

Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community

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Received 23 April 2003; accepted in revised form 9 June 2004

Key words: Agroecosystems, Biodiversity, Disturbance, Ephemeral wetlands, Removal experiment, Stress

Abstract

Empirical evidence suggests that the direction and intensity of plant–plant interactions may depend on the favourability of the environment. Previous studies have mainly focused on steep gradients of environmental stress or disturbance, while the interplay of competition and environment has not been tested for subtle environmental differences. Here, we present results from a study on plant communities of temporary wetlands in East-German farmland. Due to yearly ploughing in autumn, the vegetation is composed of annual species. Flooding does not affect adult plants and the elevation on the gradient expresses differences in the length of the growing season rather than in disturbance intensity or severe environmental stress. We tested whether such subtle differences in environmental stress may affect the importance of interspecific competition by the dominant species. Two treatments were applied at two elevations: removal of the dominant species (*Matricaria maritima* ssp. *inodora*) and reciprocal transplants of the seed-bank of the two elevations. At both elevations, removal of *Matricaria inodora* led to an increase in total species richness and number of wetland species, but the effects were substantially stronger at high elevations. Removal and the elevation on the flooding gradient significantly influenced the plant community composition. In particular, the weed communities became more similar to the wetland communities after the removal. Transplanted weed species did not emerge at low elevations. While two of four target species had significantly higher densities after the removal at high elevations, none of them was influenced by removal at low elevations. This indicates that, consistent with previous studies from other habitat types, competition by the dominant species was more intense under conditions of low environmental stress. The overall results suggest that both flooding as well as interspecific competition are important in structuring the plant communities along the freshwater gradient studied.

Introduction

Interactions among species play a major role in structuring plant communities. Therefore, much

effort has been made to achieve models of competitive interactions and their influence on plant communities (reviews in Goldberg and Barton 1992; Goldberg et al. 1999). While the importance

of competition for plant community structure is generally accepted, there is still a considerable debate about the influence of abiotic conditions, i.e. stress and disturbance, on the strength of competitive interactions. It has been argued, that the relative importance of competition is inversely proportional to the level of stress or disturbance (Grime 1973, 1974; Huston 1979; Keddy 1989; Belcher et al. 1995). Under benign conditions, a species' performance is mainly driven by competition, while abiotic determinants of fitness become more important under more stressful conditions. This model has been questioned by many authors (e.g. Newman 1973; Tilman 1982, 1988; Taylor et al. 1990) who claim that the level of competition in a community is independent of stress or disturbance. Total competition intensity is mainly determined by how close the community is to the carrying capacity (Taylor et al. 1990), while the importance of below- and above-ground competition may change along environmental gradients (Newman 1973; Tilman 1982, 1988). Empirical tests gave evidence to both models (e.g. Connell 1983; Goldberg and Barton 1992; Wilson and Tilman 1993; Goldberg et al. 1999; Tielbörger and Kadmon 2000a, b), leaving the debate unresolved.

A large number of previous studies about the interplay of abiotic and biotic control of species performance has focused on environmental gradients across shorelines where the intensity of stress or disturbance is related to elevation (e.g. Wilson and Keddy 1986; Bertness 1991; Bertness and Hacker 1994; Belcher et al. 1995; Brewer et al. 1997; Lenssen et al. 1999; Budelsky and Galatowitsch 2000). These studies outlined the importance of biotic control, i.e. competition, for plant communities at high elevations and of abiotic control, i.e. stress or disturbance, at low elevations. These studies were conducted under high intensity of stress due to salinity (e.g. Brewer et al. 1997, Bertness et al.), or disturbance caused by flooding in riverine wetlands (e.g. Lenssen et al. 1999). However, many shoreline habitats are neither influenced by salinity nor by strong flooding events that kill the existing vegetation. Also, many shoreline plant communities are dominated by annual plant species that escape the unfavourable conditions during flooding as seeds. In such communities, elevation should be less important as a

factor imposing stress than in perennial plant communities. Consequently, the intensity of competition should depend much less on the location along the flooding gradient than in previous studies. Unfortunately, little is known about the relative importance of abiotic vs. biotic factors in structuring such annual plant communities. With this study, we attempted to separate the effects of flooding and interspecific neighbours on single species performance and on plant community structure in a temporary wetland.

