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SPECIES RICHNESS, BIOMASS PRODUCTION AND RECENT VEGETATION CHANGES OF ESTONIAN FLOODPLAIN GRASSLANDS

ABSTRACT: We studied vegetation diversity and standing biomass in relation to site moisture (moist, wet) and different management regimes (regularly mown (A), recently abandoned (B), un-mown for at least 15 years but with mowing re-introduced recently (C), and abandoned for at least 15 years without re-introduction of mowing (D)) on floodplain grasslands in Soomaa National Park, SW Estonia.

A flexible quadrate size (area inhabited by 500 ramets) was used for the estimation of life-form distribution, species richness, ramet density and weight of standing biomass. The size of the actual species pool (S_{pool}) was also estimated and relative richness (S_{rel500}), mean plant unit area (*PUA*), plant unit biomass (*PUB*), ramet density per square metre and standing dry biomass per square metre were calculated. Additionally, changes in Estonian floodplain grassland vegetation between the 1960s and the 1990s were analysed by comparing the life-form distribution of frequent species on floodplain grasslands in the 1960s and 1990s.

Life-form distribution depended both on moisture conditions and on the management regime. Tussock-forming graminoids dominated in regularly mown moist sites and long-term unmown wet sites, while mat-forming graminoids dominated in sites with irregular management. The proportion of herb ramets was highest in unmanaged moist sites without regular mowing. In general, the life-form composition of floodplain grassland flora has shifted from low-growing herbaceous plants to tall-growing herbaceous plants during the abandonment period (from 1960s to 1990s).

The effect of site moisture on the standing biomass-species richness relation and *PUA* was not significant, but the effect of the management regime was notable. *PUA* varied tenfold (mean 2.6 cm^2 at moist sites with the management regime B but was 25.2 cm^2 at un-managed wet sites). Dry standing biomass varied threefold depending on the management regime (from 263 to 763 g m^{-2}). Ramet density, *PUA*, *PUB*, S_{pool}, and life-form distribution on plots with recently re-introduced mowing (regime C) differed significantly from those of plots with regime D but did not differ from regularly mown plots (regime A).

Management cessation led to a change in life-form distribution. Dominance of certain life-forms depended on site moisture but the most obvious change was the increase of vegetation height.

KEY WORDS: biomass-species richness relation, hydrology, life-forms, management relation, restoration, scale-independent quadrate size

1. INTRODUCTION

High species diversity and density are considered the most valuable properties of semi-natural grasslands. According to the model of Grace (1999), the species richness is controlled by multiple factors, e.g. disturbance, total community biomass, colonization, the species pool and spatial heterogeneity. From these multiple factors, most attention has been paid to the community biomass-species richness relation (refs. in Cornwell and Grubb 2003). The well-known 'hump-backed' model (Al-Mufti *et al.* 1977, Grime 1973, 1979) describes this relation most evidently, and it is also confirmed for different grassland communities in Estonia (Zobel and Liira 1997). However, wetland vegetation seems to be an exception, as was shown by Wheeler and Shaw (1991) for fens. One possible explanation for this is the high share of other factors controlling species diversity and density. It has been emphasized that wetland vegetation and species richness is affected by gradients in hydrology, pH and nutrient availability (Day *et al.* 1988, Wheeler and Shaw 1991), from which the moisture gradient is considered to be the most important in floodplains (Prach 1992).

Beside these abiotic ecological factors, site history and management have a significant impact on floodplain grassland communities, which have been developed in equilibrium with human influence over hundreds of years. In Estonia, they can be regarded as the oldest man impacted vegetation type (Pork 1964). Nevertheless, abandonment in the last half a century initiated a change in the grassland species composition (Pork 1981). This succession starts immediately after cessation of mowing, but the range and speed of change varies in time (Falinska 1991). First, the original species composition remains the same but frequency and abundance values of plant species begin to change. Further, total change in plant species composition can occur over time (about 15 years; Falinska 1995, Jensen and Schrautzer 1999). Today, most floodplain grasslands in Estonia are in different stages of post-management vegetation succession (Paal *et al.* 1998).

Restoration for the protection of floodplain grassland communities has been provided mainly on nature conservation areas in Estonia. The practice most often applied is mowing and removing the hay from cut areas for restoring suitable light conditions. Bush cutting and burning have also been applied occasionally on grasslands with long periods of abandonment (Lotman 1997).

In the present paper, we analyze the effects of hydrology and management on vegetation structure, standing biomass, species richness and life-form distribution of floodplain grasslands. Furthermore, the biomass-species richness relation was investigated using a scale-independent approach. Similar to some earlier studies (Grassle and Maciolek 1992, Philips *et al.* 1994, Zobel and Liira 1997), we counted species for a fixed number of plant ramets, instead for a fixed area. We also studied small-scale richness relative to the size of the actual species pool (after Pärtel *et al.* 1996).

