Do competition and selective herbivory cause replacement of *Phragmites australis* by tall forbs?

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Abstract

We investigated the role of biotic factors in determining abundance of the low marsh species *Phragmites australis* and the high marsh species *Epilobium hirsutum*. In a 2-year field experiment, at a position where *Phragmites* and *Epilobium* co-occurred, responses of both species to each other's removal were measured. In the second year, we also tested if larvae of *Archanara geminipuncta*, which feed exclusively on *Phragmites* shoots, affect the competitive ability of *Phragmites* relative to *Epilobium*.

For both species, removal of aboveground material by clipping did not enhance shoot size or decrease variability in shoot size of the removed species itself. Surprisingly however, shoot numbers of both species increased after removal of the other, which demonstrates that there was a mutual inhibition of each other's abundance. Comparing the responses of *Archanara*-infested and non-infested *Phragmites* shoots revealed no increased competitive suppression by *Epilobium* due to selective herbivory. Instead, we found that herbivore activity was lower in plots with *Epilobium*, which demonstrates that *Archanara* population size is reduced by the presence of non-host plant species.

These results contradict the common assumption that biotic factors constrain a species upper limit along flooding gradients. Instead, our result suggest that different biotic interactions may counteract each other and thus slow down replacement by successive species.
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1. Introduction

Flooding gradients are characterized by a distinct zonation of nearly monospecific stands of plant species (Spence, 1982). The range of species along these gradients is assumed to be determined by their physiological tolerance to flooding at the lower end, whereas the upper limit would result from biotic interactions such as interspecific competition and herbivory (Keddy, 1984; Grace, 1990; Bertness, 1991; Castillo et al., 2000; Rand, 2000). Hence, plant species with an optimum at relatively high positions of a shoreline, are considered to be competitively superior to species from more frequently flooded parts of the gradient. If these species come to interact because their physiological range has a certain overlap, the competitive interactions will be strongly single sided: species from higher up the gradient will affect the more flood-tolerant ones where they meet (Keddy, 1984; Grace, 1990; Crawford, 1992). Provided that competition is the main factor responsible for abundance of both species, the more flood-tolerant species will eventually be displaced to lower positions where the stronger competitor cannot endure prevailing abiotic conditions. Many studies in salt marshes, where both salinity and flooding vary with elevation, have confirmed that interspecific competition excludes low marsh species from higher elevations (Bertness, 1991; Pennings and Callaway, 1992; Rand, 2000, but see Bockelmann and Neuhaus, 1999; Emery et al., 2001). For freshwater wetlands however, there is still very little experimental evidence that a trade-off between flood tolerance and competitive ability underlies species zonation along flooding gradients: the limited number of studies includes both affirmative (Grace and Wetzel, 1981; Keddy, 1989) and contradictory results (Shipley et al., 1991; Weisner, 1993).

Species replacement may also result from a combined influence of interspecific competition and selective herbivory. Shoreline species typically grow in monocultures and are therefore likely to harbor specialist herbivores (Bernays and Graham, 1988). In isolation, these herbivores will not cause complete disappearance of the host plant but they may enhance species replacement where environmental conditions allow persistence of competitors (Louda et al., 1990; Crawley, 1997; Rodríguez and Brown, 1998). Salt marsh studies have demonstrated an important role for selective vertebrate herbivores in species replacement along flooding gradients (Bakker, 1985; Furbisch and Albano, 1994). Thus far, no study of zonation along flooding gradients has dealt with host-specific invertebrate herbivores. Selective invertebrate herbivores may have a different impact on their host plants than selective vertebrate herbivores because there is a stronger dependence of the herbivore population size on the local availability of the food plant. This is due to both their specific food requirements and their limited mobility. Consequently, interspecific plant competition may result in decreased grazing pressure by the selective herbivores (e.g. Andow, 1990; Coll and Bottrell, 1994; Haddad et al., 2001).

Here we report results of a 2-year field experiment on the role of interspecific competition and selective herbivory in determining the upper elevational limit of *Phragmites australis* (Cav.) Trin. ex Steudel on flooding gradients. Along eutrophic freshwater bodies, *Phragmites* usually dominates the permanently flooded to irregularly flooded parts of the shoreline. Towards higher positions, *Phragmites* is usually replaced by tall forbs such as *Epilobium hirsutum* L. (Fojt and Harding, 1995; Van de Rijt et al., 1996), which may be due to competitive exclusion of *Phragmites* by *Epilobium*. Competitive

interactions between both species may be mediated by selective herbivores because *Phragmites* is an exclusive food source for many insects, among which the stem borer, *Archanara geminipuncta* (Lepidoptera, Noctuidae), is the most important species (Tscharntke, 1999).