The study was carried out in an agricultural landscape in North-Eastern Germany. The temporary wetlands (ephemeral pools in agricultural fields) are flooded during winter and spring and, because yearly ploughing prevents the establishment of perennial plants, they are inhabited by annual plant communities (see Brose 2003a for a description). After drying out, vegetation develops newly on open ground. Because plants recruit from the seed-bank only during the dry months, the elevation on the flooding gradient is correlated with the duration of the growing season but not with disturbance (*sensu* Huston 1979) that may kill the existing vegetation. The elevation reflects the level of stress as 'the external constraints which limit the rate of dry matter production of all parts of the vegetation'. (Grime 1979). By measuring the responses of species richness and abundances of interstitials to the presence of the dominant species, variations in elevation, and seed-bank composition, we studied the relative importance of stress and plant interactions for the plant communities of the temporary wetlands. In particular, the following hypotheses were addressed: (1) the importance of biotic control (i.e. competition by the dominant species) for structuring the annual communities does not differ between high elevations (low stress) and low elevations (higher stress), (2) plant abundance and distribution are mainly determined by abiotic control (i.e. length of growing season).

Methods

The nomenclature of the species follows Rothmaler (1994).

Description of study site

The study was carried out in the year 2000 at a research site located close to the city Angermünde about 55 km North-East of Berlin, Germany (53 ° 22'N., 13 ° 34'E.). The temporary wetland studied had a size of approximately 2400 m². In many of the surrounding fields, temporary wetlands (sometimes called vernal pools) occur in high densities (see Brose 2001, 2003b, c). These pools are flooded throughout the winter months and start to dry out in April. The annual plant communities in these pools are dominated by wetland species in the lower sections, and by weeds at the upper end of the hydrologic gradient (see Brose 2003a).

The upper elevations (weed section) were covered by weed communities, whereas mainly wetland species were found at the lower elevations (amphibious section) that were flooded until mid-May. The plant community was dominated by *Matricaria maritima* ssp. *inodora*, which hereafter will be referred to as *Matricaria inodora*.

Experimental design

The study area was divided into two different types of habitat representing different levels of stress: the weed section at higher elevations that was flooded until mid-April, and the amphibious section at lower elevations that was flooded until mid-May. In mid-April, before the germination of the plants, four blocks (replicates) of 225 m², each extending over both sections, were marked on the study site. The first block was selected randomly, while the following three were established at regular distances of approximately 20 m from each other.

In both sections and in each block, four plots of 1 m² each were laid out with a minimum distance of 4 m from each other, and four treatments were randomly assigned to them: (1) removal of *Matricaria inodora* (hereafter referred to as open plots), (2) addition of a seed-bank mixture ('transplanting experiment'), (3) removal of *Matricaria* and addition of a seed-bank mixture, and (4) control plots (hereafter referred to as *Matricaria* plots). This resulted in eight plots per block – four plots in the weed section and four plots in the amphibious section – and a total of 32 plots across four blocks. The plots were marked at

the end of April. In the open plots, the shoots of *Matricaria inodora* were clipped to the ground. We did not remove the plants completely, in order to minimise disturbance to the soil during the experiment. There was no re-growth from clipped stems. This treatment was repeated every other week until the end of the growing season at the end of July, when harvesting and soil tillage started in the surrounding fields. Although the study site did not yield any crop in the study year, it was included in the soil tillage to enable subsequent crop sowing.