To analyze long-term vegetation changes after abandonment, we compared records of floodplain grassland flora from the 1960s (Krall *et al.* 1973), when most floodplain grasslands were regularly mown, with the end of the 1990s (Mägi and Lutsar 2001) when floodplain grasslands were mostly abandoned.

In particular, we examine the following specific questions:

1. How is vegetation structure, standing biomass, species richness and life-form distribution of Estonian floodplain grasslands affected by management and hydrology?

2. Does the biomass-species richness relation resemble the hump-back model even if a scale-independent approach is used?

3. What major vegetation changes have taken place in Estonian floodplain grasslands during the last 40 years?

4. What conclusions can be drawn from our results concerning the conservation and restoration of floodplain grasslands?

2. STUDY AREA

We analysed species richness and biomass production of floodplain grassland vegetation in relation to moisture conditions, management history and mowing regime in the Soomaa National Park in South-western Estonia (58°26'N; 25°4'E). Big bog massifs, divided by streams and tributaries with extensive and periodic spring flooding, sometimes additional in summer or winter are typical for this area. A high variety of floodplain grassland communities has developed under different

Table 1. Sampled communities – location (South-west Estonia), plant community type, moisture conditions and management regime.

Locality name and site no.	Geographical coordinates	Plant community type*	Moisture conditions**	Management regime***
Tõramaa 1	58°25'50"N 25°2'8"E	Wet floodplain grassland	Wet	A
Tõramaa 2	58°25'50"N 25°2'9"E	Moist floodplain grassland	Moist	D
Mulgi 1	58°27'5"N 25°6'15"E	Moist floodplain grassland	Moist	A
Mulgi 2	58°27'6"N 25°6'12"E	Wet floodplain grassland	Wet	A
Halliste 1	58°27'33"N 4°59'9"E	Moist floodplain grassland	Moist	C
Halliste 2	58°27'28"N 4°59'3"E	Moist floodplain grassland	Moist	D
Halliste 3	58°27'25"N °58'53"E	Wet floodplain grassland	Wet	D
Karukose 1	58°27'10"N 5°1'26"E	Moist floodplain grassland	Moist	B
Karukose 2	58°27'8'N 25°1'26"E	Wet floodplain grassland	Wet	B
Kuusekäära 1	58°26'26"N 25°6'4"E	Moist floodplain grassland	Moist	C
Kuusekäära 2	58°26'29"N 5°6'14"E	Wet floodplain grassland	Wet	C

* Plant community types are given after Paal (1997).
** Moisture and flooding conditions are characterized after Truus and Tõnisson (1995). Wet – regularly flooded, well drained; Moist – poorly drained to saturated.
*** Management regime: A – regularly mown; B – regularly mown, recently abandoned; C – un-mown over 15 years; mowing reintroduced recently; D – unmown over 15 years.

site conditions (from occasionally flooded and well drained to permanently inundated) and different management regimes (from regularly mown to abandoned). Today, there are about 20 floodplain grasslands with a total area of 2000 ha in Soomaa (Suurkask 1999).

We studied five wet and six moist floodplain grasslands, according the classification given by Paal (1997) (Table 1). The mean soil moisture content on a fine summer day (June 26th 2002) was 41.9%±5.3 for moist and 53.4%±9.5 for wet floodplain grasslands. The studied grasslands differed in management history, which we classified as regularly mown (A), recently abandoned (B), unmown for at least 15 years but recently with re-introduced mowing (C), and abandoned for at least 15 years without re-introduction of mowing (D). Characteristic species are *Deschampsia cespitosa* (L.) P. Beauv., *Carex cespitosa* L., *Calamagrostis stricta* (Timm) Koeler for the wet and *Deschampsia cespitosa*, *Festuca rubra* L., *Filipendula ulmaria* (L.) Maxim. for the moist community type.

3. MATERIAL AND METHODS

3.1. Aboveground biomass-species richness relation and life-form distribution

At each of the 11 floodplain grasslands, species richness was analyzed and standing biomass harvested from five randomly positioned quadrates, inhabited by 500 vascular plant ramets (flexible size). Altogether 55 quadrates with 26 000 ramets were counted. Zobel and Liira (1997) described the sampling procedure in detail. The reason for the selection of the flexible quadrate size was the high patchiness and diverse height of the floodplain grassland vegetation. It seemed to be especially important for a comparison of the two communities differing in moisture conditions. Sampled quadrate sizes varied from 725 to 9 900 cm^2.