At the elevation position where the upper limit of *Phragmites* coincides with the lower limit of *Epilobium*, we first tested the hypothesis that abundance of *Phragmites* is determined by competition and that abundance of *Epilobium* is only determined by abiotic factors. Accordingly, we expected a positive response of *Phragmites* to *Epilobium*-removal but no response of *Epilobium* to *Phragmites*-removal. Using natural insect infestation, we secondly tested the hypothesis that insect-inflicted damage to *Phragmites* shoots further decreases its competitive ability relative to *Epilobium*.

2. Material and methods

2.1. Site description

The study was carried out on a shoreline along the River Nieuwe Merwede in the south-western part of The Netherlands (51°45′N, 4°45′E). The river is part of the estuary of the rivers Rhine and Meuse, which used to be a freshwater tidal area before it was isolated from the North Sea in 1970 by the construction of a barrier dam. As a consequence, the daily tidal amplitude was reduced from 2 to 0.30 m and the mean high water levels were lowered. Due to these lowered water levels many monospecific *Phragmites* stands were invaded by tall forbs, *Epilobium* in particular. Since then, *Phragmites* and *Epilobium* have co-occurred for over 25 years (Van de Rijt et al., 1996; Zonneveld, 1999).

Nowadays, a small tidal water level fluctuation remains, while larger fluctuations occur because of high river discharges in winter and early spring; low water levels prevail during the growing season. During the study period, plots were flooded almost continuously during winter and occasionally in the growing season. The ground-water level was never deeper than a few centimeters below soil surface.

2.2. Experimental procedure

In a mixed stand of *Phragmites* and *Epilobium*, 30 plots of 2 m × 2 m each were marked out in October 1994 with a minimum distance of 2 m between plots. Elevation of the plots (57.2 ± 1.3 cm above sea level; means ± S.E., $n = 30$) was measured using leveling equipment. In each plot, shoots of both species were counted to determine the initial shoot density. *Phragmites* had on average 159 ± 13 shoots per plot ($n = 30$; range 80–271) and the initial density of *Epilobium* was 78 ± 7 shoots per plot ($n = 30$; range 51–154).

From the following spring onwards, three treatments were applied: (1) removal of all *Phragmites* shoots, (2) removal of all *Epilobium* shoots, and (3) no removal of shoots ('control plots'). Ten replicates of each treatment were obtained by randomly assigning each plot to a treatment. After the spring of year 2, a number of plots was severely disturbed due to deposition of woody and anthropogenic litter, so that six replicates of each treatment remained to be used in the second season.

Phragmites and *Epilobium* were removed by clipping off their shoots at ground level. This was repeated every fortnight throughout the two successive growing seasons. Seedlings and vegetative shoots of other species were removed from all plots. At the beginning of each growing season, underground rhizome connections with plants outside the plots were severed with a spade to a depth of 1 m.

2.3. Plant measurements

The number of shoots of each of the two species was counted every month of the two successive growing seasons. Shoot size measurements were taken in August of the first year and May, June, July and August of the second year. Before measuring, plots were subdivided into four quadrats from which maximum 10 shoots were randomly selected (regardless of flowering) for measurement of length (both species) and diameter (*Epilobium*); length of *Phragmites* and shoot diameter of *Epilobium* were strongly correlated with shoot dry weight of these species. For *Phragmites*, this relationship was similar for both years (tested with ANCOVA: SS year $= 0.0246$, d.f. $= 1$, $P = 0.206$ and SS residual $=1.043$ and d.f. $= 69$) and pooled for both years the following relationship was found: log(shoot dry weight) $= -0.063 + 0.06 \times$ length ($r^2 = 0.83$, $n = 72$). For *Epilobium*, relationships differed between years (ANCOVA: SS year $= 0.178$, d.f. $= 1$, $P = 0.005$ and SS residual $=1.36$, d.f. $= 69$), in 1995: log(shoot dry weight) $= -0.125 + 0.006 \times$ length ($r^2 = 0.95$, $n = 40$) and for 1996: log(shoot dry weight) $= -0.001 + 0.006 \times$ length ($r^2 = 0.87$, $n = 32$).

Data on shoot sizes collected in May, June, July and August of the second year allowed us to monitor the shoot size variability. Using the length and diameter readings of the 40 randomly selected shoots, we calculated a coefficient of variation (CV) as a measure of size variability in each plot. Higher variability would be taken as evidence for more intense competition between shoots (Weiner, 1985). A significantly higher CV in control plots would therefore indicate that interspecific competition increases the intensity of shoot interactions.