To test whether differences in the seed-banks of the two sections influence the actual vegetation, we included seed-bank transplants as a treatment in our study. For the mixture of seed-banks, the upper soil-layer was dug out to a depth of 5 cm from the surface in (a) the marked plots and (b) an area adjacent to the plots. The sample from the plot was mixed with a sample from the other section and half of the sample was re-sown into the plot. The 'adjacent sample' was used for being transplanted to the other section. Due to the quick germination of the species, the sowing had to be carried out right after the plots dried out to allow a comparison with plots without seed-bank mixture. As a consequence of the different hydroperiods in the sections, the treatment was applied at different times, and it was not possible to take only one mixed soil sample. Re-sowing of mixed soil samples had to be carried out at the end of April in the weed section, but had to wait until mid-May in the amphibious section. Note that the mixed soil samples could not be re-sown in the weed section in mid-May, because the weed species had already germinated.

Monitoring of vegetation

At the end of July, before the soil tillage started, the abundances, i.e. the number of individuals of all plant species were recorded in each of the plots (nomenclature follows Rothmaler 1994). Wetland species were classified according to Ellenberg et al. (1992) (moisture value >6). Due to its removal, *Matricaria inodora* was not included in further analyses. Total species richness, wetland species richness and weed species richness (non-wetland species) were calculated as response variables for each plot. For the analysis of individual species

responses to the treatments, four target species were chosen. Two of these target species are wetland species (*Juncus bufonius* and *Bidens tripartita*), and the other two species are weeds (*Polygonum aviculare* and *Viola arvensis*). They were selected because they were among the most abundant species at the study site and they occurred on most of the study plots. Their mean population densities (abundances hereafter) were calculated for each treatment.

Data analysis

The effect of the various treatments on species richness was analysed using ANCOVA with neighbour treatment (control vs. removal of *Matricaria inodora*), elevation (weed vs. amphibious section) and mixture of seed-banks (mixed vs. unmixed seed-banks) as main effects, mean total, wetland and weed species richness as dependent variables, and between-plot variation as error term. In order to account for differences in abundance of *Matricaria inodora*, i.e. differences in biomass removed on the open plots and abundance on other plots, we included the *Matricaria inodora* abundance as a co-variable. A statistically significant removal \times elevation interaction term was interpreted as evidence for elevation-specific differences in competition intensity. All dependent variables met the assumptions for ANCOVA.

The variation in the species composition between the plots was analysed by correspondence analysis (CA) with biplot scaling using CANOCO

4.0 (Ter Braak and Šmilauer 1998). The species' abundances were used as dependent variables and the treatments as independent variables. The influence of the removal and seed bank transplants on the densities of the target species was analysed for each of the two sections separately. In consequence of heterogeneity of variances, we used consecutive Mann-Whitney U tests to analyse the influence of our treatments on the abundances of the target species. The densities were the dependent variables, and treatment (removal vs. control, seed-bank transplanted vs. not transplanted) was the independent variable. In order to correct for excessive Type I errors due to multiple comparisons, significance levels were adjusted using the Bonferroni-correction.

Results

Species richness

A total of 15 annual plant species was recorded during the study season. In our ANCOVAs, we found significant effects of removal and elevation, whereas neither the single effect of seed-bank transplants nor any of its interaction terms had a significant impact (Table 1). Furthermore, the dependent variables were not affected by the abundance of *Matricaria inodora*.

Total species richness was mainly influenced by the removal of *Matricaria inodora*. In contrast to this, wetland and weed species richness were additionally influenced by elevation (Table 1). Not

Table 1. Results of ANCOVA (F -values) with total species richness (S), weed species richness (S_{weed}) and wetland species richness (S_{wet}) as dependent variables, and removal (control/removal of *Matricaria inodora*), elevation (weed/amphibious section) and mixture of seed-banks (mixed/unmixed seed-banks) as independent variables and *Matricaria* abundance as covariate.