The area of every 500 ramet quadrate was carefully measured following the methodology of Zobel and Liira (1997). After completing the floristic inventory of plots, standing biomass of vascular plants was harvested. Biomass samples were sorted by species and the number of ramets of every species was counted to estimate the proportion of species of different life-forms (tussock and mat-forming graminoids, herbs; morphological classification after Leht 1999). Biomass samples were air-dried (48 h at 65°C) and weighed. For convenience, standing biomass is expressed on a square metre basis.

Furthermore, relative richness was calculated as:

$$S_{rel500} = S_{pool}/S_{500}. \quad (1)$$

where S_{pool} *sensu* Pärtel *et al.* (1996) is actual species pool that was estimated by recording all plant species occurring around each quadrate on a topographically and ecologically homogenous continuous patch. S_{500} is the number of species on a flexible size quadrate inhabited by 500 plant ramets.

For each quadrate, mean plant unit area (*PUA*) which is the area occupied by a single plant ramet, calculated as:

$$PUA = \text{Area of quadrate with 500 ramets}/500\ (cm^2) \quad (2)$$

Plant unit biomass (*PUB*) which is the dry biomass of single plant ramet, calculated as:

$$PUB = \text{Biomass of 500 ramets}/500\ (g). \quad (3)$$

3.2. Changes of floodplain vegetation between the 1960s and the 1990s

We compared floristic data of Estonian floodplain grasslands from the 1960s (1950s to 1970s), and the end of 1990s. These two periods differ largely in relation to management. In the 1960s almost all river floodplains were regularly mown for hay. Afterwards, many grasslands were abandoned and at the end of the 1990s most were un-mown. We took floristic data from Krall *et al.* (1973) to describe the earlier situation. These data contain species lists of approximately 850 floodplains with frequencies of 387 species, aggregated into seven frequency classes. Because of the high species number (about 1/3 of the total Estonian vascular plant flora) we only analysed species from two frequency classes: (a) most frequent (*FQQ*) – species with 75–100% frequency in samples and (b) frequent (*FQ*) – species with 50–75% frequency in samples. *FQQ* contained 27 species or 7% of the species number and *FQ* contained 49 species or 20% of the species number. The data from the end of the 1990s were taken from Mägi and Lutsar (2001). The data set contained 236 herbaceous plant species with 25 491 records from Estonian floodplain grasslands. For comparison with the 76 *FQQ* and *FQ* species of the 1960s data set, the most frequent species were selected from the 1990s data. We analysed the life-form distribution: low (0.1–0.6 m) and tall-growing (0.8–1.5 m) tussock- and mat-forming graminoids and herbs, as well as climbers with weak, support-needing stems (morphological classification after Leht 1999).

Furthermore, we calculated mean Ellenberg Indicator Values (*EIV*; Ellenberg *et al.* 1991) and the height distribution in the 1960s and the 1990s for *FQQ* and *FQ* species with the aim to clarify major changes in the requirements of plants during the period of abandonment.

3.3. Statistical analyses

Life-form distribution, plant unit area, biomass and species richness relation on moisture and management regimes were analyzed using one-way ANOVA procedures, which were followed by post-hoc tests (Tukey's honest significance difference test for unequal n). All statistical analyses were carried out using the package STATISTICA for Windows (2nd Edition1995). Tests were considered significant at $P < 0.05$.

4. RESULTS

The mean sampled area, standing biomass, species richness and proportion of species of different life-forms of moist and wet floodplain grasslands are presented in Tables 2–4. Herbs were most abundant in moist sites without regular mowing (management regimes B, C and D). Tussock-forming graminoids dominated in regularly mown sites (regime A) and long-term un-mown sites (regime D) while mat-forming graminoids dominated in sites with irregular management (regimes B and C). The proportion of herb ramets was highest in unmanaged moist sites without regular mowing and tussock-forming graminoids in managed sites.

ANOVA results revealed that biomass per square metre was neither significantly affected by moisture conditions (F = 1.22, P = 0.27) nor by management regime (F = 2.63, P = 0.06). Standing biomass per 500 ramets did not differ between moisture classes (F = 0.41, P = 0.53), but was significantly affected by management regime (F = 7.91, P = 0.00). Mean dry standing biomass values were the lowest on regularly mown wet sites (263±108 g m^{-2}) and highest in unmanaged moist communities (763±627.5 g m^{-2}; Table 2).

Plant unit area (*PUA*) (formula 2) significantly increased and ramet density decreased if mowing ceased for 15 years (Tables 3 and 4). The lowest *PUA* was found at moist sites with management regime B, whereas this parameter was tenfold higher at wet sites which had been abandoned for more than 15 years (25.2±17.7; Table 2). On sites where mowing was re-introduced, these parameters were much more similar to those on regularly mown sites than to sites with long-term abandonment. Moisture conditions did not significantly affect *PUA*.

