Competition as a factor structuring species zonation in riparian fens – a transplantation experiment

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Abstract
Question: What is the relative importance of competition and physical factors in restricting the occurrence of different fen species to certain zones of the riparian landscape?
Location: Biebrza National Park, NE Poland.
Methods: We carried out a two-season reciprocal transplantation experiment: sod-blocks were replaced between a low-productive groundwater-fed small-sedge fen and a high-productive fluviogenous tall-sedge fen. Five treatments were applied to the transplanted sods: (1) no manipulation; (2) fertilization with NPK to exclude the effect of nutrient limitation; (3) clipping vegetation around the transplant to exclude competition for light; (4) clipping + fertilizing; (5) sods were also transplanted within their own environment.
Results: After two seasons, the small-sedge sods transplanted into the high-productive zone had a biomass two times lower than that of the control transplants, mainly due to a decrease in small sedges and bryophytes. Tall sedges of the high-productive zone did not respond significantly to transplantation in the low-productive zone. Removal of the surrounding vegetation largely enhanced the growth of small sedges and bryophytes and, to a lesser degree, of tall sedges. Fertilization, on the other hand, resulted in increased growth of tall sedges, grasses and non-graminoid herbs.
Conclusion: Species characteristic of low-productive fen communities are competitively excluded from the high-productive zone through light competition. In contrast, the performance of tall sedges in the low-productive zone is lowered by nutrient limitation. In the long run this may lead to a complete disappearance of these species from this zone. We did not find evidence that the physical stress of flooding has a direct effect on the performance and distribution of species. Results from the experiment suggest that productivity gradients and their influence on competition intensity are of primary importance for structuring vegetation patterns in lowland riparian fens.

Keywords: Biebrza; Biomass; Gradient; Light availability; Productivity; Sedge; Shoot:Root Ratio; Vegetation removal.

Abbreviations: RGR = Relative Growth Rate; SRR = Shoot : Root Ratio

Nomenclature: Names of vegetation types follow Pałczyński (1984), species names follow Mirek et al. (1997).

Introduction

It has long been recognized that competition may limit the occurrence of species to only a part of the habitats that are potentially appropriate (Ellenberg 1952, 1954; Mueller-Dombois & Ellenberg 1974; Austin & Austin 1980). However, little is still known about the relative importance of competition for structuring zonation patterns in habitats such as wetlands where other limitations may play an important role, especially physical stress (Grace & Wetzel 1981; Emery et al. 2001; Kotowski & van Diggelen 2004).

Most of the studies on competition neglect the role of non-resource factors (Emery et al. 2001) and focus on the effects of productivity on the relative intensity of above-ground and below-ground competition. Whereas general agreement exists about the central role of competition for light in nutrient-rich environments (Grime 1979; Tilman 1988), the importance of competition at the unproductive end of the gradient has always been more controversial (e.g. Grime 1979; Tilman 1988; Goldberg & Novoplansky 1997; Aerts 1999).

Recently, various authors analysed the background of these controversies and suggested that they were caused by neglecting the additional effects of gradients in non-resource factors (Emery et al. 2001) and generalizations over various types of ecosystems (Craine 2005) or species functional types (Fynn et al. 2005). Indeed, most of the classical competition studies were carried out in physically moderate habitats (mesic grasslands, old fields), which might restrict their use for interpreting patterns in more harsh habitats. When gradients in resources coincide with gradients in stress factors, disentangling the effects of competition from responses to physical factors is a key issue for understanding vegetation zonation (Wisheu 1998). Zonation patterns can be a product of (1) a segregation of species according to their competitive hierarchy (Keddy 1989; Grace & Wetzel 1981; Wisheu & Keddy

1992); (2) distinct (physiological) preferences of species for certain habitats, resulting from past competition and speciation (Karez & Chapman 1998) or (3) interaction between species responses to both physical and resource gradients (Emery et al. 2001).

In freshwater wetlands, Grace & Wetzel (1981) showed that competition from *Typha latifolia* is the main factor limiting the occurrence of *T. angustifolia* in shallower water, thus causing the zonation of these two species. On the other hand, Shipley et al. (1991) found evidence that distinct preferences rather than competition lead to the zonation of three species (*Carex crinita*, *Acorus calamus*, and *Typha angustifolia*) in a riverine marsh. Lenssen et al. (1999, 2003) analysed plant zonation along a freshwater shoreline gradient and concluded that species composition is controlled by flooding intensity in the low elevation zone and by interspecific competition at higher elevations.