Since belowground measurements would have resulted in strong disturbance of the plots we restricted ourselves to aboveground parameters. Thus, we may have overlooked a large compartment of the system, particularly in case of *Phragmites*, where belowground biomass may constitute more than two-third of the total clone biomass. However, by extending the experiment over two growing seasons we have also incorporated impact of species removal on belowground growth, because this is strongly related to shoot number and shoot sizes in the following spring (Van der Toorn and Mook, 1982).

2.4. Insect herbivory

The role of insect herbivory was investigated in the second year only, because of possible carry-over effects in the first year originating from the previous pre-treatment period: both the number of shoots suitable for *Archanara*, i.e. with a diameter > 5 mm, and the productivity of individual shoots is strongly determined by *Phragmites* peak standing crop of the previous year (Van der Toorn and Mook, 1982). Insect damage of *Phragmites* shoots in removal and control plots was assessed at four consecutive census dates in the second

year, i.e. 27 June, 15 July, 6 August and 19 August. Within each plot with *Phragmites*, a subplot, 2 m long and 0.5 m wide, was marked where infested, non-infested and dead *Phragmites* shoots were counted. At the last census date, shoot diameter and shoot length of a random sub sample of 20–30 shoots of both infested and non-infested shoots in the subplots were measured. These data allowed us to compare the survival and size of infested and non-infested shoots under both treatments (see 'data analysis' below) and estimate population size of *Archanara* larvae since this is tightly correlated with the number of infested shoots (Tscharntke, 1990).

We considered shoots to be dead if they were completely brown-colored and still had their leaves or leaf buds attached; this latter criterion was used to exclude standing litter from the previous years. Shoots without clear signs of insect damage were considered healthy. Infested shoots were identified by their brown-colored tips and/or the presence of side shoots (branches emerging from aboveground nodes of the damaged shoots), which are typical characteristics for infestation by *Archanara* larvae (Van der Toorn and Mook, 1982; Tscharntke, 1999). Regular flooding of the plots will have ruled out interference by larvae of the rhizome borer *Rhizedra lutosa* (Lepidoptera, Noctuidae) because these do not survive in flooded soils (Van der Toorn and Mook, 1982).

2.5. Data analysis

In order to test our first hypothesis, we analyzed the effect of species-removal on changes in shoot density, shoot size at the end of both growing seasons and variability in shoot size during 1996. Response of *Epilobium* and *Phragmites* shoot density to each others removal was analyzed with analysis of covariance (ANCOVA) using density before the start of the experiment (October 1994) as a covariate and census date as a within-plot repeated measures indicator. Prior to this analysis, and all other ANOVAs mentioned hereafter, we tested the assumptions of normality and homogeneity of variances (Sokal and Rohlf, 1995) and the sphericity assumption in case of ANOVAs with repeated measurements (Von Ende, 1993). For each year, the effect of removal on shoot size was tested with ANOVA using plot (nested within treatment) and treatment as predictor variables. Effects of species removal on CV of shoot length (*Phragmites*) and CV of shoot length and diameter (*Epilobium*) were analyzed with ANOVA using census date as a within-plot repeated measurement.

Because there was some among-plot variation in elevation relative to the water level, we performed separate ANCOVAs to test for possible main and interactive effects between elevation (as a covariate) and species removal treatment on shoot numbers and mean shoot dry weight. None of these tests revealed a significant influence of elevation on our dependent variables (results not shown).

To test our second hypothesis, we analyzed the effect of *Epilobium*-removal on size of both infested and non-infested shoots and on numbers of infested, non-infested and dead *Phragmites* shoots. We first tested the effect of treatment with a multivariate analysis of variance since size and number of infested, non-infested and dead shoots could not be considered as completely independent response variables. To asses significance, we used Roy's greatest root, which provides the most powerful test (Scheiner, 1993). To aid interpretation of the multivariate analysis, we also analyzed shoot categories individually. For both the

Table 1
Results of ANCOVA testing the effect of competitor removal on number of shoots of *Phragmites* and *Epilobium* during both years

	Epilobium			Phragmites		
	SS	d.f.	P	SS	d.f.	P
Initial density	33049.7	1	0.341	44317.7	1	0.076
Removal of competitor	96366.7	1	0.118	203254.2	1	**0.002**
Residual (among)	330644.8	10		113684.6	10	
Month	30837.6	8	0.305	22610.6	8	0.183
Removal × month	72725.3	8	**0.007**	110705.9	8	**0.000**
Residual (within)	255152.6	80		154208.3	80	