Independent variables (df)	Dependent variable		
	S	S_{weed}	S_{wet}
Removal (1)	50.71***	10.85**	51.84***
Elevation (1)	0.325	68.94***	58.16***
Seed-bank mixture (1)	2.66	0.24	3.68
Removal \times elevation (1)	20.54***	7.97*	14.75**
Removal \times Seed-bank mixture (1)	0.94	0.89	0.23
Elevation \times Seed-bank mixture (1)	0.13	0.001	0.26
Removal \times Elevation \times Seed-bank mixture (1)	0.11	0.22	0
<i>Matricaria</i> abundance (1)	0.05	0.02	0.04

$N = 32$; Error (df = 23); *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

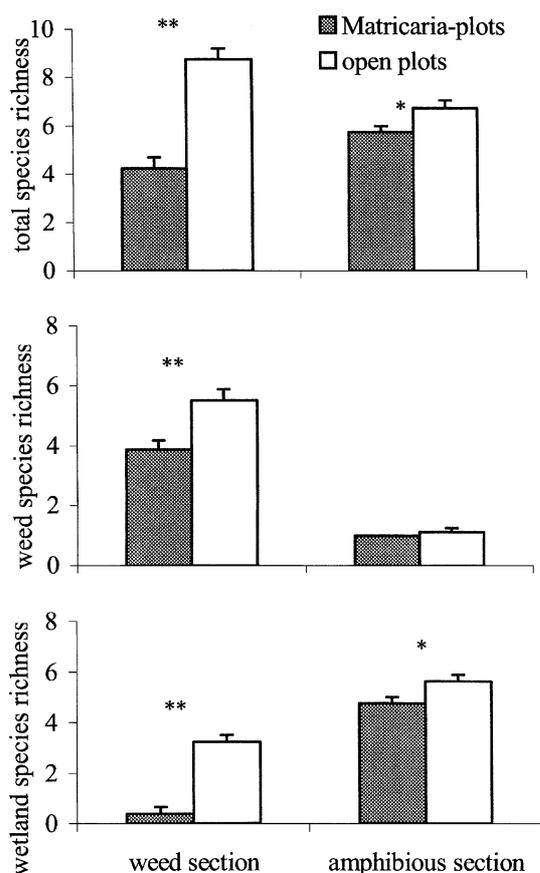


Figure 1. Effects of removal of *Matricaria inodora* on total species richness, weed species richness and wetland species richness mean \pm SE at two different elevations along a flooding gradient (weed section = upper elevation, amphibious section = lower elevation). Asterisks indicate significant differences between *Matricaria*-plots and open plots (ANOVA, * $p < 0.05$, ** $p < 0.01$).

surprisingly, we found higher values for weed and wetland species richness in the weed and amphibious section, respectively (Figure 1). Therefore, total species richness – the sum of these two measurements – did not differ significantly between the two sections when averaged for the open and *Matricaria*-plots. The removal effect was much more pronounced in the weed section with a 105% increase in species richness than in the amphibious section with a 17% increase in species richness (Figure 1). Furthermore, there were differences in the responses of wetland and weed species to the removal. In the weed section, wetland species richness was substantially higher in the open plots than in the *Matricaria*-plots where they were almost absent (Figure 1). Accordingly,

wetland species were almost restricted to the open plots and contributed most to the increase in total species richness after the removal of *Matricaria inodora* in the weed section. In contrast to this, the weed species emerged in the *Matricaria*-plots as well as in the open plots, and the differences in species richness between the two plots types were smaller, though statistically significant (Figure 1). This pattern was even more pronounced in the amphibious section: while wetland species richness slightly increased after the removal of *Matricaria inodora* in the open plots, weed species richness did not change (Figure 1). However, most of the weed species were absent from the amphibious section, irrespective of the removal of *Matricaria inodora*. These differences in the removal effect for the two sections accounted for significant removal \times elevation interaction terms in our ANCOVAs (Table 1). There were no significant effects of our seed-bank transplants indicating that the results were not affected by the abundance of specific species in the seed-bank.