Species occurrence in salt marshes is highly related to salinity and moisture gradients (Rogel et al 2000). Salinity- and anoxia-tolerant species are outcompeted in higher elevated, less harsh sites and therefore limited to sites with a lower productivity and a higher level of environmental stress (e.g. Lubchenco 1980; Hacker & Bertness 1999; Bockelmann & Neuhaus 1999; van der Wal et al. 2000; but see Karez & Chapman 1998). However, the lower-elevation species become competitively superior all over the gradient after nutrient enrichment (Emery et al. 2001), suggesting interaction between stress and competition.

To our knowledge, similar analyses are lacking for riparian fen ecosystems. Nutrient availability in lowland fens is strongly controlled by the hydrological regime through aeration of the soils and associated nutrient release from organic matter (e.g. Kulczyński 1949; Succow 1988; Wassen et al. 1990; de Mars & Wassen 1999). The zone near the river, normally occupied by reed and tall sedges, is the most productive, due to high water level fluctuations and the input of nutrient-rich surface water. The productivity declines gradually with distance from the river. Farther from the river the groundwater level remains constantly high with little fluctuation throughout the year and the vegetation is dominated by small-sedge species and brown mosses (Kotowski & van Diggelen 2004). Unlike other wetland types, the entire gradient is characterised by anoxic soil conditions for most of the year, whereas the level of disturbance and flooding stress is positively correlated with productivity.

The low-productive small-sedge zone is usually responsible for most conservation values, especially with regard to threatened plant species (Wheeler 1988; Wassen et al. 2005), whereas tall-sedge communities are dominated by few, relatively common, species. The urgency of experimental research to verify the background of fen vegetation patterns is supported additionally by arguments of increasing external eutrophication (Bedford et al. 1999) leading to further biodiversity losses in riparian landscapes. Low-productive communities decline and are overgrown by tall sedges, willows and reed (Pałczyński 1985; Fojt & Harding 1995).

Wheeler & Shaw (1991) found a strong correlation between productivity and species richness in fens and ascribed it to the effect of competition. Kotowski & van Diggelen (2004) analysed light interception profiles in different fen vegetation types and found a correlation between light availability, species distribution and diversity in functional traits of communities. Another experiment (Kotowski et al. 2001) suggested that fen species of the low productive zone performed better under higher nutrient availability and low moisture. At the same time, fen species were very sensitive to light stress. Their small size and low relative growth rate (RGR) allow them to utilize nutrients efficiently but make them poor competitors for light. This might explain their absence from the productive tall-sedge zone (Veerkamp et al. 1980; Aerts et al. 1992). Conversely, the absence of tall sedges and other high RGR species from the low productive small-sedge zone might be related to a less efficient nutrient use (Grime 1979; Aerts 1989). Aerts & de Caluwe (1994) investigated the relationship between RGR and nitrogen use efficiency in three sedge species from different parts of the gradient. Instead of the expected trade-off, they surprisingly found a positive correlation between these two traits and concluded that the field distribution of these species was due to adaptations to flooding and the chemical composition of groundwater.

In the present study, we aim to evaluate the importance of interspecific competition for light and nutrients relative to the preference for or tolerance to hydrological site conditions for fen species. We conducted a two-season reciprocal transplantation experiment across a riparian fen gradient in which we replaced sodcuttings of two fen types with contrasting productivity. We hypothesize that: (1) competition for light is the main factor excluding small sedges and other species characteristic of the low-productive groundwater-fed zone from the high-productive flooded zone; (2) low nutrient availability is the main factor that prevents the occurrence of tall sedges in the low-productive zone.

Study site

The research was carried out in the valley of the Biebrza River, a large peatland complex in NE Poland. The valley (ca. 90 000 ha) harbours a well-preserved, almost natural peatland, with a variety of marsh and fen types arranged in zones parallel to the river (Pałczyński 1984). The area has a temperate continental climate with a mean annual temperature of 6.8 °C, a mean annual rainfall of 583 mm, a growing period of ca. 200 days and severe snowy winters (Kossowska-Cezak 1984).

The research was carried out in the ca. 1 km wide floodplain near the village of Olszowa Droga (22°34' E, 53°26' N). The substrate consists of a peat layer (up to 3 m depth) on top of eolic and fluvial sand deposits. The peatland shows a smooth elevation gradient of ca. 0.1 % from the edge to the river, along which productivity increases and species composition changes. For a description of vegetation and hydrology, see Wassen et al. (1996, 2002).