The actual species pool (S_{pool}) was significantly higher (P <0.05) in moist (46±13.1) than in wet sites (33±6.2). Furthermore, it differed significantly between management regimes (F = 7.05, P <0.01, Tables 3 and 4). Here, the actual species pool continuously decreased from management regime A to management regime D.

Species richness per 500 ramets (S_{500}) and relative richness per 500 ramets (S_{rel500}) (formula 1) did not differ between moisture conditions, but were significantly affected by management regime (Table 2–4).

Species richness per square metre was highest at intermediate standing biomass levels (app. 300 g m^{-2}, Fig. 2A). The shape of the graph thus resembled the classical 'humped' shape of this relation although variability was quite large. Species richness per 500 ramets (S_{500}) was highest at lowest standing biomass per flexible quadrate (area of 500 ramets; Fig. 2B). The trend of decreasing species richness with increasing biomass was higher on wet (R^2 = 0.695) than on moist sites (R^2 = 0.178), with P <0.05 in both cases.

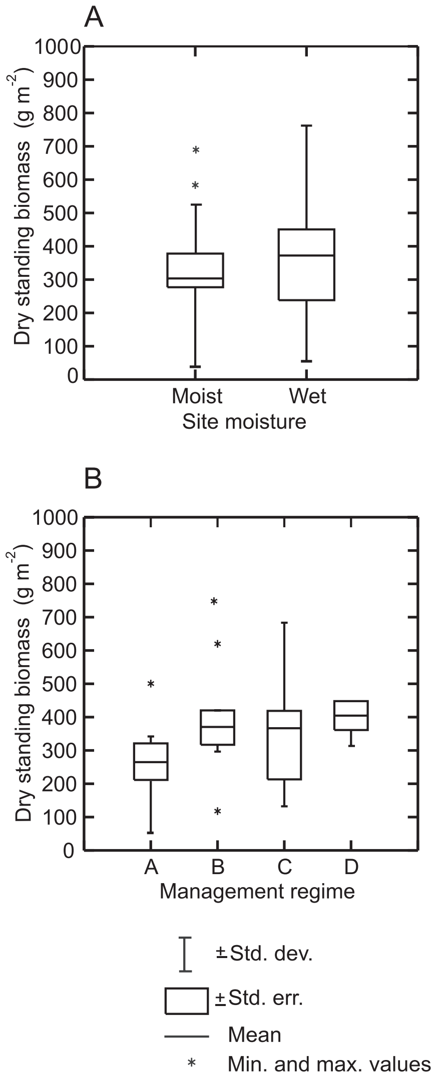

Fig. 1. Dry weight of standing biomass per 500 ramets by site moisture (A) and management regime (B). Management classes denote: A – regularly mown, B – regularly mown but recently abandoned, C – unmown over 15 years, mowing recently re-introduced, D – unmown over 15 years.

We found a slight increase in the proportion of mat-forming graminoids instead of

Table 2. Ramet density, area, standing biomass, size of actual species pool and species richness in the sampled communities and proportion of species of certain life form recorded in the sampling quadrats (flexible quadrats of 500 ramets). Numbers are means with standard errors (in parentheses).

Moisture and management regime (as in Table1)	Ramet density (ramets m^{-2})	Plant unit area *PUA* (cm^2)*	Area of quadrat including 500 ramets (m^2)	Dry standing biomass ($g\ m^{-2}$)	Actual species pool (S_{pool})	Species richness per 500 ramets (S_{500})	Relative richness per 500 ramets (S_{rel500})**	Proportion of species (% of ramets in life form)		
								Tussock-forming graminoids	Mat-forming graminoids	Herbs
Wet; A	2321 (845)	5.5 (2.76)	0.276 (0.134)	263 (108.0)	37	23 (3.6)	0.671 (0.108)	49 (19.3)	33 (25.7)	18 (16.1)
Wet; B	1012 (247)	10.4 (2.80)	0.520 (0.140)	516 (165.9)	31	12 (8.6)	0.400 (0.277)	27 (32.6)	67 (16.7)	6 (12.1)
Wet; C	2142 (1983)	7.5 (4.60)	0.378 (0.231)	452 (398.7)	40	18 (2.0)	0.450 (0.050)	19 (14.8)	66 (12.7)	15 (6.2)
Wet; D	708 (665)	25.2 (17.7)	1.258 (0.883)	447 (86.4)	16	5 (4.1)	0.375 (0.258)	82 (8.7)	1 (1.6)	17 (9.4)
Moist; A	3468 (1751)	3.4 (1.56)	0.174 (0.080)	572 (692.3)	57	24 (10.2)	0.425 (0.178)	59 (22.9)	25 (15.1)	16 (9.9)
Moist; B	5024 (2179)	2.6 (1.85)	0.321 (0.067)	333 (167.5)	69	20 (2.1)	0.588 (0.062)	24 (28.7)	34 (18.5)	43 (11.2)
Moist; C	3194 (1174)	5.3 (1.71)	0.397 (0.605)	380 (178.2)	36	17 (2.4)	0.489 (0.069)	33 (3.7)	44 (14.1)	24 (12.6)
Moist; D	745 (175)	17.0 (6.35)	0.815 (0.309)	763 (627.5)	41	13 (6.1)	0.326 (0.151)	25 (23.2)	31 (32.1)	44 (53.7)

* formula 2
** formula 1

Table 3. Mean variables of plant ramets with standard errors (in parentheses) according to moisture conditions with results of one-way ANOVA.