Community composition

In the ordination (Figure 2), distances along the first and second axes mainly indicate differences in community structure for the treatments elevation and removal, respectively (Table 2). While elevation was the most important factor for the plant community composition, the correlations between seed-banks transplants and the axes were negligible. The inflation factors of the independent variables were below two (Table 2) indicating that the internal correlations in the data set are negligible and that the analysis does not need a detrending to remove the arch effect (Jongman et al. 1995; Ter Braak and Šmilauer 1998).

Being ordinated at the upper right, the *Matricaria*-plots of the weed section were clearly separated from the other plots (Figure 2). The plots of the amphibious section were placed to the left of the origin, but within this group the plots were ordinated in close proximity and none of the treatments could be separated. The open plots of the weed section, though intermediately ordinated, were much closer to the plots of the amphibious section than to the *Matricaria*-plots of the weed section (Figure 2). The plots with transplanted

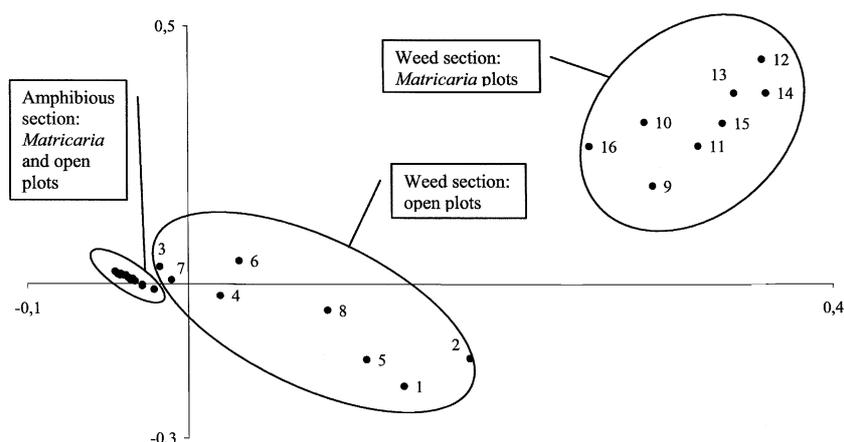


Figure 2. CA ordination of the experimental plots with removal of *Matricaria inodora* (open plots) and without removal (*Matricaria*-plots) at two different elevations along a flooding gradient (weed section = upper elevation, amphibious section = lower elevation).

seed-banks in the weed section (5–8 of the open plots and 13–16 of the *Matricaria*-plots) did not show consistent differences in their community composition compared to the plots with un-transplanted seed-banks.

Abundances of target species

There were no significant relationships between seed-bank transplants and the abundances of the target species, indicating that the results were not affected by the abundance of a species in the seed-bank. Therefore, the data were pooled for subsequent analyses. In the weed section, the mean densities of the target species *Juncus bufonius* and *Polygonum aviculare* were significantly higher in the open plots (Figure 3). *Viola arvensis* was more abundant in the *Matricaria*-plots, but this difference was not significant after Bonferroni correction. The two wetland species, *Juncus bufonius* and *Bidens tripartita* were completely absent from the *Matricaria*-plots in the weed section. However,

while the densities of *Bidens tripartita* were substantially higher in the amphibious section, *Juncus bufonius* was less abundant, even in the open plots (Figure 3). The weed species *Viola arvensis* did not emerge in the amphibious section. In contrast to the results for the weed section, there were no significant differences in the densities of the target species between the *Matricaria*-plots and open plots in the amphibious section.

Discussion

Importance of competition at different elevations

Our overall results indicate that interspecific competition by the dominant species *Matricaria inodora* was an important determinant of plant species richness, plant community composition and densities of individual plant species along the studied flooding gradient. However, in contrast to our initial hypothesis, competition intensity differed largely along the elevation gradient.