The experimental sites were situated in two vegetation zones: (1) a high-productive tall-sedge fen and (2) a low-productive small-sedge fen, described by Pałczyński (1984) as *Caricetum elatae* and *Calamagrostietum strictae*, respectively. Species composition, productivity and hydrological characteristics of both communities are summarized in Table 1. The vegetation height is ca. 1 m in the tall-sedge zone and 30 cm in the small-sedge zone. Fertilization experiments carried out in the immediate vicinity of the experimental sites showed nitrogen limitation in the low-productive zone (M. Wassen unpubl. data), while we did not find evidence for any nutrient limitation in the high-productive zone (Wassen et al. 1998). Measurements of the light transmission profiles revealed great differences between the two vegetation types (Fig. 1). Both communities used to be mown almost annually, but this practice has nearly ceased during the last decades. Disturbance by large herbivores (Elk and domestic cattle) is not intensive and at present has a negligible effect on fen vegetation (Bokdam & Sýkora 1999).
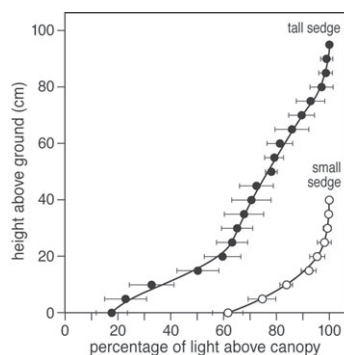

Fig. 1. Light transmission profiles in tall-sedge and small-sedge vegetation; bars show SD from mean; Measurements at three sites, each based on seven light sensors.

Table 1. Standing crop (kg.ha^{-1}dry wt.), summer and spring water table depth (cm below soil surface) (Wassen et al. 2002) and species composition in the two fen zones studied; species composition gives frequency in 16 samples of 20 cm × 20 cm; I - V = 0-20%; 20-40%; 40-60%; 60-80% and 80-100%.

	Tall-sedge zone	Small-sedge zone
Standing crop (vascular plants)	6990	3200
Standing crop (bryophytes)	65	1100
Vegetation height (cm)	90-120	30-40
Spring water level (above-ground level)	40-60	20-40
Summer water level (below-ground level)	16-24	0-16
Species composition		
Carex elata	V	
Carex acuta	II	
Menyanthes trifoliata	I	
Iris pseudacorus	I	
Carex disticha	I	
Caltha palustris	I	
Galium palustre	IV	V
Calamagrostis stricta	III	V
Lysimachia vulgaris	III	III
Equisetum fluviatile	III	III
Stellaria palustris	III	II
Myosotis scorpioides	II	II
Ranunculus lingua	I	I
Drepanocladus aduncus	I	I
Plagiomnium spec.	I	II
Potentilla palustris	II	V
Carex nigra		V
Agrostis canina		V
Calliergonella cuspidata		V
Eriophorum angustifolium		IV
Carex diandra		III
Carex lasiocarpa		III
Carex caespitosa		II
Scutellaria galericulata		II
Menyanthes trifoliata		II
Cardamine pratensis		II
Lysimachia thyrsiflora		I
Lathyrus palustris		I
Festuca rubra		I
Carex rostrata		I
Carex canescens		I

Methods

Transplantation experiment

In order to measure the ecological response of plant communities typical for the two zones of the fen we used sod-cuttings from the established vegetation instead of the more often applied technique of transplanting individual seedlings. Our results illustrate possible scenarios of fen vegetation development after the establishment of species outside their present zone of occurrence, e.g. as an effect of species invasions into canopy gaps.

The experiment was set up at the beginning of June 1998 and continued until the end of July 1999. Experimental fields (ca. 20 m × 30 m) were chosen in homogeneous and undisturbed parts of the two studied vegetation types; they were protected by enclosures to prevent

trampling by animals. Sods of 20 cm × 20 cm were cut from the vegetation in the direct surroundings of the experimental sites. The depth of the transplants was 5 cm in the small-sedge vegetation and ca. 10 cm in the tall-sedge vegetation, and comprised in both cases the dense root layer with a small amount of local soil. The sods were transplanted from the low-productive zone to the high-productive zone and *vice versa*. As a control, the sods were also transplanted close to their original site (< 20 m), to account for the effect of the transplantation process (treatment C). During the process of transplanting, the sods were kept saturated with water. Since water levels were 20 cm below the surface while transplanting in the low-productive zone, the transplanted tall-sedge sods were watered for three days after the transplantation, using water from a nearby piezometer. In the high-productive zone, watering was not necessary since water levels were at the surface. The tall-sedge transplants were furthermore supported by sticks and a cord against the wind. Litter was removed from all transplants.

