalists. *Ribautodelphax angulosa* (Rib.) was the only exception and remains enigmatic, since it was later shown to be strictly monophagous on *Anthoxanthum odoratum* L. (den Bieman, 1987). We did not find sufficient information to classify the species found by Sedlacek et al. (1988) in Ohio, although all those which are common to Europe and North America were eurytopic or oligotopic, but none was stenotopic.

Long-term effects of nitrogen fertilizing and liming were studied by Morris (1992) at Park Grass, Rothamsted (England). Neglecting species found in less than four individuals, the communities on treated plots comprised only pioneer, eurytopic and oligotopic species as well as *C. persimilis* (Edw.), which was the only stenotopic species. Species richness and total abundance were lower on plots receiving nitrogen.

Among our study plots, only the HIG sites were conventionally treated with mineral fertilizers and liquid manure. All remaining treatments received nutrients exclusively by flooding. Our design allows only a comparison of HIG and LIM sites, both of which are mown twice a year. The LIM sites show almost identical groups of generalists, but higher numbers of specialists. However, these differences are not significant, and variation is high. Achtziger and Nickel (1997) found similar results on more homogeneous study sites, with significant differences of numbers of oligotopic and stenotopic species between fertilized and unfertilized sites. Thus, there is increasing evidence for negative long-term effects of fertilizing on Auchenorrhyncha diversity, and for positive effects on the abundance of generalists.

Curry (1994) concluded that the effects of fertilizing on grassland invertebrates are mainly a consequence of vegetational changes, i.e. increased net primary production, but reduced species number, notably in dicotyledons, combined with stronger dominance of some grasses. Reduction of Auchenorrhyncha diversity can be explained by the decrease of plant species numbers and the simplification of the vegetation structure.

4.4. Effects of grazing and mowing

Like mowing, intensive grazing reduces the complexity of the vegetation structure, which in turn affects arthropod habitat conditions. For instance, spider communities in British grasslands on peat soils were twice as diverse when sheep grazing was excluded (Cherrett, 1964). On the other hand, selective feeding, trampling, and dung production have additional effects by creating patches of different microhabitats. In contrast, mowing is less selective than grazing and leads to a lower heterogeneity of structures. Negative effects are mainly due to the sudden and almost complete removal of above-ground plant biomass, which is combined with a reduction of food plants, eggs, substrates for oviposition and a dramatic change of microclimatic conditions. Insects are particularly affected when mowing takes place during sensitive phases of development (Curry, 1994).

In our study sites, Auchenorrhyncha diversity was low both in HIG sites and in LIMs, indicating a severe negative influence of mowing, particularly on specialists. Adverse effects on Auchenorrhyncha as well as on Heteroptera were also found by Morris (1981a) and Morris and Lakhani (1979), particularly if mowing had been performed twice a year or in mid-summer only. Auchenorrhyncha communities of sites no. 11 and 20 showed a close similarity to HIG and LIM sites (Fig. 5), which can be explained by unusual high disturbance due to flooding and trampling by cattle in these sites. This indicates that strong disturbance effects of mowing, flooding, grazing and trampling may be rather similar in selecting a few generalist species, and that some meadow-dwelling Auchenorrhyncha may originate from natural flood plain grasslands.

We found a number of species being confined to fallows and LIPs, e.g. *Eurybregma nigrolineata* Scott, *R. collina* (Boh.), *Graphocraerus ventralis* (Fall.), *A. argentarius* Metc., and *Jassargus pseudocellaris* (Fl.). In some cases, the lack of Auchenorrhyncha species on mown sites can be easily explained by the lack of their host plants. For instance, *Zygina hyperici* (H.-S.), a leafhopper obligatorily associated with *H. perforatum* L., is absent from meadows all over central Europe, but commonly breeds in fallows and pastures, where its host plant is usually avoided by grazing animals. Thus, regular mowing causes a long-term exclusion of some species by eliminating favoured hosts. Decrease of less specific feeders can be explained by the simplification of plant architecture combined with frequent disturbance. This is probably also true for a number of *Carex*-dwelling species, like *Kelisia* spp., *Cicadula flori* (J. Shlb.), *M. formosus* (Boh.), and *C. costalis* (Fall.). However, some of these species have been recorded in unfertilized meadows of the foothills of the Alps, which are subject to a single autumn cut (Nickel, unpublished data).