Variable	Moisture conditions (see Table 1)		ANOVA results	
	Wet	Moist	F	*P*
Ramet density (ramets m^{-2})	1700 (1260) [a]	2210 (1980) [a]	1.23	0.273
PUA (cm^2)	10.8 (10.9) [a]	9.0 (8.2) [a]	0.36	0.55
Area $_{500\ ramets}$ (m^2)	0.52 (0.54) [a]	0.46 (0.43) [a]	0.36	0.55
PUB (g)	0.5 (0.59) [a]	0.8 (2.03) [a]	0.41	0.53
S_{pool}	33 [a]	46 [b]	12.75	0.001
S_{500}	16 (8.1) [a]	19 (8.3) [a]	0.906	0.346
S_{rel500}	0.5 (0.22) [a]	0.4 (0.15) [a]	2.577	0.114
Tussock-forming graminoids (%)	42 (14.1) [a]	37 (15.2) [b]	8.072	0.006
Mat-forming graminoids (%)	44 (20.3) [a]	29 (12.5) [a]	0.101	0.752
Herbs (%)	14 (6.5) [a]	33 (17.0) [b]	19.641	0.000

Notes: Abbreviations of variables see Table 2. Mean values with different superscript letters are significantly different on the basis of pairwise comparison with Tukey's test.
PUA – formula 2; PUB – formula 3, S_{rel500} – formula 1.

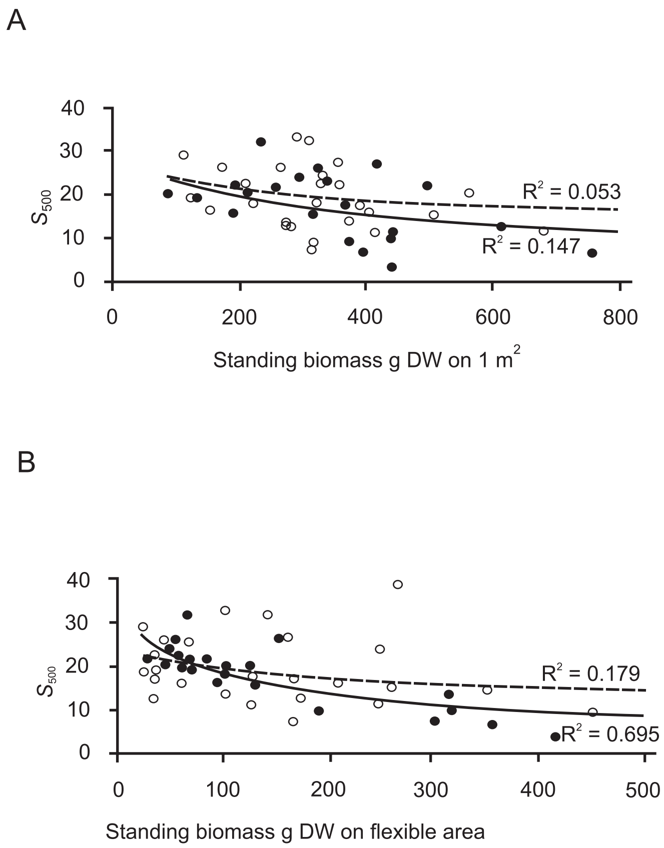

Fig. 2. Richness (i.e number of species) per 500 ramets (S_{500}) plotted against standing biomass on 1 m^2 (A), and against flexible area which is the area inhabited by 500 ramets (B). Open symbols denote moist sites and filled symbols wet sites. Trendline for moist sites is dotted and for wet sites continous.