Each of the two experimental fields contained 50 transplants situated at minimally 2 m distance. The following treatments were established in ten replicates within both small-sedge and tall-sedge transplants:
• No additional treatment of the transplanted sod (NT);
• Fertilization of the transplanted sod with NPK (F);
• Removal of the above-ground vegetation around the transplanted sod to enhance the light availability (R);
• Both fertilization and vegetation removal (RF).
For practical reasons the removal and fertilization treatments were applied to the between-sites transplants only and omitted at the within-site transplants (C), so that we were not able to compare the effects of site with those of fertilization and removal. The treatments were arranged in a blocked design, with ten plots, each containing five transplants (including the control of the other community).

In the removal treatments (R and RF) the above-ground vegetation was clipped close to the surface in a square of 1.2 m × 1.2 m in the low-productive fen and 2 m × 2 m in the high-productive fen, with the transplanted sod in the centre of the clipped areas. Clipping was continued every two weeks in the period of strongest vegetation growth (04.06 - 04.08.1998 and 15.05 - 30.07.1999). The method of pulling back competitive plants was not practical here because of the large size and tussock-growth form of the tall sedges. We believe that the potential artefacts of vegetation clipping (root decomposition and increased evaporation) were minimal because of an almost permanent water logging of peat soils in both zones. Fertilizer was supplied in amounts of 20, 8 and 20 g.m^{-1} for N, P and K, respectively. Fertilizer was applied two times in the form of a mixture of 'osmo-grains' with a 3-month release rate: in June 1998, just after the transplantation and in the be-

ginning of the second growing season in May 1999.

The total above-ground biomass was harvested from the transplants at the beginning of August 1998 and again in July 1999, when below-ground biomass was also harvested. To account for the effect of transplantation, 10 samples of the above-ground biomass were also collected from the surrounding, non-transplanted vegetation at both experimental sites (< 20 m from the experimental site) at the end of July 1999.

In the second year, the harvested above-ground biomass was split into five fractions: (1) tall sedges of the high-productive fen; (2) small sedges of the low-productive fen; (3) grasses; (4) non-graminoid herbs; (5) bryophytes. Dry weights of all above-ground biomass samples were determined after drying at 70 °C for 48 hours. The below-ground biomass was sampled from the middle of transplanted plots using a root-sampling borer of 15 cm diameter to a depth of 30 cm. The roots with soil were stored in a freezer for 5 months and afterwards rinsed with high-pressure water. Before drying (as above), dead leaves and wooden fragments of sods were removed from the below-ground biomass samples.

The light intensity measurements conducted on the removal (R and RF) plots after harvesting the transplants showed that there was no shading by the surrounding vegetation, i.e. the percentage of the light reaching the ground level was not significantly different from the light above vegetation.

Data analysis

The following response variables were used: (1) mean total above-ground biomass and mean above-ground biomass of (2) grasses, (3) bryophytes, (4) small sedges, (5) tall sedges, (6) non-graminoid herbs, (7) mean total below-ground biomass (roots + rhizomes) and (8) shoot:root ratio of the vascular plants. The mean total above-ground biomass was calculated for both experimental years, the other variables only for the second year (1999).

The effects of the treatments on the variables were analysed with the one-way and factorial 'protected ANOVA' (Scheiner 1993), i.e. univariate analyses were conducted only when MANOVA detected significant differences between groups. The effects of fertilization (F) and removal of surrounding vegetation (R), and of the interaction of the response variables, were analysed with a two-way ANOVA. One-way ANOVA, with 'treatment' as a fixed factor was conducted to compare variables between the control treatment (C) and the between-site transplants (NT, R, F, FR) by applying a simple *a priori* contrast on the C-treatment. To compare the results yielded in two experimental years for total above-ground biomass repeated-measures ANOVA

(RMANOVA) was performed with 'treatment' as the between-subject fixed factor. The shoot:root ratio, as a relative parameter, was used for a comparison of the performance of the two vegetation types using a three-way ANOVA with removal, fertilization and vegetation type as the independent variables. The shoot:root ratios of the control treatments of the two vegetation types were compared using a T-test.

In all cases, the statistical design was balanced and included only fixed factors; therefore Model 1 equations were used. In multivariate tests, Pillai's trace was used to calculate the F-statistics. All factorial analyses included only four between-site transplantation treatments (i.e. excluding C); furthermore each factor used in these analyses had only two categories (one degree of freedom), so there was no need to apply *post-hoc* comparisons. Some of the data required logarithmic or reciprocal transformation to obtain homogenous distribution of variances among groups (tested with a Levene's test). The analyses were performed using the SPSS 10 package (Anon. 2000).