In fertilized meadows in Poland with three cuts a year, individual numbers of Auchenorrhyncha declined dramatically after each cut, but recovered immediately due to survival, immigration, and emergence of the next generation. In these intensively managed sites, pioneer and eurytopic species, like *M. laevis* (Rib.), *J. pellucida* (F.), und *S. aemulans* (Kbm.), strongly dominated (Andrzejewska, 1979). We cannot demonstrate these numerical responses in our study, because of only two sampling intervals per year. But high densities of pioneer and eurytopic species in some of our sites suggest a dependance of populations on influx from surrounding habitats.

In a study on the effects of sheep grazing, Morris (1973) found significantly higher abundances of six Auchenorrhyncha species in intensively grazed sites, notably of *Anaceratagallia venosa* (Geoffr.), *Aphrodes bicincta* (Schrk.), *Arocephalus punctum* (Fl.), *R. proceps* (Kbm.), and *Eupteryx notata* Curt., whereas *Arboridia parvula* (Boh.) showed a negative response. *Stenocranus minutus* (F.), *A. flavostriatus* (Don.), and *S. aemulans* (Kbm.) were almost completely absent from grazed plots. Further species, especially those preferring tall grassland, were less abundant, but negative effects of grazing were more pronounced, when treatment was performed in autumn or winter compared to spring or summer. Effects on species of Heteroptera were not significant, although four species of grass bugs (Miridae: Stenodemini) occurred exclusively in ungrazed sites, and maximum species numbers were found on the ungrazed plots.

In our study sites, LIPs showed considerably higher species numbers of Auchenorrhyncha compared to LIMs, indicating that effects of moderate grazing (cattle densities about one livestock unit per hectare) are less severe than effects of two cuts a year. This response is even more pronounced than cessation of management, which leads to fallows often dominated by monospecific stands of tall grasses or sedges, e.g. *P. arundinacea* L. or *Carex acuta* L. Lower species numbers in fallows were also found in Bavaria in a comparison to LIMs (Achtziger et al., 1999). In contrast to our study sites, however, these meadows were mown only once a year in autumn. Maximum species diversity at intermediate disturbance levels have been observed in many ecological systems (e.g. Connell, 1978; see also Huston, 1994; Wilkinson, 1999).

We conclude that the impact of two cuts in late spring and summer on the Auchenorrhyncha fauna is rather severe, because numbers of species and, in particular, of specialists are reduced. On the other hand, grazing at low intensity offers considerable potential for higher species numbers, since cattle or sheep avoid patches harbouring less palatable plants, which may enhance diversity of plant species and architecture.

4.5. Flooding and moisture preferences

Inundations are significant constraints for the management regime in river floodplains. Mowing and grazing can take place only relatively late in the year, and cattle densities have to be kept low due to the vulnerability of the turf to trampling. Furthermore, flooding probably has a strong effect on insect communities and, hence, may blur differences between treatments.

At least 18 central European Auchenorrhyncha species are associated with habitats being subject to strong fluctuations of the water table, which may imply an ability to survive inundations (Nickel and Achtziger, 1999). In our study sites, we found evidence for further species, which showed high nymphal densities in May on plots flooded during winter and spring, e.g. *A. brachyptera* (Boh.), *A. flavostriatus* (Don.), *D. pulicaris* (Fall.), *Streptanus sordidus* (Zett.), *E. ocellaris* (Fall.), and *A. pascuellus* (Fall.). Well-designed field and laboratory experiments are needed to clarify the tolerance and requirements towards moisture and flooding in these species.

From alpine river banks, which are subject to dramatic and frequent flooding incidents, it is known that Auchenorrhyncha communities are highly adapted to river dynamics, being characterized by a high proportion of host specialists, monovoltine species and European or even Alpine endemics (Nickel, 1999). In these species, heavy population losses, which must be compensated, frequently occur due to translocation of gravel banks.