Initial density, number of shoots before the start of the experiment (October 1994), was used as a covariate. Month was treated as a within-plot repeated factor. Significant values are indicated in bold.

multivariate and univariate analysis of variance for shoot length, plot was included as a random factor nested within treatment. For shoot numbers, the effect of *Epilobium*-removal was analyzed with census time as a within-plot repeated measures. Because *Archanara*-larvae pupate around half June (Mook and Van der Toorn, 1985; Tscharntke, 1990) infestation of new shoots does no longer occur thereafter. The number of infested shoots at this time was therefore used as an estimate of the population size of *Archanara* larvae (Tscharntke, 1990) and the change in number of infested shoots between 22 June and consecutive dates was ascribed to mortality only. However, changes in numbers of non-infested shoots result from both mortality and natality.

3. Results

Shoot density of *Epilobium* was significantly affected by an interaction between month and removal of *Phragmites* (Table 1). This interaction was due to a lack of response in the first year and a strong increase in density after *Phragmites*-removal in the second year (Fig. 1). In contrast to shoot density, removal did not increase size of *Epilobium* shoots. In the second year, shoots were even significantly taller in control plots (Tables 2 and 3). Variability in shoot size was also not affected by *Phragmites* (Table 4). Both in removal
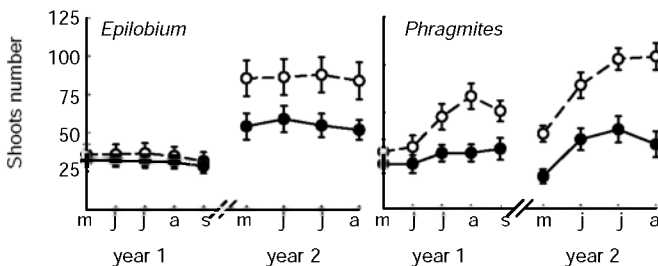

Fig. 1. Shoot number per m^2 (means ± S.E.; year 1: $n = 10$; year 2: $n = 6$) of *Phragmites* and *Epilobium* at each month of the first and second year's growing season in control (closed symbols) and removal plots (open symbols).

Table 2
Results of ANOVA for effects of plot and removal on shoot length (*Phragmites* and *Epilobium)* and shoot diameter (*Epilobium* only) in August of first and second year of the experiment

	Plot (removal)			Removal			Residual	
	SS	d.f.	*P*	SS	d.f.	*P*	SS	d.f.
Epilobium								
Shoot length								
year 1	2.053	18	**0.000**	0.101	1	0.358	5.809	766
year 2	0.442	10	**0.000**	1.370	1	**0.000**	3.382	468
Shoot diameter								
year 1	1.145	18	**0.004**	0.069	1	0.308	22.954	766
year 2	0.838	10	**0.000**	0.391	1	0.056	10.363	468
Phragmites								
Shoot length								
year 1	5.154	18	**0.000**	1.888	1	**0.019**	19.359	780
year 2	0.708	10	**0.000**	0.002	1	0.866	6.466	499

Plot was treated as a random factor nested within removal and tested against residual, removal was a fixed factor tested against plot. Significant values are indicated in bold.

and control plots variability in shoot length decreased during the growing season, but such temporal change was not clearly visible for variability in shoot diameter (Fig. 2).

Removal also significantly affected shoot density of *Phragmites* (Table 1). Already in the first year, density increased in response to *Epilobium* removal (Fig. 1). Shoot length of *Phragmites* was never increased by removal of *Epilobium* and the significant removal effect in the first year was due to a lower mean shoot length in removal plots (Tables 2 and 3). Variability in shoot length declined during the growing season in both removal and control plots (Fig. 2). Towards the end of the growing season size variability was similar in plots

Table 3
Shoot size characteristics of *Phragmites* and *Epilobium* in August of first and second year in plots with and without removal of competitor

	Removal		Control	
	n	means ± S.E.	*n*	means ± S.E.
Epilobium				
Shoot length (cm)				
year 1	388	138.2 ± 1.2	400	147.7 ± 1.7
year 2	240	111.9 ± 1.5	272	142.2 ± 1.6
Shoot diameter (mm)				
year 1	388	9.4 ± 0.2	395	9.9 ± 0.2
year 2	240	7.3 ± 0.2	240	8.3 ± 0.2
Phragmites				
Shoot length (cm)				
year 1	400	115.7 ± 2.2	400	140.1 ± 2.1
year 2	240	140.2 ± 2.3	272	142.0 ± 2.1

Means were obtained by pooling data of different plots within the same treatment, a maximum of 40 readings per plot were made.