Results

Biomass of small-sedge transplants

The transplantation process itself had no significant effect on the biomass of the small-sedge vegetation ($T_{(10.17)} = 1.72$, $p > 0.05$). The multivariate analysis of variance revealed that there were significant differences among groups, so that univariate analysis was appropriate. This was the case in the one-way design ($F_{(32, 164)} = 5.27$, $p < 0.0001$), and in the two-way design, which detected that both removal (cutting surrounding vegetation) and fertilization were significant sources of variation ($F_{(8,29)} = 12.30$, $p < 0.0001$ and $F_{(8,29)} = 6.77$, $p < 0.0001$, respectively). The interaction of removal and fertilization was not significant.

The above-ground biomass was affected by the interaction of harvesting year and treatment, while the harvesting year alone did not cause a significant effect (Table 2). Only removal caused a significant increase of the above-ground biomass in 1998 (fertilization effect was not significant), while in 1999 both factors significantly contributed to the increase of above-ground biomass (two-way ANOVA, Table 3). No significant interaction of these factors was detected, which implies that the effects of fertilization and removal on the above-ground biomass production were additive in the FR (fertilization + cutting) treatment (Fig. 2). In 1998, small-sedge sods transplanted into the tall-sedge vegetation without removal of surrounding vegetation (treatments NT and F) produced a lower above-ground biomass than the control treatment (C) (one-way ANOVA

Table 2. Repeated measures ANOVA on the effect of harvest year and treatment on the total above-ground biomass of transplants in tall-sedge transplants (**A**) and small-sedge transplants (**B**).

Source of variation	df	F	P
A. Tall-sedge transplants			
Year	1	92,321	***
Year × Treatment	4	0,508	NS
B. Small-sedge transplants			
Year	1	2,398	NS
Year × Treatment	4	4,508	**

with an *a priori* contrast, Tables 3, 4). Removal of the surrounding vegetation enhanced this production to the same level as in the control (treatments R, FR). In the second year, a significantly lower above-ground biomass as compared to the control was produced by NT sods only. The above-ground production in F and R transplants was equal to that of the control treatment, and when fertilization and removal were applied together (FR), the biomass was significantly higher than the control (Tables 3, 4).

A comparison of biomass produced by various species groups (Fig. 2) revealed that the removal of surrounding vegetation led to an increase of small sedges, bryophytes and non-graminoid herbs and had no effect on the biomass of grasses (one-way ANOVA, Table 4). By con-

Table 3. Results of two-way ANOVA for the effects of vegetation removal and fertilization on biomass variables in tall-sedge transplants (**A**) and small-sedge transplants (**B**) moved into the new environment. Effect of interaction (fertilization x removal) is not given because it was never detected as a significant source of variation by MANOVA. For all variables and both factors $df = 1, 46$; *** = $p < 0.001$, ** = $0.01 > p > 0.001$, * = $0.05 > p > 0.01$, ns = $p > 0.05$.

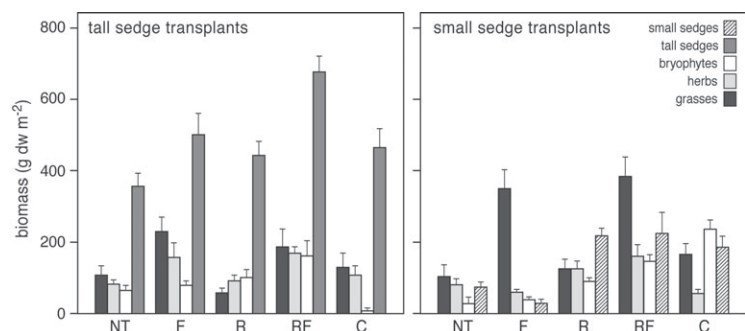| Dependent variables	Removal F	Removal P	Fertilization F	Fertilization P
A. Tall-sedge transplants				
Above-ground biomass 1998	1.13	NS	3.49	NS
Above-ground biomass 1999	4.49	*	32.24	***
Tall sedges	7.56	**	11.09	**
Grasses	3.11	NS	9.94	**
Non-graminoid herbs	0.79	NS	6.27	*
Bryophytes	4.07	NS	1.15	NS
Roots 1999	3.01	NS	0.00	NS
Shoot:root ratio 1999	2.02	NS	9.02	**
B. Small-sedge transplants				
Above-ground biomass 1998	16.90	***	0.00	NS
Above-ground biomass 1999	29.24	***	16.57	***
Small sedges	47.59	***	4.73	*
Grasses	0.21	NS	22.88	***
Non-graminoid herbs	14.20	***	0.02	NS
Bryophytes	43.90	***	7.02	*
Roots 1999	3.61	NS	2.51	NS
Shoot:root ratio 1999	4.94	*	3.93	NS