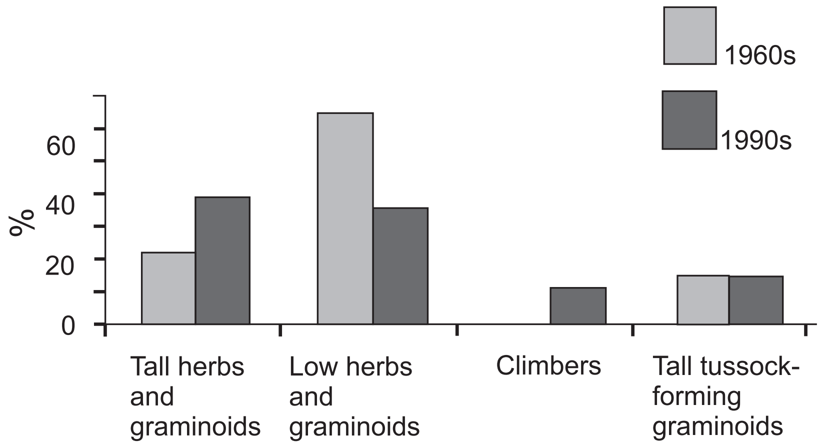

Fig. 3. Share (%) in number of species of most frequent species – 75–100% of samples (*FQQ*) of Estonian floodplain grasslands in the 1960s and at the end of the 1990s by different growth-forms.

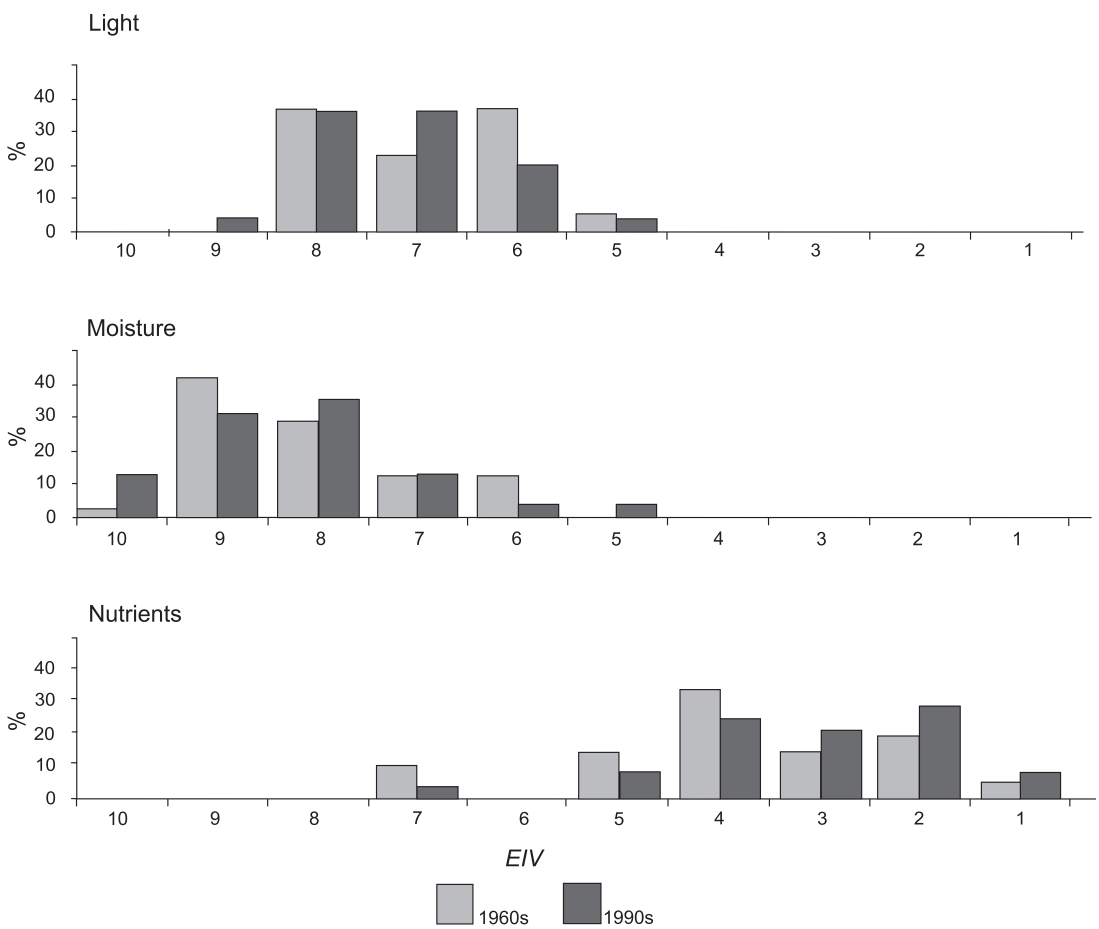

Fig. 4. Share (%) in number of species of most frequent species – 75–100% of samples (*FQQ*) of Estonian floodplain grasslands in the 1960s and at the end of the 1990s by Ellenberg Indicator Values (*EIV*) for light, moisture and nutrients.

Table 4. Mean variables of plant ramets with standard errors (in parentheses) according to management regime with results of one-way ANOVA.