Table 4
ANOVA results for effects of removal and census date on size variability (coefficient of variation, CV) of shoot length (both species) and shoot diameter (*Epilobium* only). Based on measurements of forty randomly selected shoots within each plot, one CV-value was calculated per plot and month

| | *Epilobium* | | | | | | *Phragmites* | | |
| | CV shoot diameter | | | CV shoot length | | | CV shoot length | | |
	SS	d.f.	P	SS	d.f.	P	SS	d.f.	P
Removal	78.49	1	0.322	14.99	1	0.623	7.44	1	0.603
Residual (between)	723.57	10		582.94	10		258.27	10	
Month	165.45	3	**0.024**	951.98	3	0.000	602.32	3	**0.000**
Removal × month	6.84	3	0.929	22.80	3	0.364	314.74	3	**0.004**
Residual (within)	459.00	30		207.28	30		588.91	30	

Significant values are indicated in bold, Month of the year (May, June, July and August of year 2) was treated as a within-plot repeated factor.
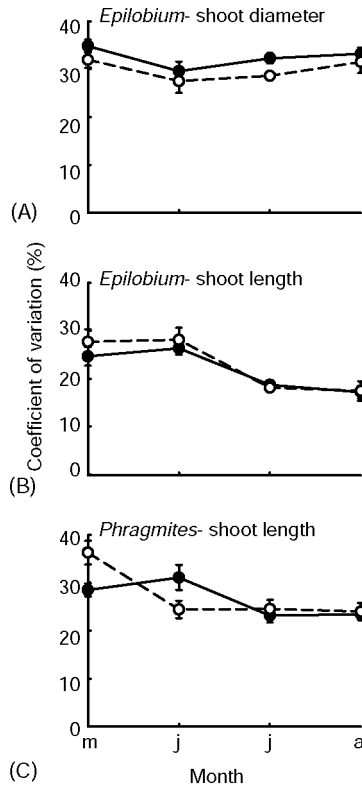

Fig. 2. Size variability (%; means ± S.E., $n = 6$–7) for *Epilobium* shoot diameter (A), *Epilobium* shoot length (B) and *Phragmites* shoot length (C) in control (closed symbols) and removal plots (open symbols) at each month of the second year' s growing season.

Table 5
Multivariate and univariate ANOVA for effects of removal and census date on number of non-infested, infested and dead *Phragmites* shoots during the growing season of the second experimental year

	Multivariate			Univariate								
				Non-infested			Infested			Dead		
	SSCP	d.f.	*P*	SS	d.f.	*P*	SS	d.f.	*P*	SS	d.f.	*P*
Removal	5.8	3	**0.001**	4294.1	1	0.126	9352.1	1	**0.005**	374.1	1	0.333
Residual (between)				15378.3	10		7620.3	10		3619.6	10	
Census	55.3	9	0.077	487.1	3	0.085	1431.4	3	**0.000**	455.8	3	**0.006**
Removal × census	9.5	9	0.362	108.4	3	0.659	6.4	3	0.985	66.8	3	0.545
Residual (within)				2012.0	30		1321.7	30		921.4	30	

In the multivariate analyses, effects were tested against the sums of squares and cross-products matrix (SSCP). In all analyses, census was analyzed as a within-plot repeated factor. Significant values are indicated in bold.

with and without competitors. Small differences in size variability earlier in the growing season probably produced the significant interaction between removal and month (Table 4).

3.1. Archanara infestation

Multivariate analysis revealed a significant change in shoot number after *Epilobium*-removal (Table 5). When analyzed for each category separately, only infested shoots appeared to be affected by removal of *Epilobium* (Table 5). After removal, more shoots were infested by *Archanara* (Fig. 3), also when number of infested shoots was expressed as a proportion of the total number of living *Phragmites* shoots (data not shown). This removal-effect was not due to a higher mortality of infested shoots before the first census since there was never a significant effect of removal on density of dead shoots (Table 5, Fig. 3). Instead, the significant removal effect (Table 5) probably indicates that less *Phragmites* shoots were attacked by *Archanara* in the presence of *Epilobium*.

MANOVA revealed no significant effect of removal on shoot length across infested and non-infested shoots (plot, nested within removal: Roy's greatest root = 3.3, d.f. = 20, $P < 0.001$ and for removal: Roy's greatest root = 0.65, d.f. = 2, $P = 0.532$). The length of infested shoots was 135.4 ± 3.0 cm in removal plots and 141.1 ± 3.5 cm in controls (both mean $\pm$ S.E., $n = 106$), non-infested shoots were taller: 161.8 ± 4.4 and 162.3 ± 4.1 (both mean $\pm$ S.E., $n = 116$) in removal and control plots, respectively. When calculated on a shoot dry weight basis, using the equation in 'plant measurements' in Section 2, there was approximately 31% reduction in shoot productivity due to *Archanara* infestation.