Fig. 2. Above-ground biomass of the transplanted sods in the second year of the experiment split into groups of species. Error bars represent standard error of the mean.

trast, fertilization largely promoted the growth of grasses and had only a small effect on small sedges and bryophytes and no effect on non-graminoid herbs (Table 3). In removal treatments (R, RF) the small sedges produced an above-ground biomass similar as in the control treatment, and non-graminoid herbs were higher than the control. Under shaded conditions (NT, F) the above-ground biomass of small sedges was significantly lower as compared to the control treatment, whereas the non-graminoid herbs did not differ (Table 4, Fig. 2). Grasses exceeded the control biomass whenever the fertilizer was applied (F, FR), whereas the bryophyte biomass was lower in all treatments than in the control (Table 4, Fig. 2).

Root biomass was not significantly affected by either removal or fertilization (two-way ANOVA, Table 3) but it was significantly higher in the RF treatment than in the control (planned comparisons, Tables 3, 4).

Table 4. Results of one-way ANOVA for the effect of all treatments on biomass variables in tall-sedge transplants (**A**) and small-sedge transplants (**B**). The treatments were: NT = no treatment, F = fertilization, R = removal, FR = fertilization + removal and C = control, with an a priori simple contrast on C. In all variables $df = 4, 45$; *** = $p < 0.001$, ** = $0.01 > p > 0.001$, * = $0.05 > p > 0.01$, ns = $p > 0.05$. Contrast: given treatments significantly (< 0.05) differed from the control (C).

Dependent variable	F	P	Contrast
A. Tall-sedge transplants			
Above-ground biomass 1998	1.28	ns	-
Above-ground biomass 1999	10.62	***	F, FR
Tall sedges	4.91	**	FR
Grasses	3.18	*	-
Non-graminoid herbs	1.79	ns	-
Bryophytes	10.30	***	NT, R, F, FR
Roots 1999	0.98	ns	-
Shoot:root ratio 1999	2.69	*	-
B. Small-sedge transplants			
Above-ground biomass 1998	5.16	**	NT, F
Above-ground biomass 1999	11.95	***	NT, FR
Small sedges	12.38	***	NT, F
Grasses	6.72	***	F, FR
Non-graminoid herbs	5.43	**	R, FR
Bryophytes	25.91	***	NT, F, R
Roots 1999	3.40	*	FR
Shoot:root ratio 1999	2.24	ns	NT

Biomass of tall-sedge transplants

No significant effect of the transplantation process was detected ($T_{(10.17)} = 1.72$, $p > 0.05$). The groups differed significantly according to the multivariate analysis of variance, both in the one-way ($F_{(32,164)} = 2.58$, $p < 0.0001$) and in the two-way analysis. In the latter test, significant effects of removal and fertilization were detected ($F_{(8, 29)} = 2.67$, $p < 0.05$ and $F_{(8, 29)} = 5.40$, $p < 0.001$ respectively), while the interaction of these two factors was not significant.

The harvest year had a highly significant effect on the above-ground biomass (Table 2), which was lower in the second year of the experiment in all treatments (Fig. 2). No interaction of the harvest year and treatment was observed. Neither removal nor fertilization significantly affected the above-ground biomass in the first year of the experiment (two-way ANOVA, Table 3) when none of the experimental treatments differed from the control (planned comparisons in one-way ANOVA, Table 4; Fig. 2). In the second year (1999), both removal and fertilization significantly increased the above-ground biomass production (Table 3), but the effect of fertilization was much more pronounced (Fig. 2). The above-ground biomass highly exceeded that of the control treatment when sods were fertilized (F, FR) (planned comparisons, Table 4), but in non-fertilized treatments (NT, R) the above-ground biomass was not different from the control.

Tall sedges responded with an increased above-ground biomass both to fertilization and to the removal of surrounding vegetation (two-way ANOVA, Table 3), but they exceeded the control above-ground biomass only when fertilizer was supplied (F, FR) (Table 4). Grasses and non-graminoid herbs were affected by fertilization only, which caused an increase of their above-ground biomass. None of the treatments differed from the control with respect to these two species groups. The bryophyte biomass was not different between NT, R, F and FR treatments (Table 3), and it was significantly higher compared to the control treatment (Table 4, Fig. 2).

No significant differences in root biomass were detected between groups (Tables 3 and 4).