Variable	Management regime (see Table 1)				ANOVA results	
	A	B	C	D	*F*	*P*
Ramet density (ramets m^{-2})	2700 (1340) ^{a}	1520 (1040) ^{a}	2360 (2130) $^{a e}$	590 (480) $^{b f}$	4.47	0.007
PUA (cm^2)	4.8 (3.07) $^{a c e}$	8.4 (3.44) $^{a c e}$	7.1 (3.84) $^{a c e}$	24.9 (13.85) $^{b d f}$	21.317	0.000
$Area_{500\ ramets}$ (m^2)	0.240 (0.15) $^{a c e}$	0.420 (0.17) $^{a c e}$	0.540 (0.54) $^{a c e}$	1.2450 (0.69) $^{b d f}$	2.331	0.000
PUB (g)	0.1 (0.12) $^{a c e}$	0.4 (0.23) $^{a c e}$	0.2 (0.14) $^{a c e}$	2.5 (3.12) $^{b d f}$	7.919	0.000
S_{pool}	46 $^{a c e}$	50 $^{a c e}$	37 $^{a d e}$	29 $^{b d f}$	7.048	0.000
S_{500}	23 (6.2) $^{a c f}$	21 (10.6) $^{a c e}$	16 (3.9) $^{b c e}$	9 (6.7) $^{b d f}$	10.374	0.000
S_{rel500}	0.57 (0.20) $^{a c f}$	0.41 (0.20) $^{a c e}$	0.45 (0.12) $^{b c e}$	0.33 (0.22 $^{b d f}$	10.374	0.000
Tussock-forming graminoids (%)	52 (10.4) $^{a d e}$	44 (27.9) $^{b c f}$	36 (14.7) $^{a d e}$	55 (28.9) $^{a d e}$	5.255	0.003
Mat-forming graminoids (%)	30.10 (11.97) $^{a d e}$	50.55 (17.45) $^{b c f}$	40.70 (10.01) $^{a d e}$	6.12 (5.46) $^{b d f}$	14.246	0.000
Herbs (%)	17 (2.3) $^{a c e}$	24 (19.5) $^{a c e}$	23 (4.7) $^{a c e}$	39 (23.9) $^{b c f}$	4.534	0.007

Notes: Abbreviations of variables see Table 2. Mean values with different superscript letters are significantly different on the basis of pairwise comparison with Tukey's test.
PUA – formula 2; PUB – formula 3, S_{rel500} – formula 1.

Table 5. Proportion of life-forms (%) of most frequent (*FQQ*) – 75–100% of samples and frequent (*FQ*) (50–75%) species in Estonian floodplain grasslands flora in 1960s and 1990s.

Life forms	*FQQ*		*FQ*	
	1960s	1990s	1960s	1990s
Herbs	66	71	66	70
Mat-forming graminoids	21	18	25	25
Tussock-forming graminoids	13	11	9	5

Table 6. Mean Ellenberg Indicator Values (*EIV*) for light, moisture and nutrient availability (Ellenberg *et al.* 1991) of most frequent (*FQQ*) – 75–100% of samples and frequent (*FQ*) (50–75%) species in Estonian floodplain grasslands flora in 1960s and 1990s.

Parameter	*FQQ*		*FQ*	
	1960s	1990s	1960s	1990s
EIV for light	7.0	6.7	7.0	7.0
EIV for moisture	7.5	6.9	7.4	6.5
EIV for nutrient availability	3.5	4.9	4.4	4.6

tussock-forming graminoids in a comparison of floodplain flora from the 1960s and 1990s (Table 5). The most obvious difference in the distribution of life-forms in floodplain floras of the 1960s and the 1990s was a higher percentage of tall-growing herbs and graminoids as well as climbers in the 1990s (Fig. 3). The mean Ellenberg Indicator Value (*EIV*) for light did not change, showing the dominance of grassland species in both periods (Table 6). However, *EIV* for nutrient availability increased for *FQQ* species ($P = 0.05$) and *EIV* for moisture decreased for *FQ* species ($P < 0.05$) from the 1960s to the 1990s.

5. DISCUSSION

5.1. Effects of hydrology and management regime on the vegetation of floodplain grasslands

We found that biomass and species richness were not affected by moisture conditions. This is not in accordance with previous data (Prach 1992, Touzard *et al.* 2002). One reason for this discrepancy might be the use of flexible quadrates considering plant size instead of a fixed area, and ramet number instead of traditional cover estimations. Another reason could be that we compared only two plant community types by moisture conditions. In wet site flood is usually more persistent than in moist site, and soil is longer saturated with water. Unfortunately, the difference was not important in our measurements in midsummer.

Management regimes significantly affected biomass, species diversity and ramet density. Surprisingly, Touzard *et al.* (2002) did not find significant differences in species richness and diversity of floodplain grasslands differing in their period of abandonment. Nevertheless, Falinska (1991, 1995) also found a decrease in species richness during succession.