4. Discussion

4.1. Mechanism of species interaction

Surprisingly, we found that shoot numbers of both species increased after removal of the other species whereas neither species had significantly increased shoot size or decreased its
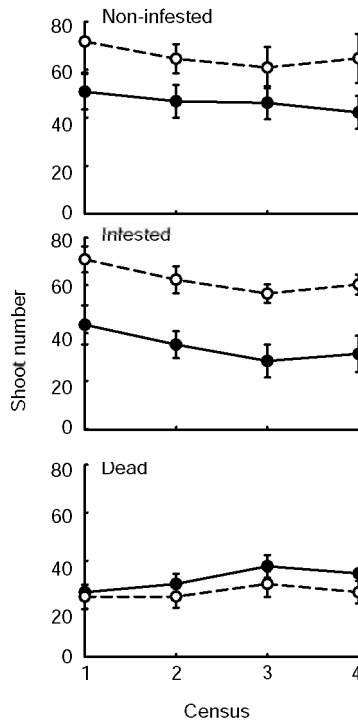
Fig. 3. Total number of non-infested, infested and dead *Phragmites* shoots per m^2 (means ± S.E., $n = 6$–7) in subplots with (closed symbols) and without (open symbols) *Epilobium* (means ± S.E., $n = 6$) at four consecutive census dates during year 2, i.e. 27 June, 15 July, 6 and 19 August.

variability after removal of the other species. The density response to removal clearly demonstrates that both species constrain each other's abundance. Shoot size dynamics indicate either absence of competition or equivalence of intraspecific and interspecific competition at the shoot level.

For *Epilobium*, we cannot fully exclude a role for interspecific interactions at the shoot level. Since the number of offspring shoots depends on the size of the parent shoot in the previous year (Shamsi and Whitehead, 1973; Lenssen et al., 2000) the increase after removal in the second year does suggest that parent shoots were more productive in the preceding year. The lack of a significant removal effect on *Epilobium* shoot size in the first year could have been due to altered allometrical relationships between diameter and dry weight. *Epilobium* may have responded to increased light availability after *Phragmites* removal by increased branching, a morphological change that remains unnoticed by measuring only diameter or shoot length (Weiner and Thomas, 1992). Removal of *Phragmites* did not enhance shoot numbers of *Epilobium* in the first year, because shoot number was already determined in the previous year as a consequence of the pseudoannual life history of *Epilobium* (Shamsi and Whitehead, 1973).

The immediate increase in *Phragmites* shoot numbers after removal of *Epilobium* indicates that inhibition of shoot formation is an important mechanism in the reduction of

Phragmites. Inhibition of shoot formation at high densities has been demonstrated before (De Kroon and Kwant, 1991; Ekstam, 1995) and is probably effected through a decrease in bud activity in response to lower light intensities and red: farred ratios (Deregibus et al., 1985; Ekstam, 1995). Others (Yamasaki, 1990; Crawford, 1992) have suggested that *Phragmites* is mainly inhibited through shoot overtopping because its shoots have to emerge from deeply buried rhizomes. Observed responses of shoot size and size variability to removal provided no evidence for inhibition through shoot interactions. Instead, mean shoot size of *Phragmites* in the first year was significantly smaller in removal plots. This can be explained by a carry-over effect: carbohydrate reserves, built up in the previous year and therefore similar for both treatments, were presumably distributed among a larger number of shoots. Size variability as measured in the second year was not affected by removal but decreased in both treatments during the growing season, probably as a consequence of physiological support of small shoots by tall shoots (see Amsberry et al., 2000 for experimental evidence) and/or a decreased growth rate of larger shoots (Hara et al., 1993; Ekstam, 1995).

4.2. Position of the experimental site

We measured effect of competition within a restricted range of the flooding gradients and our conclusion therefore seems to be of limited scope. However, *Phragmites* and *Epilobium* only co-occur within a limited range of the flooding gradient. Measuring above or below this range would have required transplantation of ramets. This method tends to overestimate shoot responses and may overlook shoot density responses, which were shown to be most important here. Moreover, our study was designed to test the competitive ability–flood tolerance trade-off hypothesis stating that the higher elevated species will competitively reduce the lower elevated, more flood-tolerant species but not vice versa (Keddy, 1984; Grace, 1990; Crawford, 1992). Following this hypothesis, reduction due to competition may change along the flooding gradient, but *Phragmites* will always be a weaker competitor than *Epilobium* (Goldberg, 1996). Hence, rejection of this trade-off hypothesis does not depend on the position of the elevation where the experiment is performed but only on how both species respond to each other's removal.