Shoot:root ratio (SRR)

Shoot:root ratio of vascular plants was analysed by a three-way ANOVA, which revealed a significant effect of fertilization ($F = 11.94, p < 0.01$) and of an interaction between vegetation type and removal of surrounding vegetation ($F = 0.50, p < 0.05$), while the separate effects of these factors and other types of interactions were not significant. The effect of fertilization was reflected in an increase of the biomass fraction allocated to shoots (table 5). When the analysis was performed separately per vegetation type, the effect of fertilization was only significant in the tall-sedge transplants (two-way ANOVA, Table 3). The significant interaction of vegetation type and removal means that the effect of removal differs depending on the vegetation types compared. Removal caused increase of SRR in small-sedge transplants and a decrease of SRR in tall-sedge transplants (Table 5), although this effect was too small to be detected by a two-way ANOVA (Table 3). One-way ANOVA revealed that the small-sedge sods that were transplanted in the tall-sedge vegetation without additional treatment (NT) had a lower SRR than the control treatment, while SRR of the tall-sedge transplants did not differ from the control. The SRR of control treatments did not differ significantly between the vegetation types ($T_{(18)} = 1.04, p = 0.331$).

Table 5. Biomass and shoot:root ratios of the transplanted vegetation. Values in parentheses are standard errors of the mean. For abbreviations see Table 4.

		Tall-sedge transplants	Small-sedge transplants
Biomass (g dw m^{-2})			
above-ground 1998	NT	1277 (114)	442 (43)
	F	1448 (157)	403 (33)
	R	1336 (130)	566 (44)
	FR	1680 (146)	613 (43)
	C	1388 (137)	608 (51)
above-ground 1999	NT	601 (55)	284 (46)
	F	939 (82)	482 (53)
	R	692 (48)	543 (39)
	FR	1191 (80)	924 (93)
	C	709 (67)	648 (54)
below-ground 1999	NT	1617 (255)	847 (100)
	F	1570 (175)	947 (92)
	R	1899 (146)	981 (122)
	FR	1949 (168)	1224 (117)
	C	2038 (278)	700 (88)
Shoot:root ratio			
	NT	0,42 (0,08)	0,33 (0,06)
	F	0,67 (0,12)	0,51 (0,08)
	R	0,32 (0,03)	0,53 (0,07)
	FR	0,54 (0,03)	0,71 (0,14)
	C	0,44 (0,09)	0,86 (0,25)

Discussion

Fen zonation: resource competition or physical stress?

Differences in groundwater flow and flooding dynamics across river valleys have long been recognized as important in vegetation zonation (Kulczyński 1949; Succow 1988; Wassen et al. 1990). Our results suggest that these correlations are not due to a direct casual relationship. We found a striking difference in response between the two vegetation types. The small-sedge sods transplanted into the nutrient-rich tall-sedge zone suffered from low light availability leading to a twofold decrease in above-ground productivity. Since this effect could be entirely reversed by increasing light availability through removal of the neighbouring above-ground vegetation, we conclude that species of the low-productive zone occupy only part of their potential habitat and their absence from the productive zone is due to a high light interception there. We did not find any evidence that the small-sedge transplants were doing less well in the second year after transplantation. This implies that they are tolerant of flooding, which occurred in the spring of 1999 for more than two months in the high-productive zone and less than three weeks in the low-productive zone.

Biomass of the tall-sedge transplants, on the other hand, decreased in the nutrient-poor zone, but increased again with fertilization or with cutting the surrounding vegetation. This suggests that low nutrient availability limits the productivity of the tall sedges in these fens. Frequent cutting, on the other hand has likely diminished the capability of the small sedges to take up nutrients, limiting below-ground competition. Thus, the absence of tall sedges from the nutrient-poor zone is likely due to nutrient limitation and below-ground competition could be an important mechanism contributing to this shortage.

This picture differs from that known from most other wetland types, where high levels of physical stress restrict the occurrence of some species in lower elevations, whereas competition prevents the establishment of other species in higher elevations (e.g. Grace & Wetzel 1981; Bockelmann & Neuhaus 1999; Emery et al. 2001). A likely explanation for this difference is the specific hydrological regime of fen systems. The high water-holding capacity of peat results in much smaller differences in anoxia in fens than in wetlands on mineral soils. The major hydrological difference between the studied zones is the water regime and associated productivity levels. The tall-sedge zone is close to the river, flooded intensively and for a long time in the spring but the water levels drop considerably in summer. Nutrient turnover rates are high and these sites are very productive. The high

groundwater levels in the low-productive zone are maintained throughout the year at a relatively constant level by upward seepage. Nutrient release through mineralization is, therefore, low (Wassen et al. 2002).

Competition for nutrients

As expected, competition for light was highest in the high-productive zone. However, we did not find any evidence for the opposite trend, i.e. increased competition for nutrients in the low-productive environment (Newman 1973; Tilman 1988). On the contrary, the effect of fertilization on the productivity of grasses was higher in the high-productive zone, suggesting that below-ground competition was also higher there. These findings are in line with the theory of Grime (1979), and are similar to those of Twolan-Strutt & Keddy (1996) from mineral wetlands.