4.6. Incongruence of botanical and zoological conservation priorities

Although floristic as well as faunistic diversity is high in many nature reserves, priority sites for conservation are not necessarily identical. Most Auchenorrhyncha, including host specialists and threatened species, live on common and widespread plants rich in biomass (Nickel, 2003). On a regional scale, faunal diversity has been found to be mainly correlated with habitat diversity and small-scale disturbance (see Rosenzweig, 1995).

In our study region, the priority sites for threatened plants, i.e. flood plain meadows with *C. dubium* (Schkuhr) Thell., *L. palustris* L., and others, were clearly different from those for threatened Auchenorrhyncha. These were mainly grazed and fallow sites with only low relevance for plant conservation. Extended grazing would promote vegetation complexes dominated by *Elymus repens* (L.) Gould and other tall grasses as well as a decline of established meadow plant communities, notably the 'Cnidion meadows'. Possible implications of such an extension of grazing on animal communities include (i) an increase of specific dwellers of tall grasses and *Elymus* specialists among Auchenorrhyncha, and (ii) new or enlarged habitats for grassland songbirds, e.g. *Alauda arvensis* (L.) (Skylark) and *Saxicola rubetra* (L.) (Whinchat). Therefore, maintaining maximum local biodiversity in grasslands requires different management regimes, including grazing at low intensity and fallowing, in order to balance issues of animal and plant conservation.

5. Conclusions

(i) The study of grassland Auchenorrhyncha can provide a useful tool for demonstrating biotic conditions of the habitat. Suction sampling produces exact figures of species numbers and abundance, whereas sweepnet samples are biased towards species of higher vegetation layers. Resident species can be recognised if nymphs are present.

(ii) Short-term effects of most grassland treatments, like mowing, grazing, fertilizing and trampling, result in a decrease of individual numbers of most Auchenorrhyncha species. Populations of a few pioneer and generalist species are capable of a rapid recovery. Long-term effects include the maintenance of plant species composition and prevention of tree growth, but also a permanent exclusion of specialists, if disturbance occurs too frequently.

(iii) Although mineral fertilizing may lead to an increase in individual numbers of generalists, its main effect is a decrease in species numbers of specialists. The underlying mechanisms are not fully understood.

(iv) Mowing and grazing at low intensity may maintain maximum diversity of Auchenorrhyncha species. However, there is increasing evidence for severe negative long-term effects of two or more cuts a year and cutting in early or mid-summer. Grazing at low intensity offers a high potential for conservation, because selective feeding, trampling, dung production, and avoidance of less palatable plants creates a diverse patchwork of microhabitats. In these patches, insect species favouring taller vegetation can permanently survive. At high-intensity, grazing (like mowing) seriously reduces insect diversity and, in particular, species numbers of specialists.

(v) Fallows may act as refuges for grassland species, which do not tolerate conventional management regimes. This is particularly true for intensively utilized regions.

(vi) We suggest that total species numbers as well as the proportion and abundance of specialists, which are all negatively correlated with management intensity, may be used as robust parameters for the indication of favourable habitat conditions in grasslands. Conversely, communities showing a high proportion and abundance of pioneer species indicate severe disturbance. Their stability is often reduced as they are subject to strong fluctuations.

(vii) Management regimes aiming at zoological and botanical conservation priorities are not necessarily identical. On a regional scale, different regimes should be employed for maintaining maximum biodiversity.

(viii) The study of Auchenorrhyncha communities is complicated by the relatively high effort required for determination, e.g. compared to grasshoppers and birds. Moreover, strong overlaying effects on communities may occur in river flood plains, because their responses to mowing, fertilizing, and flooding are principally similar and are difficult to disentangle in field experiments.

(ix) Community dynamics in river flood plains may include significant population shifts between flooded and non-flooded areas. A number of species, however, can tolerate flooding events in situ.

(x) Quantitative indicative values, like in some freshwater groups, are difficult to calculate for Auchenorrhyncha, because the overall data base is too weak. Thus, a macroecological approach is needed to study whether local patterns are robust.

(xi) In general, causal relations between management measures and community patterns of invertebrates are not yet fully understood. Although much research has been done on responses of communities and single species to treatment, little is known of the implications on meso-scale population dynamics in cultivated landscapes. More information is also needed on the effects of flooding.

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