4.3. Methodology

Our experimental treatments included removal of aboveground plant material and disruption of belowground connections with ramets. This will have caused death of belowground plant material and subsequent nutrient release through mineralization (McLellan et al., 1995). However, differences in nutrient availability will have had little impact: standing crop in control plots, as estimated by multiplying individual shoot biomass estimates (see Section 2, plant measurements') with shoot densities indicate an average standing crop of $1409 \pm 106\,\mathrm{g\,DW\,m^{-2}}$ ($\pm$S.E., $n = 6$), which corresponds to maximum values of herbaceous wetland vegetation (Wheeler and Shaw, 1991). Moreover, regular flooding with nutrient rich surface water from the river Rhine will probably have ruled out any nutrient limitation (Spink et al., 1998).

Leaving belowground connections intact would have favored *Phragmites* over *Epilobium*, because the latter has no physiological integration with other shoots. Disrupting connections first ensured that all measured responses were based within our experimental plot. Secondly, it provided a conservative test for the prediction that *Epilobium* would not respond to *Phragmites*, since a (possibly) weakened *Phragmites* stand would also exert a smaller effect on *Epilobium*.

4.4. Archanara infestation

We found no indication that *Archanara* attack decreased competitive ability of its host plant *Phragmites*. Infested shoots were smaller than non-infested shoots but shoot lengths were not further decreased in the presence of *Epilobium*. We also found no indication that damaged shoots have a higher mortality rate when growing with *Epilobium*. This is a surprising result in the light of the many examples of altered competitive ability under influence of selective herbivory (e.g. Louda et al., 1990; Bonser and Reader, 1995; Furbisch and Albano, 1994; Rodríguez and Brown, 1998). However, whether herbivory really decreases the competitive ability may strongly depend on the timing or intensity of damage (Crawley, 1997). In our system, *Archanara* larvae feed upon *Phragmites* shoots early in the growing season, i.e. from May until half June (Van der Toorn and Mook, 1982). By that time, *Epilobium* shoots will not have reached their maximum length and competition for light may therefore be less intense than later in the growing season. Competitive ability of damaged shoots may also be sustained because infested shoots are partly compensated by means of internal support from non-infested, taller shoots (Hara et al., 1993; Amsberry et al., 2000). The intensity of grazing by *Archanara* does not seem to be exceptionally low and seems comparable with grazing pressure from vertebrates such as greylag geese (*Anser anser*). *Archanara*-infested shoots reached on average 83% of the length of non-infested shoots, whereas *Phragmites* shoots grazed by geese had reached 79% of their maximum length (Van den Wyngaert et al., 2003).

Our results suggest a feed-back mechanism through which *Epilobium* reduces the grazing pressure by *Archanara*. We have no indication that reduced food quality was the cause for reduced *Archanara* abundance in plots with *Epilobium*. Shoot size, an important parameter of *Archanara* food quality (Tscharntke, 1990), was not significantly affected by competition of *Epilobium*. Instead, *Epilobium* decreased the number of *Phragmites* shoots which may imply less food availability for *Archanara* (Tscharntke, 1990). In addition, larvae require at least three shoots before pupation (Mook and Van der Toorn, 1985; Tscharntke, 1990) and migration between shoots may be constrained when *Phragmites* shoots are intermingled with other species.

Decreases in population size of selective herbivores with increasing higher plant species richness have been reported in a number of studies with experimental field plots (Andow, 1990; Schellhorn and Sork, 1997; Haddad et al., 2001), but to our knowledge we report the first evidence for naturally established communities. Usually, there is no net benefit from reduced herbivory for the food plant since it is also reduced by interspecific competition (Schellhorn and Sork, 1997). The question whether *Phragmites* is actually favored by *Epilobium* can be addressed with a simple model. Let N be the number of shoots at the end of the growing season, w_m the mean maximum shoot dry weight of a non-infested shoot and