We did not find significant differences between the biomass allocation patterns of the two transplant types. This is contrary to the predictions that plants of more fertile environments invest larger proportions of assimilates into shoots, whereas storage in roots prevails in species of nutrient-poor habitats (Tilman 1988; Wilson 1988). In general, we noticed a relatively small percentage of biomass allocated to shoots. We recorded a SRR between 0.32 and 0.86 for small-sedge transplants, whereas it ranged from 1.0 to 4.0 in other studies (Veerkamp et al. 1980; Perez-Corona & Verhoeven 1996). Aerts et al. (1992), however, obtained similar results as in our study. Our results are closer to those gathered from adult plants from the field, whereas high SRR are typical of seedlings and young plants. Saarinen (1996) applied a detailed method of isotope labelling to *in situ* analysis of vertical distribution of biomass in *Carex rostrata* and found that more than more than 90% of the biomass was allocated to the roots.

Competition in relation to plant traits

The different reactions of selected species groups to changes in light availability and site fertility are clearly related to size and life strategy. Bryophytes are the smallest fen plants and these had the largest problems at low light levels. When transplanted into a high-productive zone, cutting of the surrounding vegetation was crucial for their mere survival, although they were not able to reach the same productivity as in their typical zone. Conversely, transplantation from the high-productive zone to the low-productive zone stimulated the growth of mosses significantly.

Small sedges did not react at all to fertilization, even when the competition for light was removed. These species have a rather low RGR (Veerkamp et al. 1980;

Aerts et al. 1992) and might grow at their maximum rate even under nutrient-poor conditions.

The response of non-graminoid herbs is less clear: they react positively to vegetation removal in the small-sedge sods transplanted to the high-productive zone, as well as to enhanced fertility in the tall-sedge transplants moved into the low-productive zone. They are quite a heterogeneous group of species that occur in both vegetation types and are more common in the low-productive zone. Again, their relatively small size (as compared to *Carex elata*) explains their clear response to enhanced light supply in the high-productive zone. On the other hand, their rather frequent occurrence in this vegetation suggests that they are stronger competitors for light than small sedges, which are entirely absent from the high-productive zone.

Tall sedges, characterized by a high RGR (Aerts et al. 1992) and a large size, are the only plants with clear characteristics of good competitors for light (cf. Keddy et al. 1994). As expected, they were able to increase their size in reaction to fertilization. However, an unexpected result is that they also responded positively to vegetation removal. Even tall sedges seem to be sensitive to differences in light intensity. As the vegetation in the low-productive zone is much lower than the maximum height of tall sedges, clipping of surrounding vegetation could only affect light conditions at the bottom of the tall-sedge sods. A significant reduction in the establishment of seedlings was observed at low light levels (Spackova et al. 1998; Lepš 1999), but this could equally be true for the growth of young shoots.

Grasses reacted most clearly to fertilization, especially when transplanted to the nutrient-rich zone. In contrast to most other groups, they did not show any response to differences in light availability. Their elongate growth form may enable them to reach places with a high light availability with at least some of their leaves, even in a dense canopy (Barnes et al. 1990; Anten & Hirose 1999).

Implications for nature management

Our study shows that productivity gradients may be at least equally important as hydrological gradients for structuring vegetation patterns in riparian fens (Bedford et al. 1999; Wheeler & Proctor 2000). At present the correlation between hydrological regime and productivity in fens is often lost, especially due to external eutrophication and other forms of increased anthropogenic influence (Grootjans & van Diggelen 1995; Kotowski & van Diggelen 2004). Therefore, we see an urgent need for further research on the importance of competition in structuring fen zonation. Studies should be conducted that include a larger part of the gradient and also include

hydrologically transformed areas, Also, more attention should be focused on the role of below-ground competition. Moreover, we need to better understand the mechanisms by which vegetation management affects riparian vegetation patterns. Although both types of fen communities studied here do occur as stages of natural succession (e.g. Pałczyński 1985), small-sedge fens are usually restricted to regularly mown areas in the present landscape (Wheeler & Shaw 1995) and decline rapidly after cessation of this management (Pałczyński 1985; Fojt & Harding 1995). Our study suggests that mowing, through increasing light availability, may stimulate the development of these communities even in places nowadays occupied by tall sedges. Such a possibility should be welcomed for biodiversity conservation reasons, especially with respect to numerous rare plant species and rich communities exclusively associated with low-productive small-sedge fens (Wassen et al. 2005).

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