The effect of removal of *Matricaria inodora* on species richness was much more pronounced in the weed section (i.e. low stress) than in the amphibious section (i.e. higher stress). Responses in the abundances of the four target species to removal were restricted to the weed section and the removal treatment in the weed section led to a community structure much closer to the communities of the amphibious section than to the *Matricaria*-plots. These results indicate that the removal of

Table 2. Results of the CA: eigenvalues of the axes, inflation factors of the independent variables and weighted correlation matrix.

Variable	Axes 1	Axes 2	Inflation factors
Eigenvalues (CA)	0.577	0.348	
Removal	– 0.111	0.359	1.149
Elevation	– 0.729	0.206	1.152

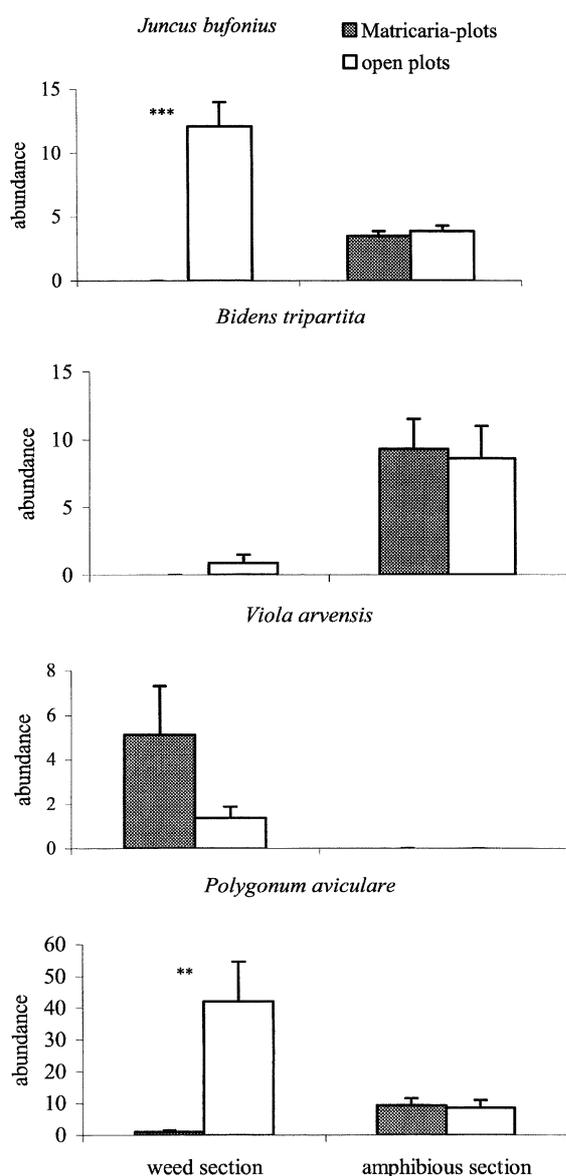


Figure 3. Mean (\pm SE) densities [N/m²] of four annual plant species with removal of *Matricaria inodora* (open plots) and without (*Matricaria*-plots) at two different elevations along a flooding gradient (weed section = upper elevation, amphibious section = lower elevation). Asterisks indicate significant differences between *Matricaria*-plots and open plots (Mann-Whitney U with Bonferroni-correction, ** $p < 0.01$, *** $p < 0.001$).

Matricaria inodora in the weed section had similar consequences for the plant community structure as the extended flooding period in the amphibious section. In contrast to this, removal effects on community composition in the amphibious section were only marginal. Our findings therefore

corroborate most previous studies carried out at riverine wetlands (Belcher et al. 1995; Lenssen et al. 1999; Budelksy and Galatowitsch 2000) and salt marshes (Bertness and Hacker 1994; Brewer et al. 1997). These studies found that biotic control of species richness predominates at high elevations where abiotic stress or disturbance due to flooding or salinity is much lower than at low elevations. Differences between our study and previous studies are mainly expressed in the strength of the interaction between stress and competition: while in previous studies, the steep environmental gradient translated into differences in plant interactions that ranged from largely negative (high elevations) to even positive (low elevations), we did not find a shift towards positive plant-plant interactions when stress increased. In our study, competition by the dominant species was more important at high elevations, while flooding limited growth of certain plant species at the lower elevations even in the absence of competition. Similar results were obtained by Budelksy and Galatowitsch (2000), who investigated the response of perennial sedges to flooding and competition in Australian temporary wetlands.