5.2. Relation between aboveground biomass and species richness

Vegetation communities in wetlands usually have a spatially patchy structure with patches of different size (Wheeler and Shaw 1991), which yields problems in describing the community structure. On wet grasslands, the variation of hydrology, pH and nutrient availability is accompanied by different types of management, or management cessation at different times. We assumed that the 'hump-backed' relation that was recorded for other grassland types in Estonia (Zobel and Liira 1997) was not valid for floodplain grasslands as a consequence of these highly variable ecological conditions. However, our data proved the 'hump-backed' relation between standing biomass and species richness, if biomass was calculated per square metre (Fig. 2A). If species richness was plotted against standing biomass per 500 ramets it revealed a continuous decrease of richness with increasing biomass. This is supported by many other authors (e.g. Moore and Keddy 1989, Tilman and Pacala 1993).

5.3. Succession of floodplain grassland flora after abandonment

Falinska (1991, 1995) used long-term studies to describe the succession of floodplain grasslands after management cessation. For Estonian floodplain grasslands, there is no such systematic long-term study, but some permanent-plot studies of shorter duration have been carried out. Comparison of species richness and cover data from 1982, when sites were managed, and in 1996 after nine years of abandonment, was carried out on permanent plots along a transect crossing the Kasari floodplain in Western Estonia (Truus 1998). A non-significant decrease in species number and change in species composition was observed. The most evident influence of abandonment was litter accumulation. In some plots, litter mass exceeded standing biomass threefold.

We tried to reveal a general trend in Estonian floodplain grassland flora for 1960s to 1990s when grasslands succeeded to abandonment. We noted the dominance of tall plant species (Fig. 3), which was also underlined by Falinska (1991). We also found some changes in the proportion of species with different Ellenberg Indicator Values (*EIV*). During the period from the 1960s to1990s, the mean *EIV* for nutrient availability for most frequent species (75–100% in samples) changed from 3.5 to 4.9. For less frequent species (50–75% in samples) *EIV* for moisture changed from 7.4 to 6.5 (Table 6). This suggests that the wet site species were suppressed by abandonment. Pork (1981) mentioned the change in plant species synecological amplitudes after abandonment of grasslands: species typical for wet sites shift to dryer conditions and vice versa.

5.4. Consequences for restoration and conclusions

One of our main findings is that a substantial decrease in species richness on long-term abandoned floodplain grasslands is inevitable. This decrease is probably mainly a consequence of increasing light competition and the build-up of dense litter layers as many small-growing grassland species are either out-competed by strong competitors, such as *Filipendula ulmaria* or *Carex cespitosa,* during succession or germination and establishment is inhibited by the presence of litter layers (see also Truus 1998, Jensen and Meyer 2001, Jensen and Gutekunst 2003). Wagner *et al.* (2003) discussed the possibilities for restoration of species richness on long-term abandoned floodplain grasslands. They concluded that restoration of grasslands with a short history of biodiversity degradation is much more effective than of grasslands that have been abandoned for a long time. Re-introducing management, either mowing or/and grazing, does not create species-rich communities in a short time. It is independent of the potential for species richness: like a rich soil seed bank as in an extensive floodplain area in Bialowieża, Poland (Falinska 1999), or via plant propagules transported by floodwater, as in Soomaa, Estonia (Wagner *et al.* 2003). However, re-introduction of management changes the main features of vegetation, including ramet density, *PUA*, *PUB*, and the proportion of life-forms (Table 4), so that grasslands where management was recently re-introduced are similar to those with regular management.

Additionally, floodplain grassland plant communities usually have no such complicated structures as other types of seminatural grasslands (Pork 1964). This difference between floodplain grasslands in comparison with other grassland types, analysed by Zobel and Liira (1997), was also revealed by our study. Therefore, maintenance of remaining species richness is preferential (Wagner *et al.* 2003), although initiating the process of diversity development is also important.

As claimed earlier (Falinska 1991), vegetation starts to change immediately after management cessation. Our study showed that the proportion of herb species starts to increase in the first years after management cessation, and the introduction of mowing increases the proportion of sprout-forming graminoids on moist sites. There is no such clear correlation between management regime and life-form distribution on wet sites. The share of mat-forming graminoids increases on recently abandoned wet sites. Regularly mown and long-term unmanaged sites are characterized by dominance of tussock-forming graminoids. On managed sites tussocks are formed by the grass *Deschampsia cespitosa*, and on unmanaged sites by species forming huge tussocks, namely *Carex cespitosa*. It seems that the role of dominant species is more important on wet grasslands that on other grassland types.

The vegetation of floodplain grasslands is diverse and variable, due to environmental and management variations. Our study shows some coinciding and some contradicted results for biomass-species richness relations with moisture and management conditions on floodplain grasslands in comparison with other studies. This shows that such relations need further discussion.

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