0.69^*w_m the maximum shoot dry weight of an infested shoot (i.e. 69% of the dry weight of a non-infested shoot, see results). The maximum standing crop in a monoculture (SC_{mono}) is then determined by the fraction of infested shoots (i) and the fraction of non-infested shoots ($1 - i$):

$$SC_{mono} = i^*N^*0.69^*w_m + (1 - i)^*N^*w_m \tag{1}$$

We have shown that *Epilobium* does not affect *Phragmites* shoot size (w_m) but reduces both the total number of *Phragmites* shoots (Fig. 1) and the number of infested *Phragmites* shoots (Fig. 3). If the competitive effect of *Epilobium* on *Phragmites* (or the proportion of *Phragmites* shoots remaining in a species mixture) is α and the proportion of infested shoots in mixture is i', then the *Phragmites* standing crop in mixtures (SC_{mix}) is:

$$SC_{mix} = \alpha^*i'^*N_i^*0.69^*w_m + \alpha^*(1 - i')^*N_i^*w_m \tag{2}$$

Eqs. (1) and (2) can be used to explore the conditions under which *Phragmites* benefits from the presence of *Epilobium*, i.e. when $SC_{mix}/SC_{mono} > 1$. After rewriting, we find that the proportion of mixture and monoculture standing crop only depends on the competitive reduction by *Epilobium* (α) and the proportion of infested shoots in monocultures (i) and mixtures (i'):

$$\frac{SC_{mix}}{SC_{mono}} = \frac{\alpha^*(0.69^*i' + (1 - i'))}{(0.69^*i + (1 - i))} \tag{3}$$

Given the infestation rate as reported here for *Phragmites* plots without *Epilobium*, the negative impacts of competition from *Epilobium* prevail (Fig. 4). However, at least in monocultures, years in which 90% of the *Phragmites* shoots are infested may occur (Mook and Van der Toorn, 1985; Tscharntke, 1990). With such high infestation rates, actual benefits for *Phragmites* in mixed stands may occur under a broader range of mixture grazing intensities (i') and competitive effects of *Epilobium* on *Phragmites* (α), although benefits are still most likely under low competition and low infestation rates in species mixture (Fig. 4). Such benefits will at best be temporary, since high infestation rates in monocultures are usually followed by a collapse of the local *Archanara* population due to overexploitation of its host (Mook and Van der Toorn, 1985; Tscharntke, 1990).

In conclusion, using the community boundary between *Phragmites* and *Epilobium* as a model system, our study relaxes the common assumption that biotic factors determine the upper limits of species ranges along flooding gradients (Keddy, 1984; Grace, 1990; Crawford, 1992). Competition did not seem to be responsible for replacement of *Phragmites* by tall forbs at the upper limit of shorelines, not even when *Phragmites* was already weakened by *Archanara*-herbivory. Instead of uni-directional suppression of *Phragmites* by the tall forb *Epilobium*, we found that both species suppressed each other's density. Rather than reinforcing the negative impact of *Archanara* on *Phragmites*, we observed that *Epilobium* restricted *Archanara* herbivore population size. Modeling suggests that this may occasionally be beneficial to *Phragmites*.
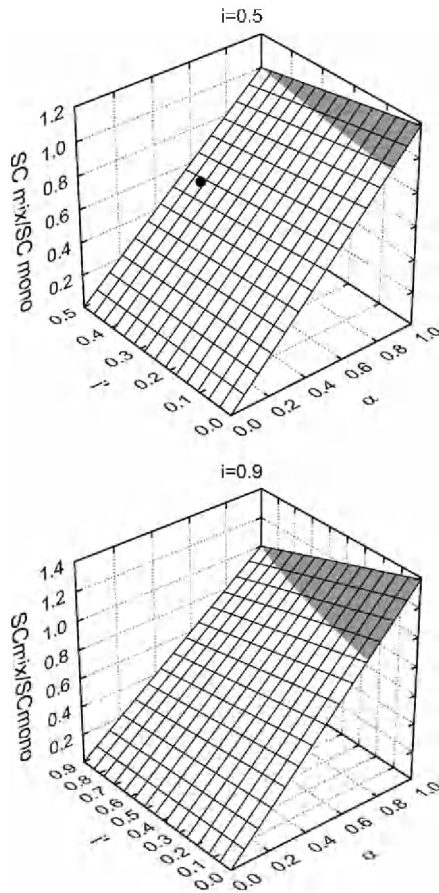
Fig. 4. Ratio between standing crop of species mixtures and monocultures (SC_{mix}/SC_{mono}) as a function of the competition coefficient α (fraction of _Phragmites_ shoots remaining in mixtures) and the infestation rate in species mixtures (i'). Both panels show results of simulation of Eq. (3) (see text) for an infestation rate in monocultures of 0.5 (upper panel) and a maximum infestation rate of 0.9 (lower panel); simulations were run with the limitation that infestation rate in mixtures would not exceed that same rate in monocultures. Black dot in upper panel indicates the conditions as found in our experiment, shaded area indicates range in which presence of _Epilobium_ is beneficial for _Phragmites_ through offering escape from herbivory.

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