In our study, the wetland species from the lower elevations were able to grow in the drier sections, when *Matricaria inodora* was absent. This is in contrast to interstitials from low elevations at riverine wetlands (Lenssen et al. 1999). The wetland species in our study were mainly excluded from the weed section by the presence of *Matricaria inodora*. In fact, they were almost absent when *Matricaria inodora* was present. One of our wetland target species, *Juncus bufonius*, even attained much higher densities in the weed section in open plots than in the amphibious section, indicating that the distribution pattern of this species is mainly ruled by competition. This clearly highlights the importance of competition by *Matricaria inodora* for structuring the annual plant communities studied.

Our overall findings are consistent with Grime's model of competition along gradients (Grime 1973, 1974; Huston 1979; Keddy 1989; Belcher et al. 1995) which claims that negative interactions are more important for structuring plant communities under benign conditions, while abiotic determinants of fitness become more important under more stressful conditions. The present study has shown that the importance of competition by

the dominant species in plant communities might decrease with increasing stress, even if the stress is not mediated by physically harsh conditions and the resulting environmental severity is low compared to previously studied habitats such as salt marshes.

Abiotic control of plant community structure

While we could show that competition by the dominant species is an important factor in shaping the studied annual communities, the location along the flooding gradient had a large influence, too. It was the most important factor for the plant community composition. In particular, the weed species that dominate the higher elevations did not emerge from the seed-bank when transplanted to the amphibious section. This indicates that the distribution pattern of weed species is mainly ruled by the abiotic environment. As these species escape the unfavourable conditions during flooding as seeds, this effect is most likely mediated by an interaction of the duration of flooding that is restricting the length of the growing season and the species' habitat predispositions. In particular, secondary dormancy of the weed species might have prohibited their germination in the amphibious section.

Previous studies have concluded that due to the dominant impact of flooding on the plant communities the composition of the seed-banks is of minor importance for the actual vegetation (Keddy and Reznicek 1982; Schneider and Sharitz 1986; Weiher and Keddy 1995; Lenssen et al. 1999). Our findings strongly corroborate these results since transplanting seed-bank did not influence species richness, plant community composition or the abundances of the four target species.

Biotic and abiotic control determine plant community structure

Our overall results indicate that abiotic and biotic controls interact in determining plant abundance and distribution in the studied temporary wetlands. While competition by the dominant species strongly influenced the species richness of the experimental plots, the elevation on the flooding gradient was the most important factor determin-

ing the community composition in terms of species' abundances. By imposing differential effects on different species groups, the two factors led to a distinct distribution pattern of plant species along the gradient. Such species-specific responses to flooding have been shown to be important in temporary wetland plant communities in Australia (Casanova and Brock 2000). Consistent with the theory of Grime (1974) there seems to be a trade-off between stress tolerance and competitiveness of species, with competitors dominating under benign conditions and stress tolerators characterising the unfavourable habitats. Interestingly, the characteristics of stress tolerance and competitiveness have usually not been attributed to annual plants, which are often considered to have similar life history strategies. In the present study, wetland species were restricted to the lower elevations, where with increasing stress they are released from competition while in consequence of their habitat predispositions, weed species cannot invade into the lower areas of prolonged flooding. Our overall findings indicate that the flooding gradient may serve as a major niche axis for the coexistence of the annual species in the studied system.

Acknowledgements

We thank Jennifer Dunne, Sarah Ellgen, Michael Glemnitz, Sándor Samu and two anonymous reviewers for their critical comments. The study was supported by a grant from the state of Brandenburg.

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